

**A peer-reviewed version of this preprint was published in PeerJ on 6 June 2017.**

[View the peer-reviewed version](https://doi.org/10.7717/peerj.3312) (peerj.com/articles/3312), which is the preferred citable publication unless you specifically need to cite this preprint.

Lieberman BS, Kurkewicz R, Shinogle H, Kimmig J, MacGabhann BA. 2017. Disc-shaped fossils resembling porpitids or eldonids from the early Cambrian (Series 2: Stage 4) of western USA. PeerJ 5:e3312 <https://doi.org/10.7717/peerj.3312>

# Disc-shaped fossils resembling porpitids (Cnidaria: Hydrozoa) or eldonids from the early Cambrian (Series 2: Stage 4) of western U.S.A.

**Bruce S Lieberman** <sup>Corresp., 1, 2</sup>, **Richard Kurkewicz** <sup>3</sup>, **Heather Shinogle** <sup>4</sup>, **Julien Kimmig** <sup>2</sup>, **Breandán Anraoi MacGabhann** <sup>5</sup>

<sup>1</sup> Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas, United States

<sup>2</sup> Biodiversity Institute, University of Kansas, Lawrence, Kansas, United States

<sup>3</sup> Pangaea Fossils, San Francisco, California, United States

<sup>4</sup> Microscopy and Analytical Imaging Laboratory, University of Kansas, Lawrence, Kansas, United States

<sup>5</sup> Department of Geography, Edge Hill University, Ormskirk, United Kingdom

Corresponding Author: Bruce S Lieberman

Email address: blieber@ku.edu

The morphology and affinities of newly discovered disc-shaped soft-bodied fossils from the early Cambrian (Series 2: Stage 4, Dyeran) Carrara Formation are discussed. These specimens show some similarity to the Ordovician *Discophyllum* Hall, 1847; traditionally this taxon had been treated as a fossil porpitid. However, recently it has instead been referred to another clade, the eldonids, which includes the enigmatic *Eldonia* Walcott, 1911 that was originally described from the Cambrian Burgess Shale. The status of various Proterozoic and Phanerozoic taxa previously referred to porpitids and eldonids is also briefly considered. To help ascertain that the specimens were not dubio- or pseudofossils, elemental mapping using energy dispersive X-ray spectroscopy (EDS) was conducted. This, in conjunction with the morphology of the specimens, 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.

**Disc-shaped fossils resembling porpitids (Cnidaria: Hydrozoa) or eldonids from the early Cambrian (Series 2: Stage 4) of western U.S.A.**

Bruce S. Lieberman<sup>1,2</sup>, Richard Kurkewicz<sup>4</sup>, Heather E. Shinogle<sup>3</sup>, Julien Kimmig<sup>2</sup>, Breandán Anraoi MacGabhann<sup>5</sup>

<sup>1</sup>Department of Ecology & Evolutionary Biology, <sup>2</sup>Biodiversity Institute, and <sup>3</sup>Microscopy and Analytical Imaging Laboratory, University of Kansas, Lawrence, Kansas 66045, USA

<sup>4</sup>Pangaea Fossils, 584 Castro St., Apt. 501, San Francisco, California 94114, USA

<sup>5</sup>Department of Geography, Edge Hill University, St. Helens Road, Ormskirk, L39 4QP, England

Corresponding Author:

Bruce S. Lieberman<sup>1</sup>

Email address: [blieber@ku.edu](mailto:blieber@ku.edu)

**Abstract**

The morphology and affinities of newly discovered disc-shaped soft-bodied fossils from the early Cambrian (Series 2: Stage 4, Dyeran) Carrara Formation are discussed. These specimens show some similarity to the Ordovician *Discophyllum* Hall, 1847; traditionally this taxon had been treated as a fossil porpitiid. However, recently it has instead been referred to another clade, the eldoniids, which includes the enigmatic *Eldonia* Walcott, 1911 that was originally described from the Cambrian Burgess Shale. The status of various Proterozoic and Phanerozoic taxa previously referred to porpitiids and eldoniids is also briefly considered. To help ascertain that the specimens were not dubio- or pseudofossils, elemental mapping using energy dispersive X-ray spectroscopy (EDS) was conducted. This, in conjunction with the morphology of the specimens, indicated that the fossils were not hematite, iron sulfide, pyrolusite, or other abiogenic mineral precipitates. Instead, their status as biogenic 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

Aspects of the Phanerozoic fossil record of disc-shaped fossils in general, and jellyfish (medusozoans) fossils in particular, 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, 2012, 2014). Recently, McGabhann (2007, 2012, 2014), Young & Hagadorn (2010), Sappenfield, Tarhan, & Droser (2016) provided a comprehensive overview of disc-shaped and medusoid fossils, such that detailed consideration of the phylogenetic affinities of a broad range of disc-shaped fossils and 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 to resemble fossil specimens at times treated as either porpitids or eldonids. As part of a discussion of the affinities of this new material, the fossil record of porpitids is also briefly considered.

**Geology and Paleoenvironment:** The Carrara Formation is a regionally extensive, relatively shallow-water, mixed carbonate-siliciclastic unit of lower to middle Cambrian (Dyeran to Delamaran; *Bonnia-Olenellus* Biozone to *Glossopleura* Biozone) age in southern Nevada and southeastern California (Fig. 1A; Barnes & Palmer, 1961; Barnes, Christiansen & Byers, 1962; Palmer & Halley, 1979; Adams, 1995; Webster, 2011; Harwood Theisen & Sumner, 2016). It

consists of mixed carbonate and siliciclastic sediments and varies in thickness between 300-500m (Adams & Grotzinger, 1996; Keller, Lehnert & Cooper, 2012). Previous investigations indicate deposition in peritidal to shallow-subtidal conditions (Palmer & Halley, 1979; Keller, Lehnert & Cooper 2012).

The Echo Shale Member was deposited in a lagoonal environment and is dominated by shales and siliceous mudstones, interbedded with silt- and sandstone beds; it is thickest in the Striped Hills area and thins out to the northwest (Palmer & Halley, 1979; Adams 1995). It lies within the *Bolbonelellus euryptaria* Biozone (Webster, 2011), overlays the Thimble Limestone Member, and in turn is overlain by the Gold Ace Limestone Member (Fig. 1B). The member is fossil poor and only a few trilobite species have been reported in the literature (Palmer & Halley, 1979).

The specimens were collected in the Nopah Range, California, U.S.A., 35° 53'35.56" N 116° 04' 39.27" W, at an elevation of about 820 meters, and derive from float closely associated with greenish siliceous mudstones of the Echo Shale Member of the Carrara Formation. The rock slab the specimens are on also contains specimens of an olenelloid trilobite, probably *Bristolia* Harrington, 1956, confirming the stratigraphic assignment.

## Materials and Methods

In any instance involving 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<sup>2</sup> 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). It has also been employed to study Ediacaran fossils by Laflamme et al. (2011) and Cai et al. (2012), and notably MacGabhann (2012) has applied it to specimens of *D. peltatum* from a different locality. 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).

The specimens in Fig. 2 were photographed using a Canon EOS 5D Mark II digital SLR camera equipped with Canon 50 mm macro lens. The specimens in Fig. 3 were photographed using an Olympus UC50 camera attached to an Olympus SZX16 stereo microscope equipped with an Olympus SDF PLAPO 0.5XPF lens. Pictures were taken with specimens submerged in alcohol. The contrast, color, and brightness of images were adjusted using Adobe Photoshop.

The biota of the Echo Shale Member consists of olenelloid trilobites, possible agnostoids, and the herein illustrated disc-shaped fossils. The disc-shaped fossils are preserved as part and

counter part of brown-grey carbonaceous films, and specimens KUMIP 389538 and KUMIP 389540 preserve some interior structure. The outer edge of KUMIP 389539 is vaguely preserved and the missing interior structure suggests partial decomposition of the type described by Kimmig & Pratt (2016). This could be due to scavenging (an unidentified phosphatic fossil is preserved next to it), pre-burial microbial decomposition, or diagenetic effects. The specimens are flattened, and that appears to have generated minor concentric wrinkles at the edge, best seen in KUMIP 389538. (MacGabhann [2012] provided a very useful and detailed discussion of the taphonomy and preservation of *Discophyllum* specimens from the Ordovician of Morocco.) The *Bristolia* specimen on the slab preserves the cephalon, and possibly part of the thorax, and appears to have been preserved completely articulated. The bulk of the thorax and pygidium are missing though because the specimen sits at the edge of the slab.

## Results

Results derived from both EDS analyses are congruent (Figs. 4, 5). The bulk mineralogy of the 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, <.1-1.1%; 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 (Figs. 4, 5). 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 (Figs. 4, 5). This, in conjunction with the fact that the sample morphology is not in line with typical, abiologic mineral precipitates, 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 (Figs. 4, 5). There are only three elements that show any consistent elevation associated with the fossil (Figs. 4, 5). 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 (Figs. 4, 5). 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 (Figs. 4, 5). The Ca could perhaps represent recent diagenetic alteration associated with weathering or early diagenetic cement. Finally, P is uniformly distributed in the fossil and the surrounding matrix at low levels, except there appears to be some elevation along the margins of the specimen (Figs. 4, 5); 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 porpitiid fossils. Notably, the EDS analyses of MacGabhann (2012) suggested that somewhat different taphonomic processes were associated with the preservation of *Discophyllum* specimens from the Ordovician of Morocco, especially involving no prominent role for C, although this is perhaps not unexpected given their different sedimentology and reconstructed paleoenvironments relative to what is known from the Cambrian Carrara Formation.

**Taxonomy:** The specimens are tentatively placed with *Discophyllum* Hall, 1847, a monospecific genus for *D. peltatum* Hall, 1847 (p. 277, pl. LXXV, fig. 3) (see also MacGabhann, 2012, figs. 4.68, 4.69), originally described from the Upper Ordovician (Mohawkian) Trenton group, near Troy, New York, U.S.A (see MacGabhann, 2012, figs. 3.28-3.30 for illustrations of the locality). The specimens are referred to *Discophyllum* sp. 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*); Fryer & Stanley (2004, p. 1117); and comprehensively in MacGabhann (2012, p. 122, figs. 4.68-4.113, figs. 5.15-5.53).

If *Discophyllum* is a porpitiid, as has been previously suggested, it would be 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 Porpitiidae Goldfuss, 1818. This follows the most up to date treatments available: Daly et al. (2007) and WoRMS (2015). However, MacGabhann (2012, 2014) suggested an alternative placement for this taxon in an enigmatic group that was formerly largely Cambrian in age, the eldonids, including the eponymous *Eldonia* Walcott, 1911. The material presented here is not sufficiently well preserved to ascertain a higher-level taxonomic assignment. For additional discussion about higher-level taxonomic assignments of fossil porpitiids see Fryer & Stanley (2004) and also MacGabhann (2012); for discussion on the early fossil record of Cnidaria see Van Iten et al. (2014).

**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. These could be akin to the radial flutes and folds of the float of modern and fossil porpitids (see Yochelson, 1984 and Fryer & Stanley, 2004 for discussion) but also might represent other structures seen in eldonids by MacGabhann (2012, 2014). In cases it appears that some of the rays or ridges may split (Fig. 3). It is not possible to determine if this was caused by post-mortem decay or represents actual biology. If the latter, it would be congruent with what MacGabhann (2012) identified as secondary or tertiary ridges in eldonids. The details of the central region are sometimes obscured, but in KUMIP 389538 and 389540 (Figs. 2, 3) there appears to be a small ovate structure from which the rays radiate. The margins of the disc show a faintly scalloped pattern. Concentric corrugations are absent. There is no evidence of a keel or sail as should be found in *Veleva* Lamarck, 1801 (see Fryer & Stanley, 2004). Evidence of structures lateral of the radial ridges or fibers 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. There is no evidence of a coiled sac or dissepiments of the type identified by MacGabhann (2012), but this could be due to relatively poor preservation. The type specimens of *D. peltatum* Hall, 1847 were originally repositied in the Troy Lyceum (see Walcott, 1898) (the Troy Lyceum became today's Rensselaer Polytechnic Institute) and are now at the Field Museum of Natural History (see MacGabhann, 2012). We have provided two alternative taxonomic assignments, and 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.

## Discussion

Most discoidal unbiomineralized fossils of Paleozoic age have been compared or referred to one of three groups: cnidarian medusae (Young and Hagadorn, 2010), the capitate hydrozoans (Fryer and Stanley, 2004) (previously referred to as chondrophorines), or the eldonids (MacGabhann, 2012). Comparisons are also made to discoidal specimens of Ediacaran age (e.g. Kirkland et al., 2016).

**Comparison with discoidal taxa of Ediacaran age:** The vast majority of described unbiomineralized discoidal fossils have been found in sedimentary rocks of Ediacaran age. The Carrara specimens bear little resemblance to any material known from the Ediacaran (MacGabhann, 2007). The most apparent distinction is taphonomic, with Ediacaran discoidal specimens generally preserved as positive hyporelief casts or negative epirelief molds on bedding surfaces (MacGabhann, 2014), fundamentally different from the preservation of the Carrara specimens as carbonaceous compressions. This does not preclude a comparison, as species can, of course, have specimens preserved in more than one taphonomic style (e.g. Zhu et al., 2008; MacGabhann, 2012). However, more importantly, there is little morphological data to suggest a link between these specimens and any of Ediacaran age.

Certain discoidal impressions of Ediacaran-aged taxa have at times been assigned to the Hydrozoa in general and the Porpitidae in particular (for additional information on such Ediacaran-aged specimens see Sprigg, 1947, Wade, 1972, Glaessner, 1979, Fedonkin, 1981, Stanley & Kanie, 1985, and Sun, 1986). There are few similarities between these specimens and

those described herein, except for the overall discoidal shape. For example, *Eoporpita medusa* Wade, 1972 consists of a small concentrically ornamented disc surrounded by radial structures, while *Hiemalora* Fedonkin, 1982 has a prominent and generally smooth central disc, with much wider radial structures that show prominent relief (Narbonne, 1994). *Cyclomedusa davidi* possesses radial striations, but these do not continue into the central circular zone (Sprigg, 1947, 1949). None of these resemble the material described herein, which lacks concentric structures.

Comparison is rendered difficult, however, by the taxonomic irregularities and complexity between and within Ediacaran discoidal genera and species (MacGabhann, 2007). Many specimens assigned to *Cyclomedusa* Sprigg, 1947 consist solely of concentric rings and lack radial features entirely. The same is true of species referred to *Spriggia* Southcott, 1958. It is also true of *Kullingia delicata* (Fedonkin, 1981), which occurs in both Ediacaran rocks and in Lower Cambrian strata in Newfoundland (Narbonne et al., 1991). Notably, *Kullingia* appears to be a trace fossil (scratch circle) that was produced by an anchored, tubular organism (Jensen et al., 2002; Sappenfield, Tarhan, & Droser, 2016). Other Ediacaran discoidal forms are now known to be pseudofossils (e.g. Menon et al., 2016).

None of these Ediacaran specimens are still thought to represent hydrozoans (e.g. Zhang, Hua, & Reitner 2006, Cartwright et al., 2007, MacGabhann, 2007, and references therein). Young & Hagadorn (2010) reiterated this perspective when they noted that in many of these taxa the radial structures cannot be interpreted as radial canals. Indeed, the Ediacaran discoidal fossils have been recognized as benthic organisms, rather than pelagic forms, since Seilacher (1984).

In fact, most discoidal Ediacaran fossils are now thought to represent holdfasts of epibenthic stalked organisms, with the differences between specimens often due simply to taphonomic variation. For instance, Gehling, Narbonne, & Anderson (2000) identified three major morphs of *Aspidella* Billings, 1872, which they suggested represent holdfast taphonomic variants (see also Tarhan et al. 2015, but see MacGabhann, 2007). The specimens described herein differ from the *Aspidella* ‘type’ morph by the lack of a prominent central slit, from the ‘flat’ morph by the lack of concentric rings, and from the ‘convex’ morph by the lack of a prominent central boss (Gehling, Narbonne, & Anderson (2000). Indeed, there is no *prima facie* reason to suggest a holdfast nature for these fossils, with no evidence for a benthic habit or stalk attachment (Gehling, Narbonne, & Anderson, 2000; Sappenfield, Tarhan, & Droser, 2016). For similar reasons, *Discophyllum* sp. 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.

**Comparison to cnidarian medusae:** Cambrian cnidarian medusae have been described from several localities, including multiple sites in the United States (Hagadorn, Dott, and Damrow, 2002; Cartwright et al., 2007; Hagadorn and Belt, 2008; Lacelle, Hagadorn, and Groulx, 2008; Young and Hagadorn, 2010; Hagadorn and Miller, 2011; Sappenfield, Tarhan, & Droser, 2016). These are generally large, preserved as molds and casts, with convex sediment rings, and have quadripartite cracks. Clear criteria for the recognition of ancient medusae have been outlined by Young and Hagadorn (2010). Other *bona fide* medusae preserve considerably more anatomy than seen in the Carrara discs (e.g. Cartwright et al., 2007; Adler and Röper, 2012). As for the

comparison to Ediacaran discoidal taxa, the fossils described herein resemble *bona fide* medusae only in terms of the overall discoidal shape, making such an affinity unlikely.

**Comparisons with fossil capitates:** *Discophyllum* sp. also differs from what seem to be *bona fide* fossil capitates. For instance, it differs from the capitate *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. valentinei* has well defined concentric circles, whereas these are lacking in *Discophyllum* sp. 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. MacGabhann (2012) noted that some specimens of *Plectodiscus* may represent scratch circles.

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.

Finally, Caster (1942) considered *Palaeoscia floweri* Caster, 1942 from the Upper Ordovician of the Cincinnati region to be a porpitiid. 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 *Discophyllum* sp. Again, some specimens of *Palaeoscia* are almost certainly scratch circles, as is *Aysenspriggia* Bell, Angseesing, & Townsend, 2001, from the Cretaceous of Chile.

**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 capitate, and we endorse her interpretation. These differ from *Discophyllum* sp. by the absence of prominent radial structures.

In terms of their relief, the Cararra 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 *Discophyllum* sp. 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 specimens discussed here.

**Comparisons with eldonids:** The most apt comparisons for the Carrara specimens seem to lie with several post-Cambrian taxa that have previously been treated as porpitids, but seem instead to have affinities with the eldonids (Conway Morris & Robison, 1988; Dzik, 1991; Conway Morris, 1993; Masiak & Żylińska, 1994; Zhu, Zhao, & Chen, 2002; and see MacGabhann, 2012, for a detailed discussion of the eldonids, including a phylogeny). These are characterized by a coiled sac near the center of a discoidal body, representing the digestive tract suspended within a coelomic cavity.

The Carrara specimens are somewhat different from the Cambrian *Rotadiscus* Zhao & Zhu, 1994, and *Pararotadiscus* Zhu, Zhao, & Chen, 2002, both of which display clear concentric structures and have a dorsal surface which was stiffened. Our specimens also differ from the Cambrian *Velumbrella* Stasińska 1960 (previously considered as a porpitid, but which may also be an eldonid), due to the lack of a prominent annulus dividing inner and outer areas of the disc, and differing style of radial structures; *Velumbrella* may also have had a stiffened disc surface, as may the potential Ordovician eldonid *Seputus* MacGabhann and Murray, 2010.

Other eldonids are dominated by radial structures, including internal radial fibers and internal lobes. The Cambrian *Eldonia* Walcott, 1911, and *Stellostomites* Sun & Hou, 1987, both display these structures, with post-Cambrian eldonids including *Discophyllum* Hall, 1847, and *Paropsonema* Clarke, 1900, displaying radial ridges ornamenting the dorsal surface (MacGabhann, 2012). The radially-arranged features of the Carrara specimens could represent poorly preserved examples of internal lobes or dorsal ornamentation. However, specimens of *Eldonia* and *Stellostomites* exhibiting internal lobes universally also preserve the coiled sac even more prominently, with many additional specimens preserving the coiled sac but not the internal lobes (MacGabhann, 2012). It is difficult to envisage how the radial structures in our specimens could represent eldonid internal lobes without also preserving a coiled sac. An affinity with *Eldonia* or *Stellostomites* thus seems unlikely.

However, it may be possible that the radial structures (Figs. 2, 3) could represent dorsal surface ornamentation. Such ornamentation is seen in post-Cambrian eldonids, including *Discophyllum peltatum* Hall, 1847, originally described from the Ordovician of New York; *Paropsonema cryptophya* Clarke, 1900 from the Upper Devonian of New York (see also Ruedemann, 1916); and *Paropsonema mirabile* Chapman, 1926, from the Silurian of Victoria, Australia. All of these display ridges radiating from a central point, with the coiled sac generally only visible where it is preserved with relief from the surface. It is not inconceivable that the Carrara Formation specimens could be preserving eldonid dorsal surface ornamentation without the relief necessary to highlight the coiled sac.

389 Both species of *Paropsonema* show multiple cycles of radial ridges on the surface  
 390 (MacGabhann, 2012), unlike the specimens described herein. *Discophyllum peltatum*, however,  
 391 exhibits only a single cycle of radial ridges extending from the center to the margin. Although  
 392 the ridges of the Carrara Formation specimens appear to be more irregular than those of  
 393 *Discophyllum peltatum*, this could simply be a consequence of a different taphonomic style and  
 394 poor preservation in the Carrara material. The size and semi-ovate shape of the type material of  
 395 *D. peltatum* is also similar to the Carrara discs. A relationship therefore cannot be ruled out, and  
 396 the Carrara discs are certainly more similar to *D. peltatum* than any other previously described  
 397 discoidal fossils.  
 398 Due to the lack of clear diagnostic features of *D. peltatum* in the Carrara material, and the fact  
 399 that so far only three specimens have been collected from the Carrara Formation, it seems most  
 400 prudent to refer the Carrara material to *Discophyllum* sp. The age differences between the  
 401 material from the Carrara Formation and the Ordovician of New York State may also suggest  
 402 they are unlikely to represent the same species.

## Acknowledgements

We thank Pauly Cartwright (University of Kansas) for discussions about hydrozoan morphology and taxonomy; Jisuo Jin, Brian Pratt, Graham Young, Kenneth De Baets, and an anonymous reviewer for comments on an earlier version of the manuscript; Perry and Maria Damiani for details on locality and site information; and Lisa Amati (NYSM), Bushra Hussein (AMNH), Greg Dietl and Leslie Skibinski (PRI), and Daniel Levin (USNM) for information about the whereabouts of specimens of *Discophyllum peltatum*.

## References

- Adams RD. 1995.** Sequence-stratigraphy of Early-Middle Cambrian Grand Cycles in the Carrara Formation, southwest basin and range, California and Nevada. In: Haq BU, ed. *Sequence Stratigraphy and Depositional Response to Eustatic, Tectonic and Climatic Forcing*. Amsterdam: Kluwer Academic, 277—328.
- Adams RD, Grotzinger JP. 1996.** Lateral continuity of facies and parasequences in Middle Cambrian platform carbonates, Carrara Formation, southeastern California, U.S.A. *Journal of Sedimentary Research* **66**:1079—1090.
- Adler L, Röper, M. 2012.** Description of a new potential fossil hydromedusa *Palaequorea rygoli* and revision of the fossil medusa *Hydrocraspedota mayri* from the Plattenkalks of the Franconian Alb, Southern Germany. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen* **264**:249—262.

- 426 **Babcock LE, Robison RA. 1988.** Taxonomy and paleobiology of some Middle Cambrian  
427 *Scenella* (Cnidaria) and hyolithids (Mollusca). *University of Kansas Paleontological*  
428 *Contributions* **121**:1—22.
- 429 **Barnes H, Palmer AR. 1961.** Revision of stratigraphic nomenclature of Cambrian rocks,  
430 Nevada test site and vicinity, Nevada. *U.S. Geological Survey Professional Paper* **424-**  
431 **C**:C100-105.
- 432 **Barnes H, Christiansen RL, Byers FM Jr. 1962.** Cambrian Carrara Formation, Bonanza King  
433 Formation, and Dunderberg Shale east of Yucca Flat, Nye County, Nevada. *U.S. Geological*  
434 *Survey Professional Paper* **450-D**:D27—31.
- 435 **Bartels C, Briggs DEG, Brassel G. 1998.** *The Fossils of the Hunsrück Slate*. New York:  
436 Cambridge University Press.
- 437 **Bell CJ, Angeesing J., Townsend M. 2001.** A chondrophorine (medusoid hydrozoan) from the  
438 Lower Cretaceous of Chile. *Palaeontology* **44**:1011—1023.
- 439 **Billings E. 1872.** On some fossils from the primordial rocks of Newfoundland. *Canadian*  
440 *Naturalist and Quarterly Journal of Science* **new series 6**:465—479.
- 441 **Butterfield NJ. 1990.** Organic preservation of non-mineralizing organisms and the taphonomy  
442 of the Burgess Shale. *Paleobiology* **16**:272—286.
- 443 **Cai Y, Schiffbauer JD, Hua H, Xiao S. 2012.** Preservational modes in the Ediacaran  
444 Gaojiashan Lagerstätte: Pyritization, aluminosilicification, and carbonaceous compression.  
445 *Palaeogeography, Palaeoclimatology, Palaeoecology* **326**:109—117.
- 446 **Cartwright P, Halgedahl SL, Hendricks JR, Jarrard RD, Marques AC, Collins AG,**  
447 **Lieberman BS. 2007.** Exceptionally preserved jellyfishes from the Middle Cambrian. *PLoS*  
448 *One* **2**:e1121.

- 449 **Caster KE. 1942.** Two siphonophores from the Paleozoic. *Palaeontologica Americana*  
450 **3(14):**60—90.
- 451 **Chapman F. 1926.** New or little known fossils in the National Museum. Part XXX. —A  
452 Silurian jelly-fish. *Proceedings of the Royal Society of Victoria* **39:**13—17.
- 453 **Cherns L. 1994.** A medusoid from the Late Ordovician or Early Silurian of Jämtland, central  
454 Sweden. *Journal of Paleontology* **68:**716—721.
- 455 **Clarke JM. 1900.** *Paropsonema cryptophya*, a peculiar echinoderm from the *Intumescens* zone  
456 (Portage beds) of western New York. *New York State Museum, Bulletin* **39:**172—186.
- 457 **Clarke JM, Ruedemann R. 1903.** Catalogue of type specimens of Paleozoic fossils in New  
458 York State Museum. *New York State Museum, Bulletin* **65:**1—847.
- 459 **Collins AG. 2002.** Phylogeny of Medusozoa and the evolution of cnidarian life cycles. *Journal*  
460 *of Evolutionary Biology* **15:**418—432.
- 461 **Conway Morris S. 1993.** Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North  
462 America, *Palaeontology* **36:**593—635.
- 463 **Conway Morris S, Robison RA. 1988.** More soft-bodied animals and algae from the Middle  
464 Cambrian of Utah and British Columbia. *University of Kansas Paleontological Contributions*  
465 **122:**23—48.
- 466 **Conway Morris S, Savoy LE, Harris AG. 1991.** An enigmatic organism from the ‘Exshaw’  
467 Formation (Devonian-Carboniferous), Alberta, Canada. *Lethaia* **24:**139—152.
- 468 **Cornelius PFS. 1992.** Medusa loss in leptolid hydrozoan (Cnidaria) hydroid rafting, and  
469 abbreviated life-cycles among their remote-island fauna: an interim review. *Scientia Marina*  
470 **56:**245—261.

- 471 **Daly M, Brugler MR, Cartwright P, Collins AG, Dawson MN, France SC, McFadden, SC,**  
472 **Opresko NM, Rodriguez E, Romano S, Stake J. 2007.** The Phylum Cnidaria: A review of  
473 phylogenetic patterns and diversity three hundred years after Linnaeus. *Zootaxa* **1668**:127—  
474 182.
- 475 **Dzik J. 1991.** Is fossil evidence consistent with traditional views of early metazoan phylogeny.  
476 In: Simonetta A, Conway Morris S, eds. *The Early Evolution of Metazoa and the Significance*  
477 *of Problematic Taxa*. New York: Cambridge University Press, 47—56.
- 478 **Etter W. 2002.** Hunsrück Slate: Widespread pyritization of a Devonian fauna. In: Bottjer DJ,  
479 Etter W, Hagadorn JW, Tang CM, eds. *Exceptional Fossil Preservation: A Unique View on*  
480 *the Evolution of Marine Life*. New York: Columbia University Press, 143—165.
- 481 **Fedonkin MA. 1981.** Belomorskaya biota vendi [The Vendian White Sea biota]. *Trudy*  
482 *Geological Institute, Academy Nauk SSSR* **342**:1—100.
- 483 **Fedonkin MA. 1982.** Novoye rodovoye nazvaniye dokembriyskikh kishchnopolostnykh [A  
484 new generic name for some Precambrian coelenterates]: *Paleontologicheskij Zhurnal*  
485 **1982(2)**:137.
- 486 **Fryer G, Stanley GD Jr. 2004.** A Silurian porpitoïd hydrozoan from Cumbria, England, and a  
487 note on porpitoïd relationships. *Palaeontology* **47**:1109—1119.
- 488 **Gabbott SE, Xiang-guang H, Norry MJ, Siveter DJ. 2004.** Preservation of Early Cambrian  
489 animals of the Chengjiang biota. *Geology* **32**:901—904.
- 490 **Gehling JG, Narbonne GM, Anderson MM. 2000.** The first named Ediacaran body fossil,  
491 *Aspidella terranova*. *Palaeontology* **43**:427—456.
- 492 **Glaessner MF. 1971.** The genus *Conomedusites* Glaessner and Wade and the diversification of  
493 the Cnidaria. *Paläontologische Zeitschrift* **45**:1—17.



- 494 **Glaessner MF. 1979.** Precambrian. In: Robison RA, Teichert C, eds. *Treatise on Invertebrate*  
495 *Paleontology Part A*. Lawrence, Kansas: Geological Society of America and University of  
496 Kansas Press, A79—A118.
- 497 **Goldfuss GA. 1818.** Ueber die classification der zoophyten. *Isis*:1008—1013.
- 498 **Hagadorn JW, Belt ES. 2008.** Stranded in upstate New York: Cambrian scyphomedusae from  
499 the Potsdam Sandstone. *Palaaios* **23**:424—441.
- 500 **Hagadorn JW, Miller RF. 2011.** Hypothesized Cambrian medusae from Saint John, New  
501 Brunswick, reinterpreted as sedimentary structures. *Atlantic Geology* **47**:66—80.
- 502 **Hagadorn JW, Fedo CM, Waggoner BM. 2000.** Early Cambrian Ediacaran-type fossils from  
503 California. *Journal of Paleontology* **74**:731—740.
- 504 Hagadorn JW, Dott RH Jr, Damrow D. 2002. Stranded on a Late Cambrian shoreline: medusae  
505 from central Wisconsin. *Geology* **30**:147—150.
- 506 **Hall J. 1847.** *Natural History of New York, part 6; Paleontology of New York, volume 1*;  
507 *Descriptions of the organic remains of the lower division of the New York System*. Albany,  
508 New York: Carrol and Cook.
- 509 **Harrington HJ. 1956.** Olenellidae with advanced cephalic spines. *Journal of Paleontology*  
510 **30**:56—61.
- 511 **Harwood Theisen C, Sumner DY. 2016.** Thrombolite fabrics and origins: Influences of diverse  
512 microbial and metazoan processes on Cambrian thrombolite variability in the Great Basin,  
513 California and Nevada. *Sedimentology* **63**:2217—2252.
- 514 **Hofmann HJ. 1971.** Precambrian fossil, pseudofossils, and problematica in Canada. *Geological*  
515 *Survey of Canada, Bulletin* **189**:1—146.

- 516 **Hofmann HJ, Mountjoy EW, Teitz MW. 1991.** Ediacaran fossils and dubiofossils, Miette  
517 Group of Mount Fitzwilliam area, British Columbia, *Canadian Journal of Earth Sciences*  
518 **28**:1541—1552.
- 519 **Jensen S, Gehling JG, Droser ML, Grant SWF. 2002.** A scratch circle origin for the medusoid  
520 fossil *Kullingia*. *Lethaia* **35**:291—299.
- 521 **Keller M, Lehnert O, Cooper JD. 2012.** Sauk megasequence supersequences, southern Great  
522 Basin: Second-order accommodation events on the southwestern Cordilleran margin platform.  
523 *American Association of Petroleum Geologists Memoir* **98**:873—896.
- 524 **Kimmig J, Pratt BR. 2016.** Taphonomy of the middle Cambrian (Drumian) Ravens Throat  
525 River Lagerstätte, Rockslide Formation, Mackenzie Mountains, Northwest Territories,  
526 Canada. *Lethaia* **49**:150—169.
- 527 **Kirkland CL, MacGabhann BA, Kirkland BL, Daly JS. 2016.** Cryptic disc structures  
528 resembling Ediacaran discoidal fossils from the Lower Silurian Hellefjord Schist, Arctic  
529 Norway. *PLoS One* **11**:e0164071.
- 530 **Kuhn A. 1913.** Entwicklungsgeschichte und verwandschaftsbeziehungen der hydrozoan. I. Teil:  
531 Die Hydroiden. *Ergebnisse der Fortschritte Zoologische* **4**:1—284.
- 532 **Lacelle MA, Hagadorn JW, Groulx P. 2008.** The widespread distribution of Cambrian  
533 medusae: Scyphomedusae strandings in the Potsdam Group of southwestern Quebec.  
534 *Geological Society of America Abstracts with Programs* **40**:369.
- 535 **Laflamme, M, Narbonne, GM, Greentree, C, Anderson, MM. 2007.** Morphology and  
536 taphonomy of an Ediacaran frond: *Charnia* from the Avalon Peninsula of Newfoundland:  
537 acaran frond: *Charnia* from the Avalon Peninsula of Newfoundland. In: Vickers-Rich P,

- 538 Komarower P, eds. *The Rise and Fall of the Ediacaran Biota*, vol. 286. London: Geological  
539 Society Special Publication, 237–257.
- 540 **Lamarck, J-B. 1801.** *Système des Animaux sans Vertèbres*: Paris: Lamarck and Deterville.
- 541 **Landing E, Narbonne GM. 1992.** *Scenella* and “A chondrophorine (medusoid hydrozoan) from  
542 the basal Cambrian (Placentian) of Newfoundland”. *Journal of Paleontology* **66**:338.
- 543 **Liu AG, Matthews JJ, Menon LR, McIlroy D, Brasier MD. 2014.** *Haotia quadriformis* n.  
544 gen., n. sp., interpreted as a muscular cnidarian impression from the Late Ediacaran period  
545 (approx. 560Ma). *Proceedings of the Royal Society, Series B, Biological Sciences*  
546 **281**:20141202.
- 547 **MacGabhann BA. 2007.** Discoidal fossils of the Ediacaran biota: a review of current  
548 understanding. In: Vickers-Rich P, Komarower P, eds. *The Rise and Fall of the Ediacaran*  
549 *Biota*, vol. 286. London: Geological Society Special Publication, 297—313.
- 550 **MacGabhann BA. 2012.** A solution to Darwin’s dilemma: Differential taphonomy of Ediacaran  
551 and Palaeozoic non-mineralised discoidal fossils. PhD Thesis, National University of Ireland,  
552 Galway.
- 553 **MacGabhann BA. 2014.** There is no such thing as the ‘Ediacara Biota’. *Geoscience Frontiers*  
554 **5**:53—62.
- 555 **MacGabhann BA, Murray,J. 2010.** Non-mineralised discoidal fossils from the Ordovician  
556 Bardahessiagh Formation, Co. Tyrone, Ireland. *Irish Journal of Earth Sciences* **28**:1—12.
- 557 **Masiak M, Zylinska A. 1994.** Burgess Shale-type fossils in Cambrian sandstones of the Holy  
558 Cross Mountains. *Acta Palaeontologica Polonica* **39**:329—340.

- 559 **Menon LR, McIlroy D, Liu AG, Brasier MD. 2016.** The dynamic influence of microbial mats  
560 on sediments: fluid escape and pseudofossil formation in the Ediacaran Longmyndian  
561 Supergroup, UK. *Journal of the Geological Society* **173**:177—185.
- 562 **Moore RA, Lieberman BS. 2009.** Preservation of early and Middle Cambrian soft-bodied  
563 fossils from the Pioche Shale, Nevada, USA. *Palaeogeography, Palaeoecology,*  
564 *Palaeoclimatology* **277**:57—62.
- 565 **Narbonne GM. 1994.** New Ediacaran fossils from the Mackenzie Mountains, northwestern  
566 Canada. *Journal of Paleontology* **68**:411—416.
- 567 **Narbonne GM, Myrow P, Landing E, Anderson MM. 1991.** A chondrophorine (medusoid  
568 hydrozoan) from the basal Cambrian (Placentian) of Newfoundland. *Journal of Paleontology*  
569 **65**:186—191.
- 570 **Oliver WA Jr. 1984.** *Conchopeltis*, its affinities and significance. *Palaeontographica*  
571 *Americana* **54**:141—147.
- 572 **Orr PJ, Briggs DEG, Kearns SL. 1998.** Cambrian Burgess Shale animals replicated in clay  
573 minerals. *Science* **281**:1173—1175.
- 574 **Ossian CR. 1973.** New Pennsylvanian scyphomedusan from western Iowa, *Journal of*  
575 *Paleontology* **77**:990—995.
- 576 **Owen R. 1843.** *Lectures on the Comparative Anatomy and Physiology of the Invertebrate*  
577 *Animals, Delivered at the Royal College of Surgeons*: London: Longman, Brown, Green, and  
578 Longmans.
- 579 **Palmer AR, Halley RB. 1979.** Physical stratigraphy and trilobite biostratigraphy of the Carrara  
580 Formation (Lower and Middle Cambrian) in the southern Great Basin. *U. S. Geological*  
581 *Survey Professional Paper* **1047**:1—131.

- Rauff H. 1939.** *Palaeonectris discoidea* Rauff, eine siphonophore medusa aus dem rheinischen Unterdevon nebst bemerkungen zur umstrittenen *Brooksella rhenana* Kinkelin. *Paläontologische Zeitschrift* **21**:194—213.
- Ruedemann R. 1916.** Account of some new or little-known species of fossils. *New York State Museum, Bulletin* **189**:7—97.
- Ruedemann R. 1934.** Paleozoic plankton of North America. *Geological Society of America Memoir* **2**:1—141.
- Ruiz JMG, Carnerup A, Christy AG, Wilhelm NJ, Hyde ST. 2004.** Morphology: An ambiguous indicator of biogenicity. *Astrobiology* **2**:353—369.
- Sappenfield, AR, Tarhan LG, Droser ML. 2016.** Earth’s oldest jellyfish strandings: a unique taphonomic window or just another day at the beach? *Geological Magazine* In Press DOI [10.1017/s0016756816000443](https://doi.org/10.1017/s0016756816000443).
- Schuchert P. 2015.** World Hydrozoa: *Porpita porpita* (Linnaeus, 1758). Accessed through World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=117831> (accessed on 06 March 2016).
- Southcott RV. 1958** South Australian jellyfish. *The South Australian Naturalist* **32**:53—61.
- Sprigg RC. 1947.** Early Cambrian (?) jellyfishes from the Flinders Ranges, South Australia. *Transactions of the Royal Society of South Australia* **71**:212—224.
- Stanley GD. 1982.** Paleozoic chondrophores (medusoid hydrozoans) and their implications for problematic mollusk-like fossils. *Third North American Paleontological Convention, Proceedings* **2**:501—504.

- 605 **Stanley GD, Kanie Y. 1985.** The first Mesozoic chondrophorine (medusoid hydrozoan) from  
606 the Lower Cretaceous of Japan. *Palaeontology* **28**:101—109.
- 607 **Stasinska A. 1960.** *Velumbrella czarnockii* n. gen. n. sp. Méduse du Cambrien inférieur des  
608 Monts de Sainte-Croix. *Acta Palaeontologica Polonica* **5**:337—346.
- 609 **Sun WG. 1986.** Precambrian medusoids: the *Cyclomedusa*-plexus and *Cyclomedusa*-like  
610 pseudofossils. *Precambrian Research* **31**:325—360.
- 611 **Sun WG, Hou X. 1987.** Early Cambrian medusae from Chengjiang, Yunnan, China. *Acta*  
612 *Palaeontologica Sinica* **26**:257—271.
- 613 **Tarhan LG, Droser ML, Gehling JG, Dzaugis MP. 2015.** Taphonomy and morphology of the  
614 Ediacara form genus *Aspidella*. *Precambrian Research* **257**:124—136.
- 615 **Van Iten H, Marques A, de Moraes Leme J, Forancelli Pacheco MLA, Guimares Simões**  
616 **M. 2014.** Origin and early diversification of the Phylum Cnidaria Verrill: Major developments  
617 in the analysis of the taxon's Proterozoic-Cambrian history. *Palaeontology* **57**:677—690.
- 618 **Verrill AE. 1865.** Classification of polyps. *Communications of the Essex Institute* **4**:145—152.
- 619 **Wade M. 1972.** Hydrozoa and Scyphozoa and other medusoids from the Precambrian Ediacara  
620 fauna, South Australia. *Palaeontology* **15**:197—225.
- 621 **Waggoner BJ, Collins AG. 1995.** A new chondrophorine (Cnidaria, Hydrozoa) from the Cadiz  
622 Formation (Middle Cambrian) of California. *Paläontologische Zeitschrift* **69**:7—17.
- 623 **Walcott CD. 1876.** Descriptions of new species of fossils from the Trenton Limestone. *New*  
624 *York State Museum of Natural History, 28<sup>th</sup> Annual Report*:93—97.
- 625 **Walcott CD. 1884.** Paleontology of the Eureka district. *United States Geological Survey,*  
626 *Monographs* **8**:1—298.
- 627 **Walcott CD. 1898.** Fossil medusa. *United States Geological Survey, Monographs* **30**:1—201.

- 628 **Walcott CD. 1911.** Middle Cambrian Holothurians and medusa. *Smithsonian Miscellaneous*  
629 *Collections* **57**:41—68.
- 630 **Webster M. 2011.** Trilobite biostratigraphy and sequence stratigraphy of the upper Dyeran  
631 (traditional Laurentian ‘Lower Cambrian’) in the southern Great Basin, U.S.A. *Museum of*  
632 *Northern Arizona Bulletin* **67**:121—154.
- 633 **Xiao S, Zhang Y, Knoll AH. 1998.** Three-dimensional preservation of algae and animal  
634 embryos in a Neoproterozoic phosphorite. *Nature* **391**:553—558.
- 635 **Yochelson EL. 1984.** North American Middle Ordovician *Scenella* and *Macroscenella* as  
636 possible chondrophorine coelenterates. *Palaeontographica Americana* **54**:148—153.
- 637 **Yochelson EL, Gil Cid D. 1984.** Reevaluation of the systematic position of *Scenella*. *Lethaia*  
638 **17**:331—340.
- 639 **Yochelson EL, Mason CE. 1986.** A chondrophorine coelenterate from the Borden Formation  
640 (Lower Mississippian) of Kentucky. *Journal of Paleontology* **60**:1025—1028.
- 641 **Yochelson EL, Stürmer W, Stanley GD. 1983.** *Plectodiscus discoideus* (Rauff): a redescription  
642 of a chondrophorine from the Early Devonian Hunsrück Slate, West Germany.  
643 *Paläontologische Zeitschrift* **57**:39—68.
- 644 **Young GA, Hagadorn JW. 2010.** The fossil record of cnidarian medusae. *Palaeoworld*  
645 **19**:212—221.
- 646 **Zhang X, Hua H, Reitner J. 2006.** A new type of Precambrian megascopic fossils: the Jinxian  
647 biota from northeastern China. *Facies* **52**:169—181.
- 648 **Zhao Y-L, Zhu, M-Y. 1994.** Discoidal fossils of Kaili fauna from Taijiang, Guizhou. *Acta*  
649 *Palaeontologica Sinica* **33**:272—280.

**Zhu M-Y, Zhao Y-L, Chen J-Y. 2002.** Revision of the Cambrian discoidal animals  
*Stellostomites eumorphus* and *Pararotadiscus guizhouensis* from South China. *Geobios*  
**35**:165—185.

## Figure captions

### Figure 1: Locality and stratigraphy.

(A) Map indicating where the specimens were derived from in the Nopah Range, Nevada, U.S.A,  
with locality indicated by the star which represents 35° 53'35.56" N 116° 04' 39.27" W; (B) A  
generalized stratigraphic chart for the Carrara Formation, with the star indicating the member the  
specimens were collected from.

### Figure 2: The slab containing the fossil specimens.

(A) Part and (B) counterpart, where 1 = KUMIP 389538, 2 = KUMIP 389539, 3 = KUMIP  
389540. Scale bar is 10mm.

### Figure 3: *Discophyllum* sp. Hall, 1847 from the Echo Shale Member of the Carrara Formation.

(A-D) Dorsal view of the part of KUMIP 389538. In (A) scale bar is 1mm, the boxes surrounded  
in black represent locations of C and D, and the boxes surrounded in blue were the regions



subjected to EDS analysis with the results from these shown in Figures 4 and 5, respectively; (B) Line drawing illustrating the preserved structures; (C, D) Close-ups of different portions of the specimen; scale bars are 500µm; (E) Dorsal view of the part of KUMIP 389540; scale bar is 1mm; (F) Dorsal view of the part of KUMIP 389539; scale bar is 1mm.

**Figure 4: Element maps of KUMIP 389538 and surrounding rock matrix.**

The region demarcated by the blue box labeled “Fig. 4” in Figure 3a was analyzed. 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 5: Element maps of a different portion of KUMIP 389538 and surrounding rock matrix.**

The region demarcated by the blue box labeled “Fig. 5” in Figure 3a was analyzed. 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 1**(on next page)

Locality and stratigraphy.

(A) Map indicating where the specimens were derived from in the Nopah Range, Nevada, U.S.A, with locality indicated by the star which represents 35°53'35.56" N 116°04' 39.27" W;  
 (B) A generalized stratigraphic chart for the Carrara Formation, with the star indicating the member the specimens were collected from.

A

B

# United States of America

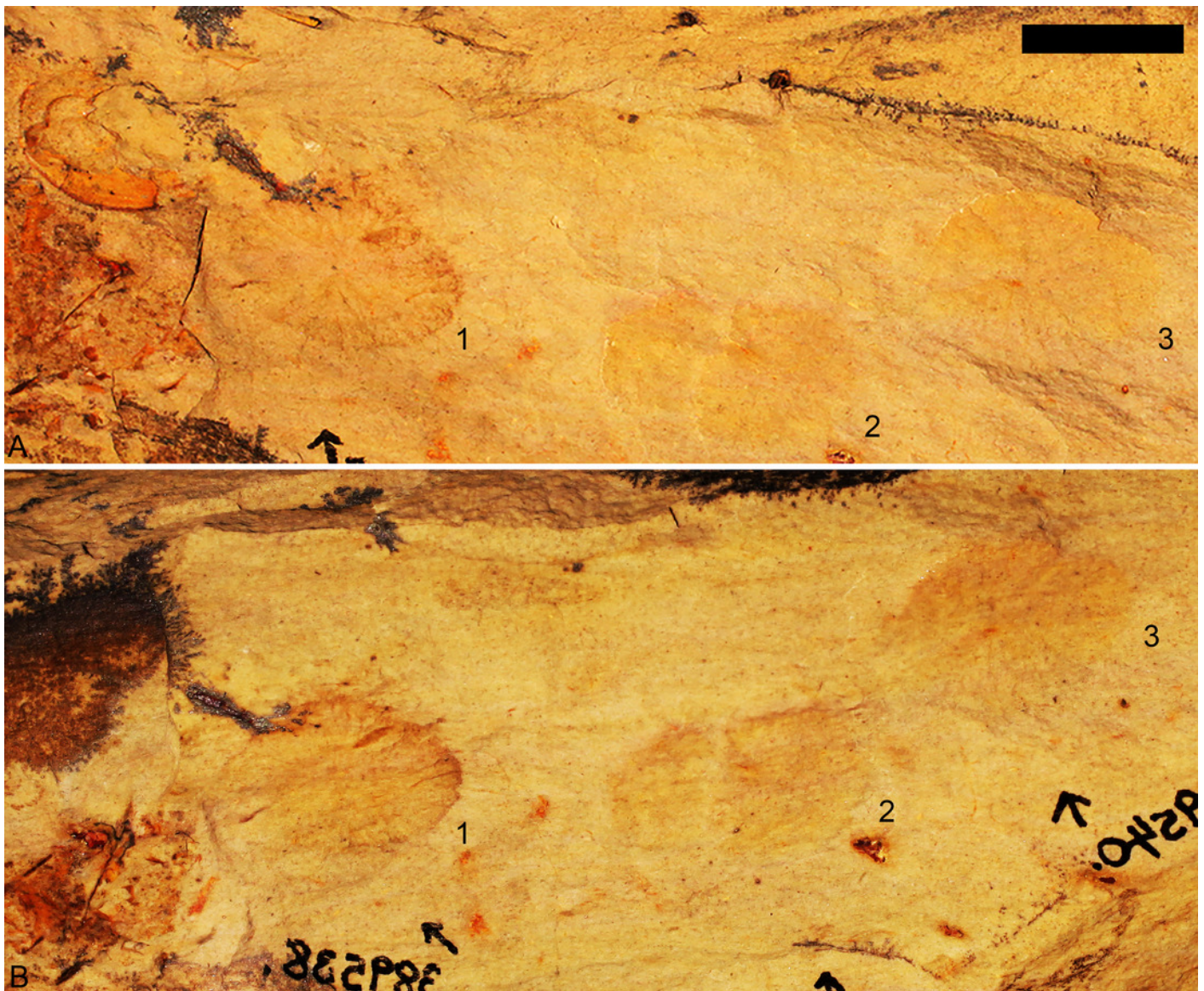


Cambrian	Delamaran Stage		Carrara Formation	Desert Range Limestone Member
	Dyeran Stage			Jangle Limestone Member
				Pahrump Hills Shale Member
				Red Pass Limestone Member
				Pyramid Shale Member
				Gold Ace Limestone Member
				Echo Shale Member ★
				Thimble Limestone Member
				Eagle Mountain Shale Member

# Figure 2

The slab containing the fossil specimens.

(A) Part and (B) counterpart, where 1 = KUMIP 389538, 2 = KUMIP 389539, 3 = KUMIP 389540. Scale bar is 10mm.

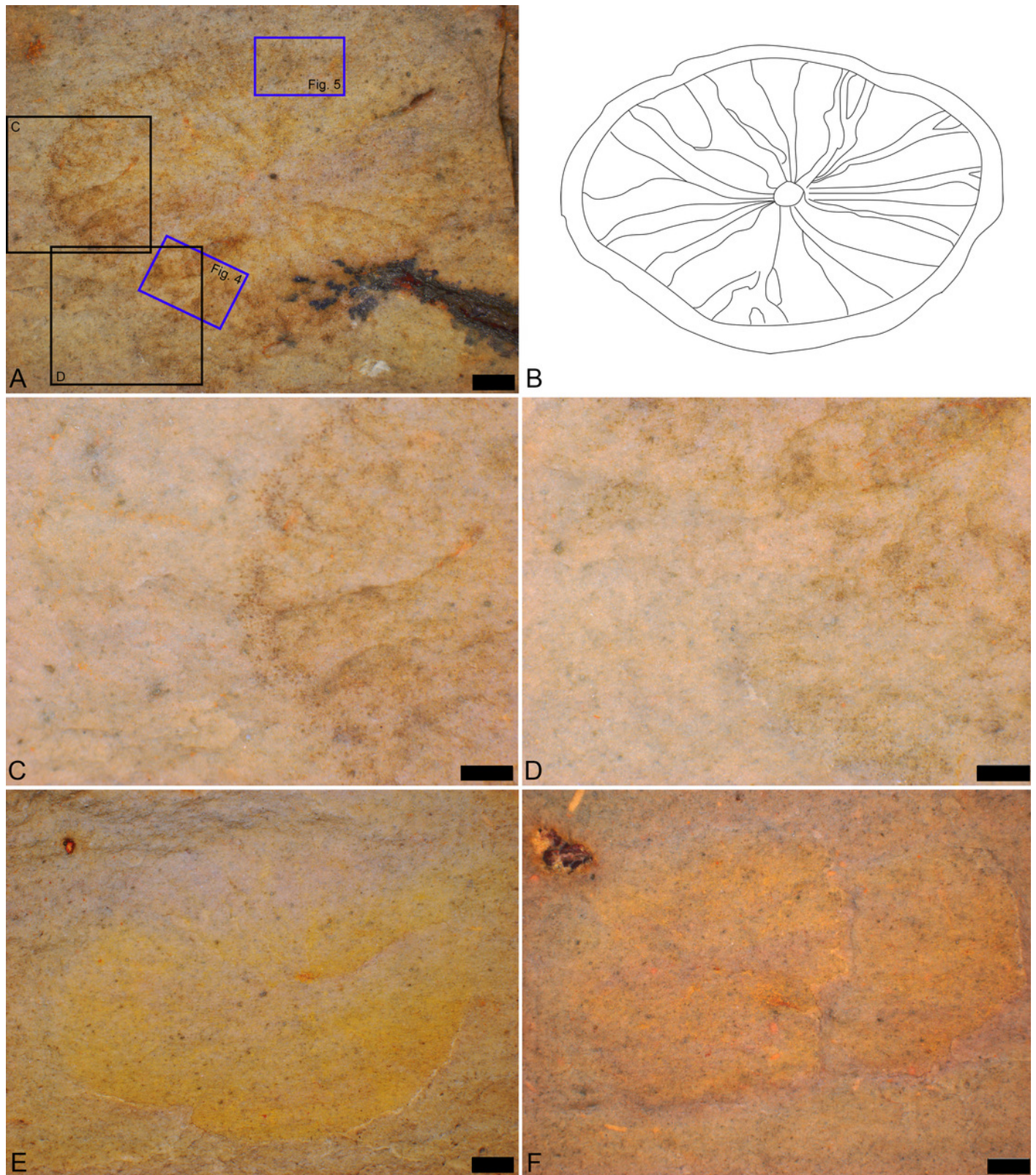


# Figure 3

*Discophyllum* sp. Hall, 1847 from the Echo Shale Member of the Carrara Formation.

(A-D) Dorsal view of the part of KUMIP 389538. In (A) scale bar is 1mm, the boxes surrounded in black represent locations of C and D, and the boxes surrounded in blue were the regions subjected to EDS analysis with the results from these shown in Figures 4 and 5, respectively; (B) Line drawing illustrating the preserved structures; (C, D) Close-ups of different portions of the specimen; scale bars are 500µm; (E) Dorsal view of the part of KUMIP 389540; scale bar is 1mm; (F) Dorsal view of the part of KUMIP 389539; scale bar is 1mm.





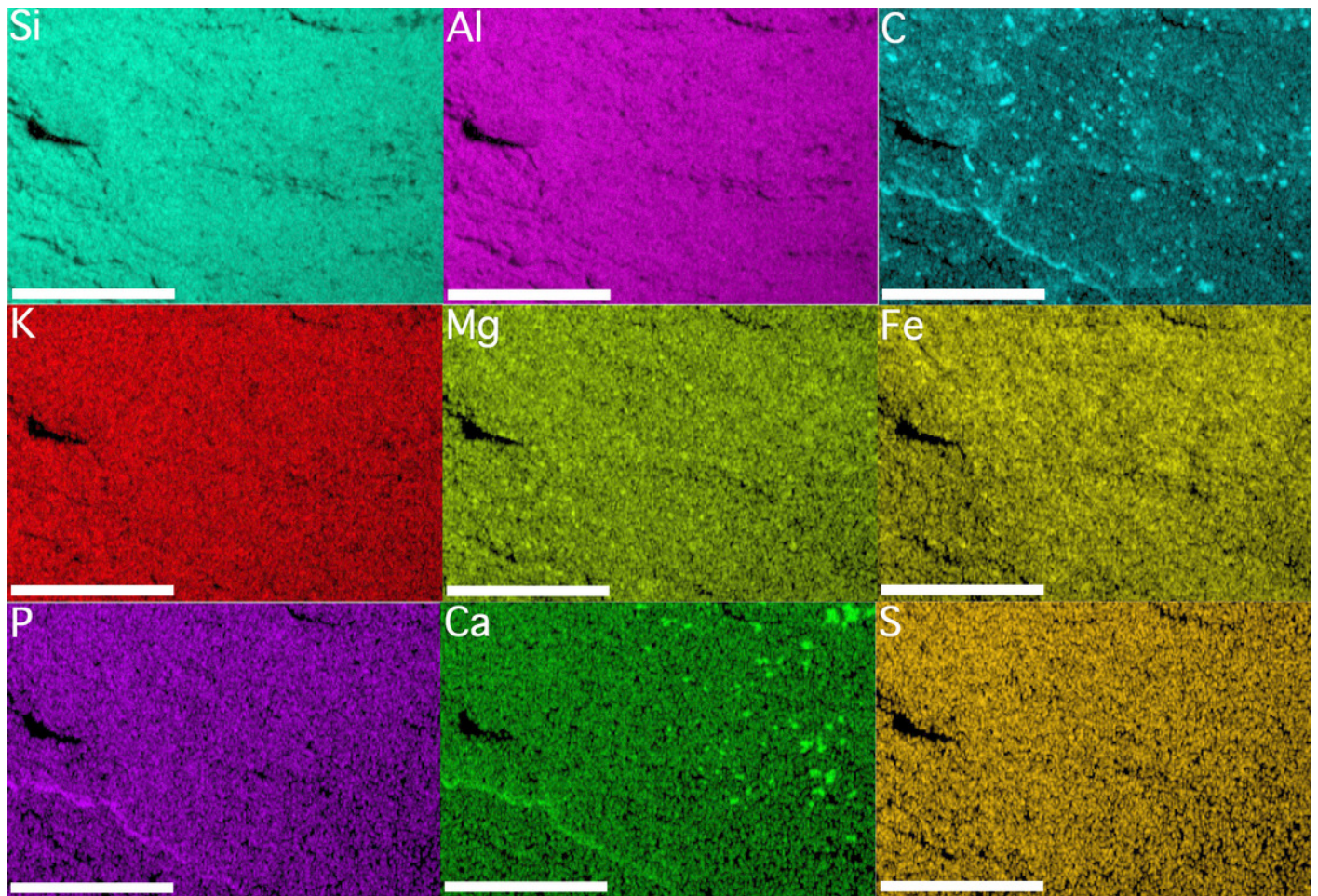


# Figure 4

Element maps of KUMIP 389538 and surrounding rock matrix.

The region demarcated by the blue box labeled “Fig. 4” in Figure 3a was analyzed. 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.

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





# Figure 5

Element maps of a different portion of KUMIP 389538 and surrounding rock matrix.

The region demarcated by the blue box labeled “Fig. 5” in Figure 3a was analyzed. 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.

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

