

An enigmatic euchelicerate from the Mississippian (Serpukhovian) and insights into invertebrate preservation in the Bear Gulch Limestone, Montana

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ABSTRACT

The Bear Gulch Limestone houses a diverse, exceptionally preserved marine fauna from the early Carboniferous. A wealth of vertebrate and invertebrate forms has previously been recorded from this deposit, including fish, annelids, and several arthropods. To expand the record of Bear Gulch marine arthropods, a new enigmatic, possibly blind euchelicerate, *Titano-prosoma edgecombei*, gen. et sp. nov., is described. The new euchelicerate taxon displays a hypertrophied, ovate, and structureless prosoma—a morphology unique among marine euchelicerates. We explore how the large prosoma and lack of ocular structures reflect possible adaptations to an infaunal, burrowing lifestyle. This species represents the fourth euchelicerate genus described from the Bear Gulch Limestone, further highlighting the impressive disparity of marine arthropods preserved in the deposit. The addition of novel invertebrate forms found in previously unknown museum material suggests that the Bear Gulch Limestone likely houses a still undocumented diversity of Carboniferous arthropods.

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INTRODUCTION

The Bear Gulch Limestone houses intervals of exceptional preservation—so-called Konservat-Lagerstätten (Seilacher, 1970; Seilacher et al., 1985)—from the Mississippian (Serpukhovian) of Montana that record a diverse fauna (Williams, 1983; Grogan and Lund, 2002; Hagadorn, 2002). In addition to the well-known cartilaginous fishes (Lund, 1989; Grogan and Lund, 2000), many invertebrates are known from the deposit (Singer, 2021). Recent examination of the Bear Gulch invertebrates has also uncovered novel records of various molluscs (Mapes et al., 2019; Conway Morris and Caron, 2022; Whalen and Landman, 2022), suggesting a still undocumented record of other invertebrates. One apparently rare, but diverse animal group preserved within the Bear Gulch Limestone are the euchelicerate arthropods. To date, three euchelicerate species have been documented—the synziphosurine *Anderella parva* Moore et al., 2007, and two xiphosurids: *Boeotiaspis longispinus* (Schram, 1979), and *Euproops* sp. (Hagadorn, 2002; Moore et al., 2007; Haug et al., 2012; Bicknell et al., 2022). All of these are known from limited material. To expand this already impressive diversity of aquatic euchelicerates, here we document a new enigmatic, synziphosurine-like euchelicerate from the deposit.

GEOLOGICAL SETTING

The specimen was collected from the Bear Gulch Limestone in Fergus County, central Montana. However, the precise collecting locality of the specimen is unknown. The Bear Gulch Limestone beds have been placed within both the Heath Formation and the overlying Tyler Formation (Williams, 1983; Cox, 1986; Lund et al., 1993; Singer et al., 2019). The current consensus, based on cephalopod, conodont, and palynomorph occurrences, as well as regional stratigraphic relationships, places the Bear Gulch Limestone within the Tyler Formation (Singer et al., 2019; Singer, 2021), dating the deposit as Serpukhovian (late Mississippian) in age. The Bear Gulch Limestone is part of a transgressive sequence that was likely deposited in the Big Snowy Trough (Williams, 1983; Hagadorn, 2002; Singer et al., 2019). This trough connected the Big Snowy Basin to a N-S trending Cordilleran Miogeosyncline to the west, 12° N of the equator during deposition (Williams, 1983; Hagadorn, 2002; Singer et al., 2019).

The Bear Gulch Limestone is a plattenkalk, or lithographic limestone, consisting of nearly horizontal alternating massive argillaceous silty dolomitic micritic limestone beds and platy clayey dolomitic micritic beds (Williams, 1983; Hagadorn, 2002; Singer et al., 2019; Singer, 2021). These alternating units are typical of the Flinz and Fäule style of bedding made famous in other fine-grained lithographic limestones, for example, Solnhofen (Munnecke et al., 2008). Similar to Solnhofen, Bear Gulch also has layers with exceptional preservation, making it one of the most important Konservat-Lagerstätten in the early Carboniferous (Hagadorn, 2002). Preservation information on Bear Gulch specimens is scarce, but scanning electron microscopy (SEM) and elemental energy-dispersive X-ray spectroscopy (EDS) analyses of 23 specimens, covering invertebrates and vertebrates, have shown that most specimens were replaced by

either calcium carbonate, calcium phosphate, or carbonate fluorapatite, with a couple of specimens preserving traces of carbon (Thomas, 2004). This suggests that many specimens have a diagenetic overprint, but some might preserve original carbon.

MATERIAL AND METHODS

The examined specimen (part and counterpart) was collected by commercial collectors and sold in 1995 to the Staatliche Museum für Naturkunde Karlsruhe by Henzel Fossils, Celle, Germany. The specimen is currently housed in the Staatliche Museum für Naturkunde, Karlsruhe, palaeontological collections. The specimen was photographed with a Canon EOS R5 camera mounted with an EF 100 f/2.8 Macro IS USM lens. The specimen was photographed under white light and 365 nm UV light in two mediums—air and immersed in ethanol. The color, contrast, and brightness of the images were adjusted using Adobe Photoshop Lightroom. Specimen measurements were made from photographs in ImageJ (Schneider et al., 2012).

The specimen was examined using SEM, and integrated EDS from Oxford Instruments (AZTEC-EDS) using a ZEISS LEO 1530 SEM at the Institute of Nanotechnology, Karlsruhe Institute of Technology. The fossil was secured to an SEM stub with copper tape and first investigated uncoated. This led to a high degree of charging because the electron beam point of impact was not earthed effectively by the natural conductivity of the specimen. To reduce the effects of charging, the specimen was wrapped in copper tape, so that only the analysed region was visible. To improve conductivity, the copper tape was placed in contact with the stage to earth the electrical charge. The specimen was then coated with carbon (10 nm). Analyses were conducted with the following operating conditions: accelerating voltage 20 keV with an aperture of 60 μm , a working distance of 10 mm, and 60 μm aperture for imaging and EDS analyses. A standard Everhart-Thornley Detector (ETD) and an InLens-SE-detector were used for secondary (topographic) electron imaging. EDS analyses were conducted using mainly the ETD, thus avoiding artifacts from charging. SEM maps have been recorded using an acquisition time of 100 μs /pixel for 20 frames with a resolution of 512 \times 384 pixels. With an image width of 3.2 mm and height of 2.4 mm, 169 scan fields were constructed at this resolution to encompass the fossil. These parameters resulted in ~6.5 minutes per scan field and a total acquisition time of 18.5 hours. Scan fields were stitched together for the total element distribution map. For EDS data evaluation the software AZTEC 6.1 (Oxford Instruments) was used. When mapping elements, a detector dead time of ~30 % was used. For each pixel, 20 X-ray spectra were recorded with element-specific X-ray spectral lines displayed in a concentration-proportional image. This resulted in the spatial distribution of elements on the sample surface.

When describing the material, we followed the systematic taxonomy of Dunlop and Lamsdell (2017) and the descriptive terminology from Moore et al. (2007), Lamsdell (2013), Bicknell and Pates (2020), and Bicknell and Smith (2021).

INSTITUTIONAL ABBREVIATIONS: **CM**, Carnegie Museum of Natural History, Pittsburgh, PA. **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany.

SYSTEMATIC PALAEONTOLOGY

Subphylum: Chelicerata Heymons, 1901

Euchelicerata: Weygoldt and Paulus, 1979

Class: Incertae sedis

Titanoprosoma edgecombei, gen. et sp. nov.

Figures 1–3

ETYMOLOGY: The generic name reflects the hypertrophied (*titan*), ovate head-shield (*pro-soma*). The specific name was selected in recognition of Gregory Edgecombe who has committed his career to the examination and documentation of arthropods.

HOLOTYPE: SMNK-PAL 1271 (part and counterpart).

TYPE LOCALITY, FORMATION, AND AGE: Fergus County, central Montana; Bear Gulch Limestone, Serpukhovian, Late Mississippian, Carboniferous.

DIAGNOSIS: Distinguished from other euchelicerates by the presence of an effaced (structureless) ovate prosoma that is over half the length of the fossil and no discernable pretelson.

PRESERVATION: The specimen is preserved as a compressed, two-dimensional exoskeleton in part and counterpart on brownish/gray micritic limestone.

DESCRIPTION: Articulated prosoma, partial opisthosoma, and partial telson (fig. 1). Part more complete than counterpart (fig. 1A, D). SMNK-PAL 1271 is 38.1 mm long. Prosoma ovate, completely preserved, 22.0 mm long, 17.5 mm wide. Possible prosomal doublure observed. No other dorsal prosomal features noted, indicating an effaced (structureless) prosoma. Impressions of two prosomal appendages on the right side of prosoma noted under UV light, both ~2.6 mm long and ~0.4 mm wide.

Opisthosoma triangular, 8.4 mm long and 11.8 mm wide, tapering to 2.8 mm. Seven opisthosomal tergites are observed. Anteriormost tergite largest section, 2.6 mm long, 11.6 mm wide. Section of first tergite removed on right side. Tergites 2–7 between 1.8–0.6 mm long, 6.7–3.2 mm wide (table 1). Tergal boundaries pronounced in more anterior tergites. No opisthosomal axial lobe, pleural lobes, or marginal rim noted. Telson 8.4 mm long, tapering from 3.1 mm wide to rock edge.

TABLE 1. Measurements of SMNK-PAL 1271 opisthosomal tergites.

Tergites: Dimensions	1	2	3	4	5	6	7
Length	2.6	1.1	0.8	1.4	1.5	1.8	0.6
Width	11.6	6.7	5.1	4.9	4.8	4.3	3.2

REMARKS: The prosomal morphology of most euchelicerates is typically quadrate to crescentic (Tollerton, 1989; Anderson and Selden, 1997), with fewer examples of ovate (Eldredge, 1974; Selden et al., 2019; Lustri et al., 2021) or rounded (Lustri et

al., 2021) shapes. Further, prosomal sections commonly comprise ~30% of the exoskeleton. To date, the combination of an ovate prosoma consisting of half the body length is

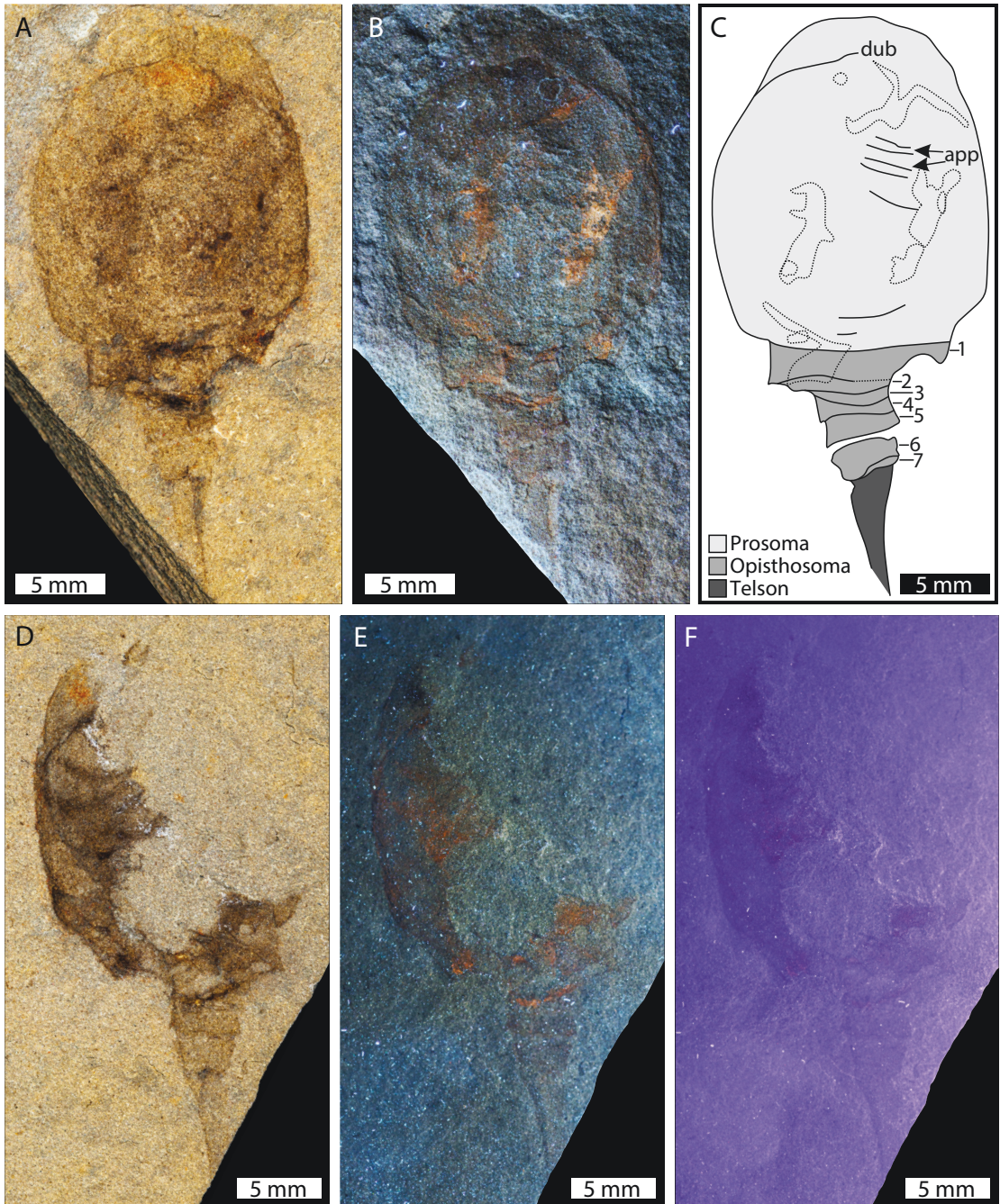


FIGURE 1. *Titanoprosoma edgecombei*, gen. et sp. nov., holotype from the Bear Gulch Limestone, Carboniferous (Serpukhovian), Montana. (A–C) SMNK-PAL 1271, part. **A**. Specimen imaged under ethanol and LED light. **B**. Specimen imaged dry under UV light. **C**. Interpretative drawing of part showing three main exoskeletal divisions. Numbers indicate expressed tergites. (D–F) SMNK-PAL 1271, counterpart. **D**. Specimen imaged under ethanol and LED light. **E**. Specimen imaged dry under UV light. **F**. Specimen imaged under ethanol and UV light. Abbreviations: **app**, appendage; **dub**, doublure. Image credit: Mathias Vielsäcker.

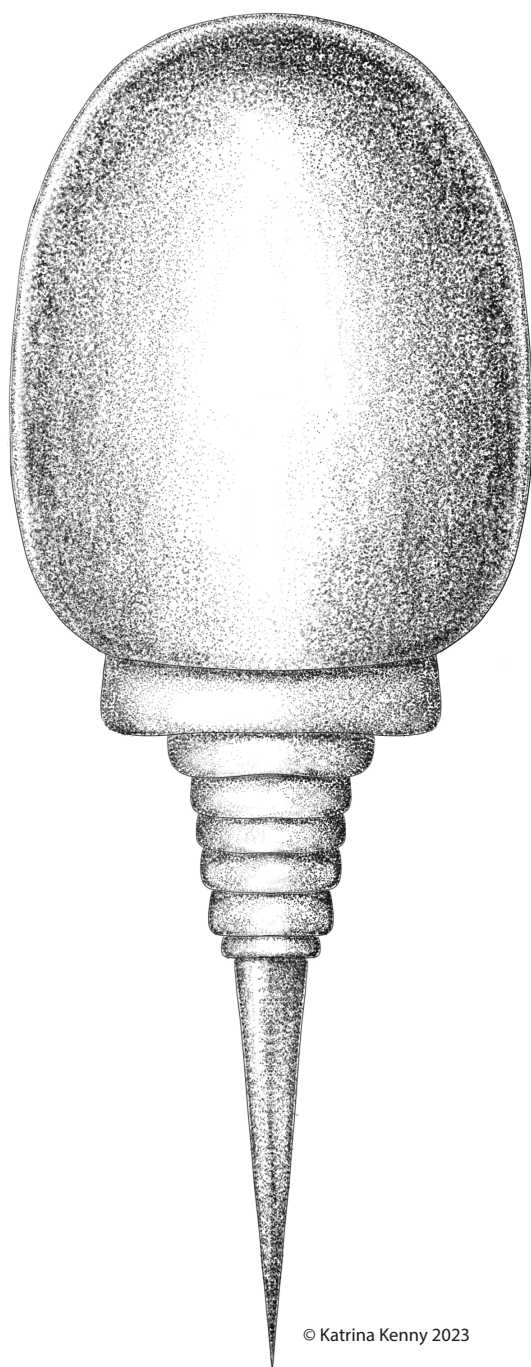
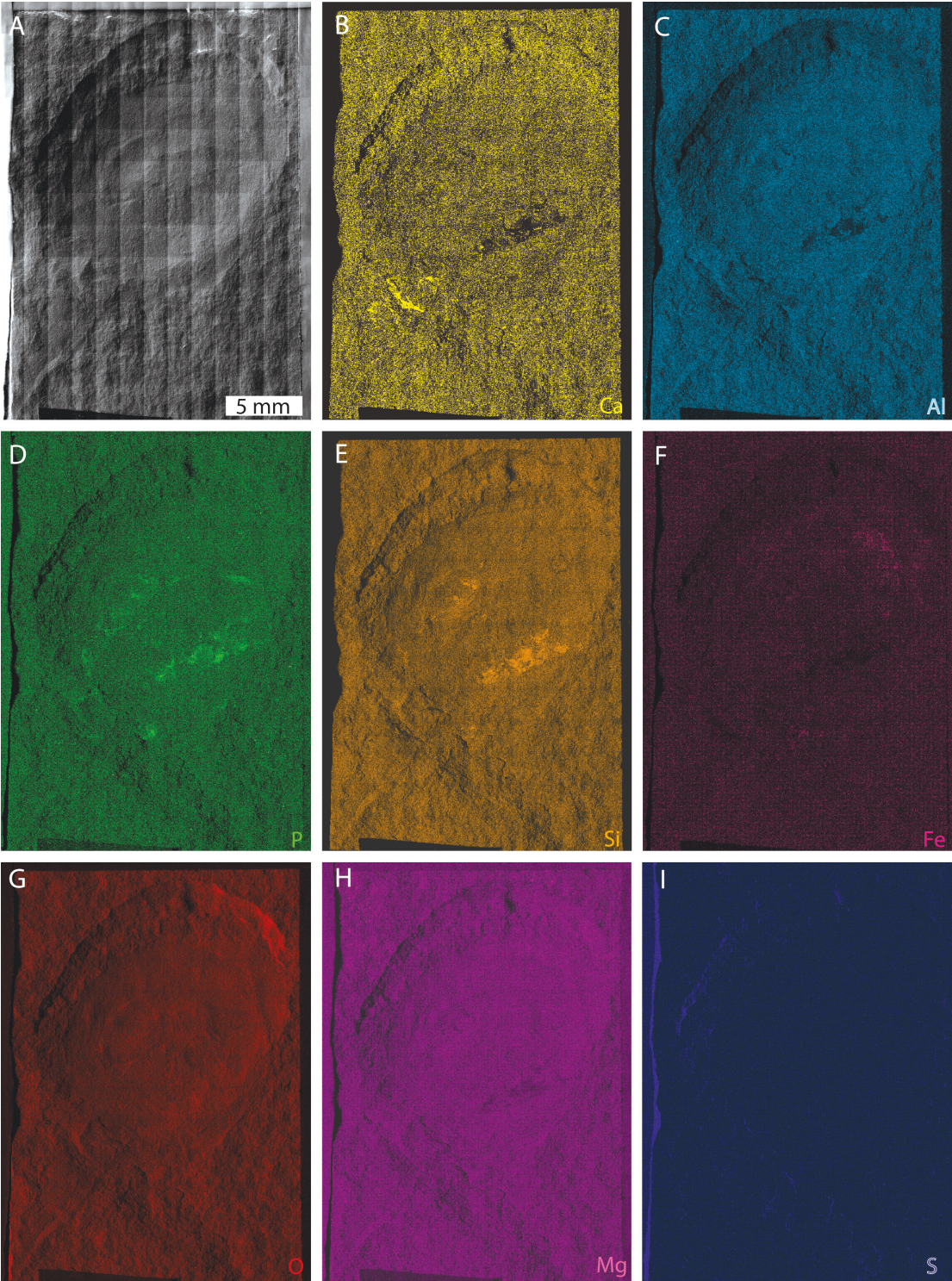


FIGURE 2. Proposed reconstruction of *Titanoprosoma edgecombei*. Image credit: Katrina Kenny.

unknown, distinguishing *Titanoprosoma edgecombei*, gen. et sp. nov., from other euehelicercates. Nonetheless, comparisons with other Paleozoic euehelicercates are required. The new taxon is distinct from Eurypterida (sea scorpions) as *T. edgecombei* lacks a demonstrable metasoma, excluding the material from Eurypterida (Snodgrass, 1952; Dunlop and Lamsdell, 2017). Although SMNK-PAL 1271 is superficially comparable to Xiphosurida (true horseshoe crabs), the lack of an opisthosoma fused into a plate (= thoracetrone) excludes the new material from xiphosurids (Dunlop and Lamsdell, 2017; Bicknell and Pates, 2020; Bicknell et al., 2021). Chasmataspidida is another possibility. However, the lack of a bucklerlike morphology along the opisthosoma (Marshall et al., 2014; Lamsdell, 2020) and nine postabdominal segments (Dunlop and Lamsdell, 2017) excludes the Bear Gulch material from the chasmataspidids. We can also consider the synziphosurines (Bicknell and Pates, 2020)—a paraphyletic assemblage containing basal crown-group euehelicercates (Giribet and Edgecombe, 2019). Morphologically, *T. edgecombei* is most comparable to synziphosurine taxa (Bicknell and Pates, 2020). However, synziphosurine species have at least eight expressed tergites, a pretelson, and lack ovate prosomas. This suggests SMNK-PAL 1271 is not a synziphosurine (Bergström, 1975; Moore et al., 2005; Dunlop and Lamsdell, 2017). Alternatively, if this animal is a synziphosurine, the morphology

FIGURE 3. SEM micrograph and SEM-EDS elemental maps of *Titanoprosoma edgecombei* holotype from the Bear Gulch Limestone, Carboniferous (Serpukhovian), Montana. **A.** SEM micrograph of SMNK-PAL 1271, part. **B–I.** SEM-EDS elemental maps of Ca, Al, P, Si, Fe, O, Mg, and S, respectively. Scale bar in A applies to all panels.



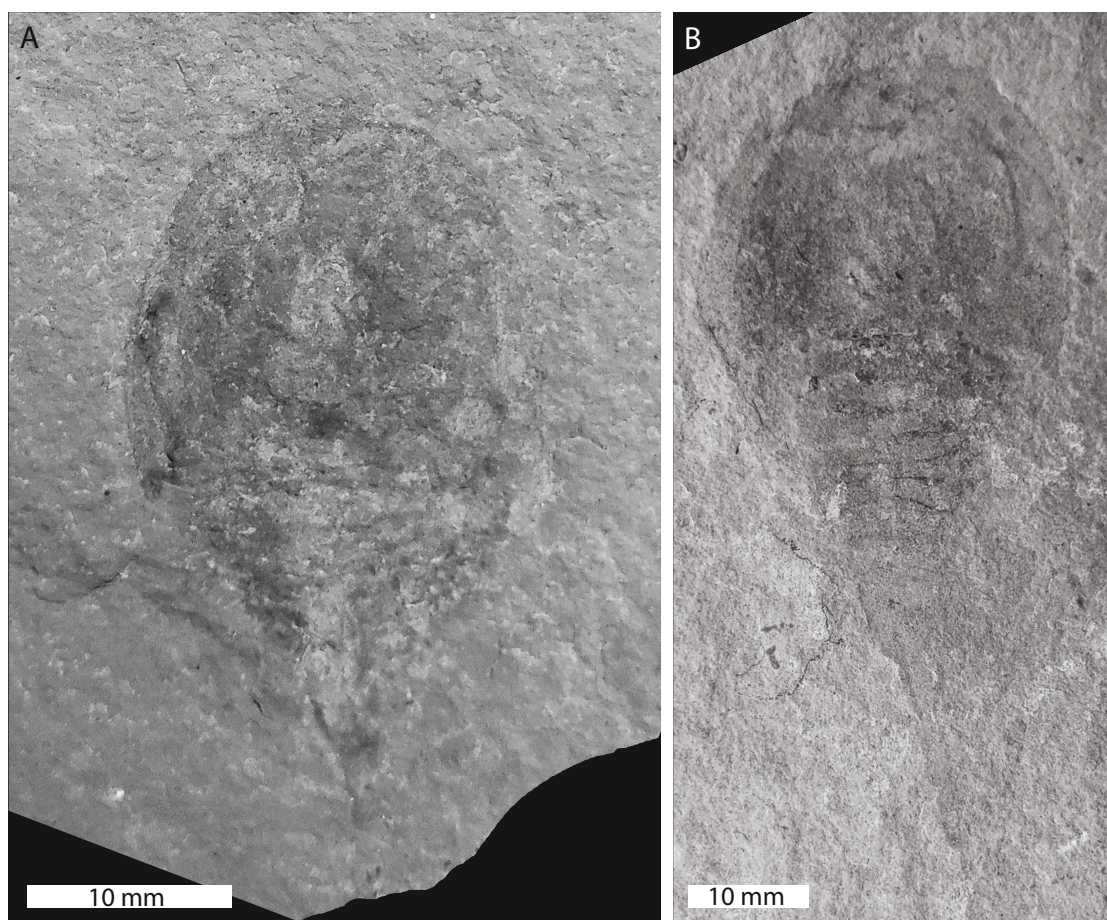


FIGURE 4. *Anderella parva* from the Bear Gulch Limestone. **A.** CM54200 (holotype), internal mould. **B.** CM54201 (paratype), external mould. Both panels have been converted to grayscale. Image credit: Albert Kollar.

is distinct from other forms. Finally, the ovate prosomal morphology contrasts the co-occurring *Anderella parva* that has a much more crescent-shaped prosoma, excluding SMNK-PAL 1271 from the known Bear Gulch synziphosurine (fig. 4). In sum, SMNK-PAL 1271 is distinct from all other Paleozoic euchelicerates. An additional consideration is that the specimen has a broad, horseshoe shape akin to *Lunataspis* Rudkin et al., 2008, followed by the thoracetrone and then a pretelson region (Rudkin et al., 2008; Lamsdell et al., 2023). The holotype does not preserve evidence for these morphologies.

The euchelicerate fossil record contains forms that have not been placed within a higher-order grouping due to aberrant morphologies. This includes genera such as *Bembicosoma* Laurie, 1899, *Maldybulakia* Tesakov and Alekseev, 1992, and *Offacolus* Orr et al., 2000. We have taken a similarly conservative position in our placement of *Titanoprosoma edgcombei* within Euchelicerata as the holotype shows seven opisthosomal tergites; a morphology not observed in any marine Paleozoic euchelicerate groups (Dunlop and Lamsdell, 2017). One conservative

perspective is that the additional tergites were telescoped under the large prosoma. However, more material of this rare animal is needed to confirm this assumption and additional specimens are likely to shed more light on the taxonomic position of this species.

One final possibility is that *Titanoprosoma edgecombei* could belong within Aglaspidida. At least *Brachyaglaspis singularis* Ortega-Hernández et al., 2016, shows a larger cephalic region and a reduced number of trunk tergites. However, our material shows no evidence of postventral plates, a morphological characteristic observed in all aglaspidids (Van Roy, 2005; Ortega-Hernández et al., 2013, 2016; Lerosey-Aubril et al., 2017; Siveter et al., 2018). As such, we can confidently exclude *T. edgecombei* from Aglaspidida.

PRESERVATION

The more complete part of *Titanoprosoma edgecombei* was analyzed using SEM-EDS (fig. 3). This specimen is preserved as a compressed, two-dimensional exoskeleton in part and counterpart on brownish/gray micritic limestone, parallel to bedding. The elemental composition of the host rock reveals it is a carbonate.

The anterior of the specimen, as well as regions along the exoskeleton edge, are preserved as iron oxide and/or oxyhydroxide. These represent pyrite weathering products. Some unweathered pyrite is present on the left side of the prosoma, as indicated by the presence of sulfur and iron (fig. 3). The structures that are well visible under UV light (fig. 1B) are preserved as phosphorus, silica, and calcium, reflecting taphonomic phosphatization (fig. 3B, D, E). We suggest this is likely some form of apatite (Whitaker et al., 2022). The composition is similar to the apatite preservation in Bear Gulch polychaetae worms and the carbonate fluorapatite preservation of Bear Gulch shrimp specimens (Thomas, 2004), as well as Cambrian bradoriid carapaces (Streng et al., 2008; Peel et al., 2021; Whitaker et al., 2022). However, this preservational mode is restricted to the thicker exoskeletal regions. This suggests that fossil material in other regions of the specimen were too thin to be completely preserved and records a mix of carbonates and clay—the host sediment. In addition to this, the uncoated specimen preserved small patchy carbonaceous areas, which did not exist as consistent film and likely reflected weathering and/or metamorphic alteration of the rock.

DISCUSSION

The large, ovate prosoma observed in *Titanoprosoma edgecombei* represents an extreme morphology for benthic euhelicerates. The larger prosomal size may have allowed the animal to burrow effectively, similar to modern xiphosurans (Vosatka, 1970; Chiu and Morton, 2004; Jackson et al., 2005). Burrowing would also have functioned as a means of protection. This contrasts the hypotheses that benthic Paleozoic euhelicerates may have enrolled to protect themselves (Fisher, 1977; Bicknell and Smith, 2021), at least for this taxon. Evidence for novel infaunal consumers indicates that benthic animals from the Bear Gulch Limestone are likely

underdocumented and additional examination of the formation may uncover novel bottom-dwelling species. The Bear Gulch Limestone has distinctive collection and publication bias (sensu Whitaker and Kimmig, 2020) toward the exceptionally preserved fishes (e.g., Lund 1989; Grogan and Lund, 2000) and it is likely that future collections, and maybe museum digitization efforts, will yield more euchelicerates.

The lack of ocular structures in *Titanoprosoma edgecombei* is worth considering. Lateral compound eyes in basal Paleozoic crown-group euchelicerates are rare, with the structures known from *Pseudoniscus roosevelti* Clarke, 1902, and *Legrandella lombardii* Eldredge, 1974, and putative evidence in other forms (Stürmer and Bergström, 1981; Krzemiński et al., 2010; Bicknell et al., 2019). It is possible that the lack of lateral compound eyes in *T. edgecombei* is taphonomic. However, the Lagerstätten intervals of the Bear Gulch Limestone have preserved fossils in exceptional detail (Hagadorn, 2002; Moore et al., 2007; Conway et al., 2022). Given the preservation of this fossil, the presence of compound eyes cannot be completely ruled out, especially if they lacked an ocular tubercle. We suggest that this lack of lateral compound eyes reinforces the aforementioned infaunal lifestyle, aligning with select trilobites and other possibly blind euchelicerates (Thomas, 2005; Bicknell et al., 2019).

An alternative explanation for a lack of ocular structures is that *Titanoprosoma edgecombei* had a benthic epifaunal lifestyle similar to Silurian euchelicerates *Offacolus kingi* Orr et al., 2000, and *Dibasterium durgae* Briggs et al., 2012. *Offacolus*, in particular, has been reconstructed as a relatively slow-moving animal that either preyed on slow-moving or sessile benthos, stirred up soft sediment for the infauna, or functioned as a scavenger (Orr et al., 2000). However, *Offacolus* and *Dibasterium* inhabited dim light conditions (Siveter et al., 2020), while *T. edgecombei* lived within a well-lit, shallow basin (Williams, 1983; Hagadorn, 2002). As such, we can exclude this as an explanation for the lack of lateral compound eyes in *T. edgecombei*.

It is important to consider whether the lower-than-expected number of opisthosomal segments in *Titanoprosoma edgecombei* could be an artifact of telescoping. Telescoping of thoracic segments is relatively common in some post-Ordovician trilobites, which have highly vaulted exoskeletons or fused facial sutures (Henningsmoen, 1975). Similarly, telescoped chasmatspidids are common enough that in one species (*Octoberaspis ushakovi* Dunlop, 2002) the telescoped nature was initially considered evidence for possible sexual dimorphism (Dunlop, 2002). Conversely, taphonomic experiments on modern xiphosurans and scorpions demonstrated that telescoping is rare in these chelicerates (McCoy and Brandt, 2009). Likewise, telescoped eurypterids are extremely rare, with records known from six to eight species (Lamsdell, 2011). This disparity in telescoping, particularly between eurypterids and chasmatspidids, is thought to reflect differences in molting techniques caused by fused opisthosomal structures (Lamsdell, 2011). As there is no evidence of fused structures in *Titanoprosoma edgecombei*, there is less evidence to support opisthosomal telescoping. Hence, we suggest that the seven segments documented here could reflect the true number of segments obtained by the animal in its adult stage. However, as mentioned above, more material of this rare animal is needed to confirm this assumption.

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REFERENCES

- Anderson, L.I., and P.A. Selden. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia* 30: 19–31.
- Bergström, J. 1975. Functional morphology and evolution of xiphosurids. *Fossils and Strata* 4: 291–305.
- Bicknell, R.D.C., and S. Pates. 2020. Pictorial atlas of fossil and extant horseshoe crabs, with focus on Xiphosurida. *Frontiers in Earth Science* 8: 98.
- Bicknell, R.D.C., and P.M. Smith. 2021. *Patesia* n. gen., a new Late Devonian stem xiphosurid genus. *Palaeoworld* 30: 440–450.
- Bicknell, R.D.C., L. Amati, and J. Ortega Hernández. 2019. New insights into the evolution of lateral compound eyes in Palaeozoic horseshoe crabs. *Zoological Journal of the Linnean Society* 187: 1061–1077.
- Bicknell, R.D.C., B. Błazejowski, O. Wings, T. Hitij, and M.L. Botton. 2021. Critical re-evaluation of Limulidae reveals limited *Limulus* diversity. *Papers in Palaeontology* 7: 1525–1556.
- Bicknell, R.D.C., S.V. Naugolnykh, and S.C. McKenzie. 2022. On *Paleolimulus* from the Mazon Creek Konservat-Lagerstätte. *Comptes Rendus Palevol* 21: 303–322.
- Briggs, D.E.G., et al. 2012. Silurian horseshoe crab illuminates the evolution of arthropod limbs. *Proceedings of the National Academy of Sciences of the United States of America* 109: 15702–15705.
- Chiu, H., and B. Morton. 2004. The behaviour of juvenile horseshoe crabs, *Tachypileus tridentatus* (Xiphosura), on a nursery beach at Shui Hau Wan, Hong Kong. *Hydrobiologia* 523: 29–35.
- Clarke, J.M. 1902. Notes on Paleozoic crustaceans. *New York State Museum Report* 54: 83–110.
- Conway Morris, S., and J.-B. Caron. 2022. A possible home for a bizarre Carboniferous animal: is *Typhloesus* a pelagic gastropod? *Biology Letters* 18: 20220179.
- Cox, R.S. 1986. Preliminary report on the age and palynology of the Bear Gulch Limestone (Mississippian, Montana). *Journal of Paleontology* 60: 952–956.
- Dunlop, J.A. 2002. Arthropods from the Lower Devonian Severnaya Zemlya Formation of October Revolution Island (Russia). *Geodiversitas* 24: 349–379.
- Dunlop, J.A., and J.C. Lamsdell. 2017. Segmentation and tagmosis in Chelicerata. *Arthropod Structure and Development* 46: 396–418.
- Eldredge, N. 1974. Revision of the suborder Synziphosurina (Chelicerata, Merostomata), with remarks on merostome phylogeny. *American Museum Novitates* 2543: 1–41.
- Fisher, D.C. 1977. Functional significance of spines in the Pennsylvanian horseshoe crab *Euproops danae*. *Paleobiology* 3: 175–195.
- Giribet, G., and G.D. Edgecombe. 2019. The phylogeny and evolutionary history of arthropods. *Current Biology* 29: R592–R602.
- Grogan, E.D., and R. Lund. 2000. *Debeerius ellefseni* (fam. nov., gen. nov., spec. nov.), an autodiastyle chondrichthyan from the Mississippian Bear Gulch Limestone of Montana (USA), the relationships

- of the Chondrichthyes, and comments on gnathostome evolution. *Journal of Morphology* 243: 219–245.
- Grogan, E.D., and R. Lund. 2002. The geological and biological environment of the Bear Gulch Limestone (Mississippian of Montana, USA) and a model for its deposition. *Geodiversitas* 24: 295–315.
- Hagadorn, J.W. 2002. Bear Gulch: an exceptional upper Carboniferous plattenkalk. In D.J. Bottjer, W. Etter, J.W. Hagadorn, and C.M. Tang (editors), *Exceptional fossil preservation: a unique view on the evolution of marine life*: 167–183. New York: Columbia University Press.
- Haug, C., et al. 2012. A holomorph approach to xiphosuran evolution—a case study on the ontogeny of *Euproops*. *Development Genes and Evolution* 222: 253–268.
- Henningsmoen, G. 1975. Moulting in trilobites. *Fossils and Strata* 4: 179–200.
- Heymons, R. 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica* 13: 1–244.
- Jackson, N.L., K.F. Nordstrom, and D.R. Smith. 2005. Influence of waves and horseshoe crab spawning on beach morphology and sediment grain-size characteristics on a sandy estuarine beach. *Sedimentology* 52: 1097–1108.
- Krzemiński, W., E. Krzemińska, and D. Wojciechowski. 2010. Silurian synziphosurine horseshoe crab *Pasternakevia* revisited. *Acta Palaeontologica Polonica* 55: 133–139.
- Lamsdell, J.C. 2011. The eurypterid *Stoermeropterus conicus* from the lower Silurian Pentland Hills, Scotland. *Palaeontographical Society Monograph* 165: 1–84.
- Lamsdell, J.C. 2013. Revised systematics of Palaeozoic ‘horseshoe crabs’ and the myth of monophyletic Xiphosura. *Zoological Journal of the Linnean Society* 167: 1–27.
- Lamsdell, J.C. 2020. A chasmataspidid affinity for the putative xiphosuran *Kiaeria* Størmer, 1934. *PalZ* 94: 449–453.
- Lamsdell, J.C., P.A. Isotalo, D.M. Rudkin, and M.J. Martin. 2023. A new species of the Ordovician horseshoe crab *Lunataspis*. *Geological Magazine* 160: 167–171.
- Laurie, M. 1899. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. *Transactions of the Royal Society of Edinburgh* 39: 575–590.
- Lerosey-Aubril, R., J.R. Paterson, S. Gibb, and B.D. Chatterton. 2017. Exceptionally-preserved late Cambrian fossils from the McKay Group (British Columbia, Canada) and the evolution of tagmosis in aglaspidid arthropods. *Gondwana Research* 42: 264–279.
- Lund, R. 1989. New petalodonts (Chondrichthyes) from the Upper Mississippian Bear Gulch Limestone (Namurian E2b) of Montana. *Journal of Vertebrate Paleontology* 9: 350–368.
- Lund, R., H. Feldman, W.L. Lund, and C.G. Maples. 1993. The depositional environment of the Bear Gulch Limestone, Fergus County, Montana. In 1993 Field conference guidebook: old timers’ rendezvous edition: energy and mineral resources of central Montana: 87–96. Billings, MT: Montana Geological Society.
- Lustri, L., L. Laibl, and R.D.C. Bicknell. 2021. A revision of *Prolimulus woodwardi* Fritsch, 1899 with comparison to other paedomorphic belinurids. *PeerJ* 9: e10980.
- Mapes, R.H., N.H. Landman, and C. Klug. 2019. Caught in the act? Distraction sinking in ammonoid cephalopods. *Swiss Journal of Palaeontology* 138: 141–149.
- Marshall, D.J., J.C. Lamsdell, E. Shpinev, and S.J. Braddy. 2014. A diverse chasmataspidid (Arthropoda: Chelicerata) fauna from the Early Devonian (Lochkovian) of Siberia. *Palaeontology* 57: 631–655.
- McCoy, V.E., and D.S. Brandt. 2009. Scorpion taphonomy: criteria for distinguishing fossil scorpion molts and carcasses. *The Journal of Arachnology* 37: 312–320.

- Moore, R.A., D.E.G. Briggs, and C. Bartels. 2005. A new specimen of *Weinbergina opitzi* (Chelicerata: Xiphosura) from the Lower Devonian Hunsrück Slate, Germany. *Paläontologische Zeitschrift* 79: 399–408.
- Moore, R.A., S.C. McKenzie, and B.S. Lieberman. 2007. A Carboniferous synziphosurine (Xiphosura) from the Bear Gulch Limestone, Montana, USA. *Palaeontology* 50: 1013–1019.
- Munnecke, A., H. Westphal, and M. Kölbl-Ebert. 2008. Diagenesis of plattenkalk: examples from the Solnhofen area (Upper Jurassic, southern Germany). *Sedimentology* 55: 1931–1946.
- Orr, P.J., D.J. Siveter, D.E.G. Briggs, D.J. Siveter, and M.D. Sutton. 2000. A new arthropod from the Silurian Konservat-Lagerstätte of Herefordshire, UK. *Proceedings of the Royal Society of London B, Biological Sciences* 267: 1497–1504.
- Ortega-Hernández, J., D.A. Legg, and S.J. Braddy. 2013. The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics* 29: 15–45.
- Ortega-Hernández, J., P. Van Roy, and R. Lerosey-Aubril. 2016. A new aglaspidid euarthropod with a six-segmented trunk from the Lower Ordovician Fezouata Konservat-Lagerstätte, Morocco. *Geological Magazine* 153: 524–536.
- Peel, J.S., C.B. Skovsted, and E. Walset. 2021. Morphology and ecology of the bradoriid arthropods *Spinospitella* and *Nikolarites* from the Cambrian (Series 2, Stage 4) of North Greenland (Laurentia). *PalZ* 95: 413–427.
- Rudkin, D.M., G.A. Young, and G.S. Nowlan. 2008. The oldest horseshoe crab: a new xiphosurid from Late Ordovician Konservat-Lagerstätten deposits, Manitoba, Canada. *Palaeontology* 51: 1–9.
- Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.
- Schram, F.R. 1979. Limulines of the Mississippian Bear Gulch Limestone of Central Montana, USA. *Transactions of the San Diego Society of Natural History* 19: 67–74.
- Seilacher, A. 1970. Begriff und Bedeutung der Fossil-Lagerstätten. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 7: 34–39.
- Seilacher, A., et al. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 311: 5–24.
- Selden, P.A., L. Simonetto, and G. Marsiglio. 2019. An effaced horseshoe crab (Arthropoda: Chelicerata: Xiphosura) from the Upper Carboniferous of the Carnic Alps (Friuli, NE Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 125: 333–342.
- Singer, A., G.D. Stanley, and N.W. Hinman. 2019. Anatomy of the Book Canyon conglomerate: a sequence boundary at the top of the Bear Gulch Limestone in the Big Snowy Trough. *Facies* 65: 1–13.
- Singer, A.E. 2021. Benthic invertebrate paleontology of the Late Mississippian (Serpukhovian) Bear Gulch Limestone, Central Montana. Ph.D. dissertation, Geosciences Department, University of Montana, Missoula.
- Siveter, D.J., R.A. Fortey, X. Zhu, and Z. Zhou. 2018. A three-dimensionally preserved aglaspidid euarthropod with a calcitic cuticle from the Ordovician of China. *Geological Magazine* 155: 1427–1441.
- Siveter, D.J., D.E.G. Briggs, D.J. Siveter, and M.D. Sutton. 2020. The Herefordshire Lagerstätte: fleshing out Silurian marine life. *Journal of the Geological Society* 177: 1–13.
- Snodgrass, R.E. 1952. A textbook of arthropod anatomy. Ithaca, NY: Cornell University Press.
- Streng, M., J.O.R. Ebbestad, and M. Moczyłowska. 2008. A *Walcottella*-like bradoriid (Arthropoda) from the lower Cambrian of Sweden. *GFF* 130: 11–19.

- Stürmer, W., and J. Bergström. 1981. *Weinbergina*, a xiphosuran arthropod from the Devonian Hunsrück Slate. *Paläontologische Zeitschrift* 55: 237–255.
- Tesakov, A.S., and A.S. Alekseev. 1992. Myriapod-like arthropods from the Lower Devonian of central Kazakhstan. *Paleontologicheskii Zhurnal* 26: 18–23.
- Thomas, A.T. 2005. Developmental palaeobiology of trilobite eyes and its evolutionary significance. *Earth-Science Reviews* 71: 77–93.
- Thomas, N. 2004. The taphonomy of a Carboniferous Lagerstätte: the invertebrates of the Bear Gulch Limestone Member. Ph.D. dissertation, Department of Geology, University of Leicester.
- Tollerton, V.P. 1989. Morphology, taxonomy, and classification of the order Eurypterida Burmeister, 1843. *Journal of Paleontology* 63: 642–657.
- Van Roy, P. 2005. An aglaspidid arthropod from the Upper Ordovician of Morocco with remarks on the affinities and limitations of Aglaspidida. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 96: 327–350.
- Vosatka, E.D. 1970. Observations on the swimming, righting, and burrowing movements of young horseshoe crabs, *Limulus polyphemus*. *Ohio Journal of Science* 70: 276–283.
- Weygoldt, P., and H.F. Paulus. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 17: 85–115, 177–200.
- Whalen, C.D., and N.H. Landman. 2022. Fossil coleoid cephalopod from the Mississippian Bear Gulch Lagerstätte sheds light on early vampyropod evolution. *Nature Communications* 13: 1–11.
- Whitaker, A.F., and J. Kimmig. 2020. Anthropologically introduced biases in natural history collections, with a case study on the invertebrate paleontology collections from the middle Cambrian Spence Shale Lagerstätte. *Palaeontologia Electronica* 23: a58.
- Whitaker, A.F., J.D. Schiffbauer, D.E.G. Briggs, W.W. Leibach, and J. Kimmig. 2022. Preservation and diagenesis of soft-bodied fossils and the occurrence of phosphate-associated rare earth elements in the Cambrian (Wuliuan) Spence Shale Lagerstätte. *Palaeogeography, Palaeoclimatology, Palaeoecology* 592: 110909.
- Williams, L.A. 1983. Deposition of the Bear Gulch Limestone: a Carboniferous plattenkalk from central Montana. *Sedimentology* 30: 843–860.

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