

Central nervous system of a 310-m.y.-old horseshoe crab: Expanding the taphonomic window for nervous system preservation

Russell D.C. Bicknell^{1*}, Javier Ortega-Hernández², Gregory D. Edgecombe³, Robert R. Gaines⁴ and John R. Paterson¹

¹Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

²Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA

³Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

⁴Geology Department, Pomona College, 185 E. Sixth Street, Claremont, California 91711, USA

ABSTRACT

The central nervous system (CNS) presents unique insight into the behaviors and ecology of extant and extinct animal groups. However, neurological tissues are delicate and prone to rapid decay, and thus their occurrence as fossils is mostly confined to Cambrian Burgess Shale-type deposits and Cenozoic amber inclusions. We describe an exceptionally preserved CNS in the horseshoe crab *Euproops danae* from the late Carboniferous (Moscovian) Mazon Creek Konservat-Lagerstätte in Illinois, USA. The *E. danae* CNS demonstrates that the general prosomal synganglion organization has remained essentially unchanged in horseshoe crabs for >300 m.y., despite substantial morphological and ecological diversification in that time. Furthermore, it reveals that the euarthropod CNS can be preserved by molding in siderite and suggests that further examples may be present in the Mazon Creek fauna. This discovery fills a significant temporal gap in the fossil record of euarthropod CNSs and expands the taphonomic scope for preservation of detailed paleoneuroanatomical data in the Paleozoic to siderite concretion Lagerstätten of marginal marine deposits.

INTRODUCTION

The central nervous system (CNS) plays a critical role in animal functions, behavior, and ecology, and contains valuable morphological data that inform the evolution of complex organisms (Schmidt-Rhaesa et al., 2015). Although the lipid-rich composition of the CNS makes it prone to rapid decay (Sansom, 2016), recent research demonstrates that neurological tissues can be preserved as carbonaceous compressions in Cambrian animal macrofossils from open-marine deposits (Edgecombe et al., 2015; Strausfeld et al., 2016; Ortega-Hernández et al., 2019; Table S1 in the Supplemental Material¹). Paleoneuroanatomical remains are extremely rare in younger deposits before Cenozoic ambers, leaving profound gaps in our

understanding of CNS evolution. Notable exceptions include the putative brain described for the Carboniferous *Tullimonstrum gregarium* Richardson, 1966 (McCoy et al., 2016) and a phosphatized ventral nerve cord in a Triassic insect (Montagna et al., 2017), suggesting that paleoneuroanatomical structures can be captured by taphonomic pathways other than Burgess Shale-type preservation in the Paleozoic (Butterfield, 1995; Gaines, 2014), albeit extremely rarely.

We describe an exceptionally well-preserved CNS in the belinurid *Euproops danae* (Meek and Worthen, 1865) from the Pennsylvanian (Moscovian) Mazon Creek Konservat-Lagerstätte in Illinois, USA. The discovery of paleoneuroanatomy in *E. danae* is significant because xiphosurids (horseshoe crabs) are the only wholly aquatic extant order of euchelicerates, and their fossil record is critical for

reconstructing the complex evolutionary history of Euarthropoda (Lamsdell, 2016). *Euproops danae* shares similar prosomal appendage organization with the extant *Limulus polyphemus* (Linnaeus, 1758) (Haug and Rötzer, 2018) and is one of the best-documented fossil xiphosurids both within Mazon Creek (Raymond, 1945) and globally (Haug and Rötzer, 2018; Bicknell and Pates, 2020). Therefore, these new data on *E. danae* inform on the internal anatomy of this major euchelicerate group, represent the first occurrence of CNS preservation in a fossil horseshoe crab, and shed new light on preservational modes for fossilized neural tissue.

MATERIALS AND METHODS

We reviewed *E. danae* specimens in the Yale Peabody Museum (New Haven, Connecticut, USA) Division of Invertebrate Paleontology (YMP IP). One specimen (YMP IP 168040) showing evidence of preserved internal anatomy was identified. This specimen was photographed as a series of stacked images under normal LED light using a Canon EOS 5DS digital SLR camera fitted with a Canon MP-E 65 mm macro lens (complete specimen) and a Canon MP-E 65 mm 1×–5× macro lens (close-up on CNS) and a Cognisys StackShot 3X stacking system. Photos were stacked and stitched using Helicon Focus 7 (<https://www.heliconsoft.com/heliconsoft-products/helicon-focus/>). Backscatter and energy dispersive X-ray spectroscopy (EDS) analyses were conducted to examine composition of the CNS with a JEOL JSM-6010LA

*E-mail: rbickne2@une.edu.au

¹Supplemental Material. Figures S1 and S2, and Table S1. Please visit <https://doi.org/10.1130/GEOL.S.14925225> to access the supplemental material, and contact editing@geosociety.org with any questions.

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scanning electron microscope (SEM) under low vacuum at a voltage of 20 kV. The specimen was not coated.

RESULTS

Specimen YPM IP 168040 contains the first known record of *E. danae* internal anatomy, aspects of which are preserved on both the part and counterpart (Fig. 1; Fig. S1 in the Supplemental Material). The specimen is a fully articulated individual in dorsal view, preserved with limited relief in a siderite concretion, as is typical for Mazon Creek fossils (Clements et al., 2019). The prosoma is 6.9 mm long and 16.8 mm wide, the opisthosoma is 7.3 mm long and 11.2 mm wide, and the telson is 7.9 mm long. Based on opisthosomal size, the specimen likely represents the third *Euproops* developmental stage (*sensu* Haug and Rötzer, 2018). The axial region of the prosoma features a bilaterally symmetrical complex structure with a white coloration (Figs. 1A, 1B, and 1G). Elemental mapping indicates that this feature is enriched in aluminum and silicon (Clements et al., 2019; Figs. 1I and 1J) and depleted in iron, potassium, and magnesium relative to the siderite matrix (Figs. 1H, 1M, and 1N). The morphology of the internal structure consists of a fusiform ring oriented along the sagittal axis with seven paired and regularly spaced lobe-like lateral extensions that generally increase in length posteriorly (Figs. 1B and 1D). Although the anterior-most third of the structure is broken and displaced laterally, there is direct continuity between the lateral extensions on both sides and the width of the aluminosilicates defining the ring boundaries. White coloration is also noted at the prosoma-opisthosoma and opisthosoma-telson articulations.

DISCUSSION

The internal structure preserved in specimen YPM IP 168040 is morphologically comparable to the CNS of *L. polyphemus* early juveniles and more mature individuals, specifically the synganglion formed by the fusion of the segmental ganglia in the prosoma (Harzsch et al., 2005; Göpel and Wirkner, 2015; Fig. 1E). The seven paired lateral extensions correspond to the segmental nerves of the protocerebrum (optic nerves), deutocerebrum (chelicerae), four walking legs, and the pushing leg. The opening of the fusiform ring structure represents the esophageal foramen (Figs. 1B and 1D). There is no evidence of a preserved opisthosomal CNS in specimen YPM IP 168040. An alternative interpretation of the internal axial structure as a gut is discounted because the conspicuous opening corresponding to the esophageal foramen is a feature without an analogue in the euarthropod digestive tract, and the *L. polyphemus* gut lacks a metameric organization (Zacari et al., 2016).

Euproops danae offers valuable insights into the CNS of extinct euchelicerates. The

correspondence between the synganglia of *E. danae* and *L. polyphemus* suggests close functional and behavioral similarities between modern and extinct xiphosurids, despite the substantial temporal and phylogenetic gaps between their respective clades (Bicknell and Pates, 2020). This fossil shows that the fundamental organization of the xiphosurid CNS has essentially remained unchanged for >300 m.y. Furthermore, close anatomical parallels between the CNS organization of *L. polyphemus*, *E. danae*, and the great appendage stem-group chelicerates (Tanaka et al., 2013; Ortega-Hernández et al., 2019) suggest that euchelicerates have sustained this conserved neuroanatomy since the Cambrian.

This unique *E. danae* specimen represents the earliest unequivocal evidence of preserved euarthropod neuroanatomy from a brackish marginal-marine deposit (Clements et al., 2019). Elemental mapping indicates that the CNS—which is white in visible light (Fig. 1G)—is enriched in aluminum, silicon, and oxygen (Figs. 1I–1K). Further, SEM imaging reveals that vermiciform stacks of platy, micron-sized crystallites compose the white material (Fig. 1F). These observations, coupled with depletion in potassium and magnesium relative to matrix, indicate that the white mineral highlighting the CNS is kaolinite.

Kaolinite is well documented in Mazon Creek fossils (Baird et al., 1986; Cotroneo et al., 2016; Clements et al., 2019). It commonly occurs as a void-filling mineral that precipitated within concretion cavities. This includes voids inside fossils where bones had dissolved, where plant stems were carbonized and undergone volume loss, leaving spaces, and where aragonitic bivalve shells dissolved within the concretion matrix (Baird et al., 1986; Cotroneo et al., 2016; Clements et al., 2019). In Mazon Creek material, kaolinite is associated occasionally with sphalerite and galena, indicative of later-stage mineralization during burial (Keller, 1988), and more commonly with pyrite, which may form during early diagenesis or later mineralization. Based on these aspects of its occurrence, kaolinite in Mazon Creek fossils has been consistently interpreted as being late diagenetic in origin (Baird et al., 1986, 1997; Clements et al., 2019), precipitating in voids long after fossilization was complete.

Morphology of kaolinite crystallites within the examined CNS (Fig. 1F) confirms the late-stage precipitate origin, consistent with previous interpretations. However, kaolinite was not a component of the original fossilization process that captured the paleoneuroanatomical information. Instead, kaolinite precipitated in a void that remained long after the decay of neural tissue. The CNS was therefore preserved originally as a mold, captured as minerals grew around the highly labile tissues prior to loss of structural integrity during decomposition. Elemental mapping (Figs. 1H–1N; Fig. S2) shows that the outer

CNS margin is sharp and the matrix is composed of siderite, as indicated by enrichment in iron, carbon, and oxygen (Figs. 1H and 1K; Fig. S2). The siderite surrounding the CNS has the same composition and texture as the matrix of the concretion enveloping the specimen.

The preservation of the examined CNS requires that siderite grew rapidly around the decomposing organism, molding the CNS in three dimensions. The CNS was then lost to decay, leaving a void inside its external mold that was stabilized by the siderite mineral matrix. This void was subsequently filled by the precipitation of kaolinite (Fig. 2). Such a pathway has two important implications.

(1) The siderite matrix must have been emplaced very quickly to capture neural tissue. While this rapid growth could be difficult to account for (e.g., Berner, 1968; Yoshida et al., 2020), it is currently the accepted mode of exceptional preservation within the Mazon Creek *Konservat-Lagerstätte* (Clements et al., 2019). Such a preservational pathway is thought to have produced the flattened composite molds observed in the Mazon Creek concretions, particularly of dermal, cuticular, and other external structures (Baird et al., 1986; Clements et al., 2019). However, this pathway can also preserve more labile internal tissues, such as the observed CNS, which is very rare in Mazon Creek fossils. Rapid precipitation of the concretionary matrix is consistent with the notably narrow range of $\delta^{13}\text{C}$ values reported from the fossiliferous concretions (Cotroneo et al., 2016). During prolonged concretion growth, changes in pore-water biogeochemistry due to exhaustion of oxidants and switching of primary bacterial metabolic pathways commonly result in pronounced variation in carbon isotope values across concretions from the center to the edge (Raiswell and Fisher, 2000). Although similarly suppressed $\delta^{13}\text{C}$ variation might result from protracted pervasive growth, rather than from rapid concentric growth (Mozley and Burns, 1993), the robust molding of the CNS in siderite suggests rapid pervasive concretion growth is far more likely (Sellés-Martínez, 1996). The limited range of isotopic variation observed in Mazon Creek concretions is therefore noteworthy (Cotroneo et al., 2016) and supports rapid siderite development around decaying organisms.

(2) CNS preservation by molding implies a loss of other soft tissues beneath the prosomal shield prior to CNS decay. In modern xiphosurids, the CNS is sheathed by a thick vascular membrane (Göpel and Wirkner, 2015). Such a membrane in *E. danae* may have slowed the decay of the synganglion (relative to other internal structures) and facilitated the rapid molding of these delicate tissues. Given the ferruginous pore-water conditions that led to the precipitation of siderite, it is also possible that dissolved Fe^{2+} may have played a role

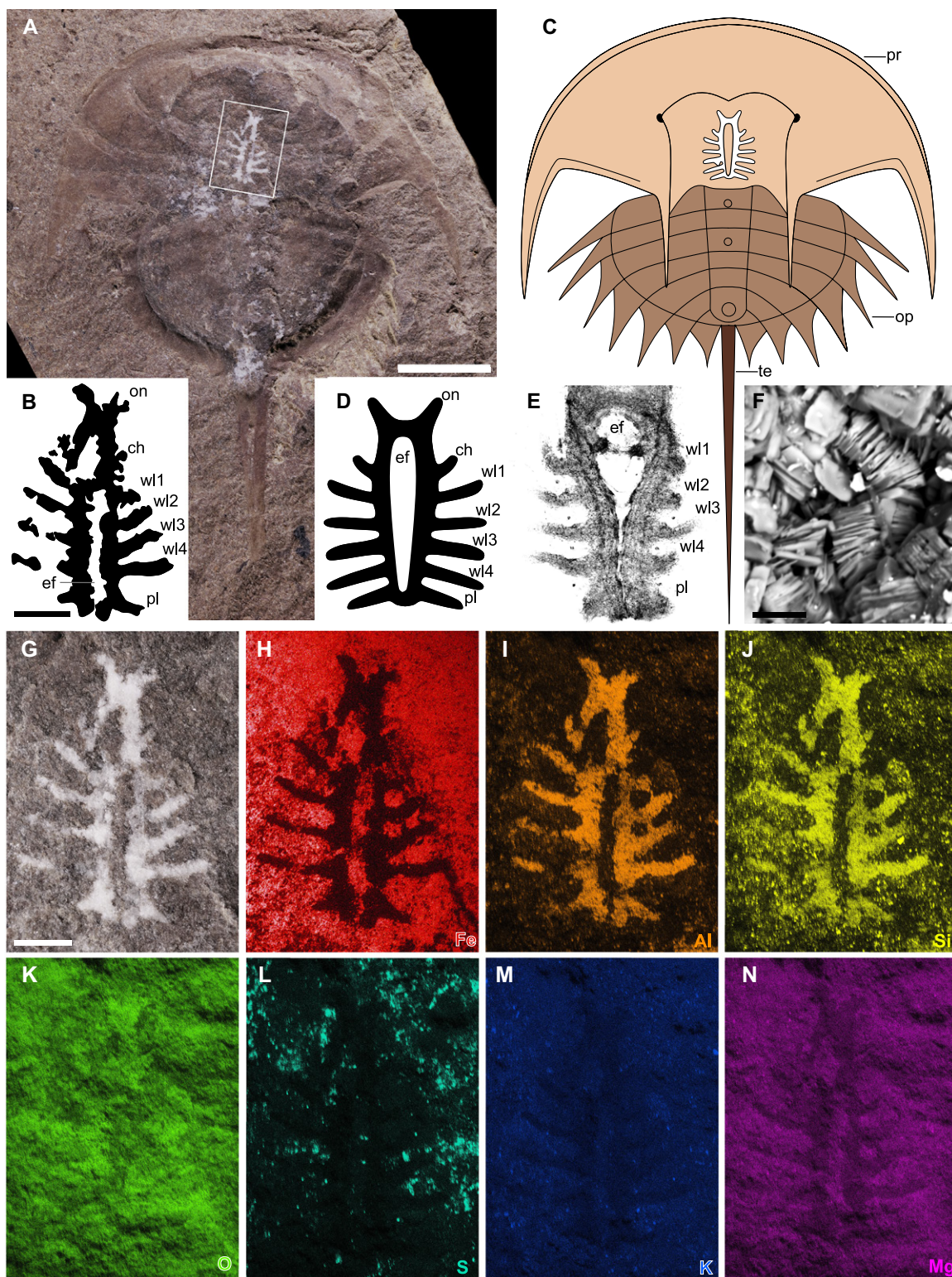


Figure 1. The central nervous system (CNS) of *Euproops danae* from the Carboniferous (Moscovian) Mazon Creek Konservat-Lagerstätte in Illinois, USA. (A) Part of Yale Peabody Museum Division of Invertebrate Paleontology specimen YPM IP 168040; complete specimen preserved in dorsal view. Box indicates close-up shown in B and G–N. (B) Interpretative drawing of the CNS in specimen YPM IP 168040. (C) Reconstruction of *E. danae* showing CNS position. (D) Reconstruction of observed CNS. (E) *Limulus polyphemus* early juvenile nervous system imaged using confocal laser scan; from Harzsch et al. (2005, their figure 6A; reproduced with permission from S. Harzsch). (F) Backscattered secondary electron image of vermiform stacks of platy crystallites of kaolinite replicating the CNS. (G) Close-up of the CNS under normal lighting. (H–N) Elemental maps of iron, aluminum, silicon, oxygen, sulfur, potassium, and magnesium, respectively. Dark areas indicate low elemental abundance, and bright areas indicate high elemental abundance. Scale bars: A—2 mm; B,G—500 μ m; F—10 μ m. Scale bar in G also applies to H–N. Abbreviations: ch—chelicerae; ef—esophageal foramen; on—optic nerve; op—opisthosoma; pl—pushing leg; pr—prosoma; te—telson; wl1–wl4—walking leg 1–4.

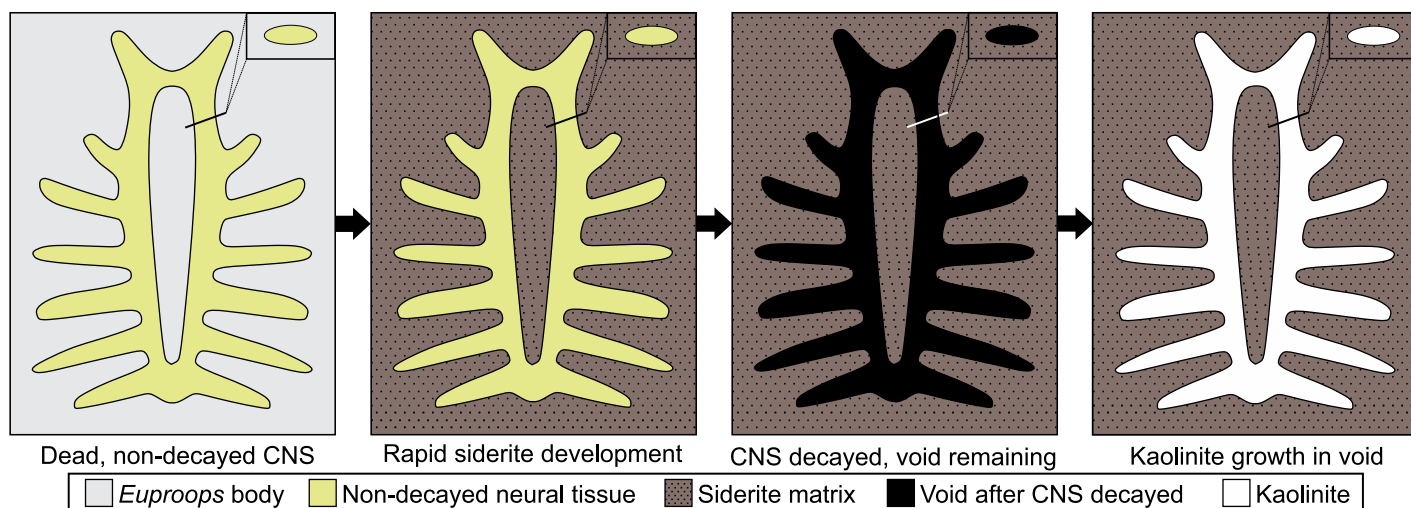


Figure 2. Diagrammatic representation of the taphonomic pathway for the preserved central nervous system (CNS) of *Euproops danae*. Both dorsal and cross-sectional (inset) perspectives are presented.

in delaying decay of neural tissue (Schweitzer et al., 2014; Saleh et al., 2020). It is also possible that reduction of porosity around the CNS via the rapid growth of concretion matrix further delayed its decay until after the neural tissue was robustly molded (McCoy et al., 2015a, 2015b). The present Carboniferous example validates earlier observations of euarthropod CNS tissues preserved through a fundamentally different taphonomic pathway (see Table S1).

This proposed taphonomic pathway also explains the presence of kaolinite along the exoskeletal articulations between the prosoma and opisthosoma as well as between the opisthosoma and telson (Fig. 1A; Figs. S1A and S1B). In life, these articulation sites would have contained arthrodial membrane, which is markedly softer than the carapace. Such material may have also been molded by siderite and subsequently decayed, leaving voids that were partially filled by the growth of kaolinite.

The presence of kaolinite in the examined CNS was not essential to its fossilization but was critical to its recognition because of its contrasting color compared to the remainder of the fossil and its host concretion. This record suggests that other examples of molded neural tissue could be preserved in Mazon Creek fossils. However, such evidence may be more cryptic and difficult to recognize, represented only by slight topographic variation in the siderite matrix in the absence of substantial mineral infillings. Hence, future studies on the Mazon Creek *Konservat-Lagerstätte* should consider careful exploration of the subtle topographic features on fossil surfaces that may assist in the possible detection of exceptionally preserved labile tissues.

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REFERENCES CITED

- Baird, G.C., Sroka, S.D., Shabica, C.W., and Kuecher, G.J., 1986, Taphonomy of Middle Pennsylvanian Mazon Creek area fossil localities, Northeast Illinois: Significance of exceptional fossil preservation in syngenetic concretions: *Palaos*, v. 1, p. 271–285, <https://doi.org/10.2307/3514690>.
- Baird, G.C., Shabica, C.W., and Hay, A.A., 1997, Francis Creek diagenetic events, in Shabica, C.W., and Hay, A.A., eds., *Richardson's Guide to the Fossil Fauna of Mazon Creek*: Chicago, Northeastern Illinois University, p. 30–34.
- Berner, R.A., 1968, Rate of concretion growth: *Geochimica et Cosmochimica Acta*, v. 32, p. 477–483, [https://doi.org/10.1016/0016-7037\(68\)90040-9](https://doi.org/10.1016/0016-7037(68)90040-9).
- Bicknell, R.D.C., and Pates, S., 2020, Pictorial atlas of fossil and extant horseshoe crabs, with focus on Xiphosurida: *Frontiers in Earth Science*, v. 8, 98, <https://doi.org/10.3389/feart.2020.00098>.
- Butterfield, N.J., 1995, Secular distribution of Burgess-Shale-type preservation: *Lethaia*, v. 28, p. 1–13, <https://doi.org/10.1111/j.1502-3931.1995.tb01587.x>.
- Clements, T., Purnell, M., and Gabbott, S., 2019, The Mazon Creek Lagerstätte: A diverse late Paleozoic ecosystem entombed within siderite concretions: *Journal of the Geological Society*, v. 176, p. 1–11, <https://doi.org/10.1144/jgs2018-088>.
- Cotroneo, S., Schiffbauer, J.D., McCoy, V.E., Wortmann, U.G., Darroch, S.A.F., Peng, Y., and Laflamme, M., 2016, A new model of the formation of Pennsylvanian iron carbonate concretions hosting exceptional soft-bodied fossils in Mazon Creek, Illinois: *Geobiology*, v. 14, p. 543–555, <https://doi.org/10.1111/gbi.12197>.
- Edgecombe, G.D., Ma, X., and Strausfeld, N.J., 2015, Unlocking the early fossil record of the arthropod central nervous system: *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, v. 370, 20150038, <https://doi.org/10.1098/rstb.2015.0038>.
- Gaines, R.R., 2014, Burgess Shale-type preservation and its distribution in space and time: *Paleontological Society Papers*, v. 20, p. 123–146, <https://doi.org/10.1017/S1089332600002837>.
- Göpel, T., and Wirkner, C.S., 2015, An “ancient” complexity? Evolutionary morphology of the circulatory system in Xiphosura: *Zoology (Jena, Germany)*, v. 118, p. 221–238, <https://doi.org/10.1016/j.zool.2014.12.004>.
- Harzsch, S., Wildt, M., Battelle, B., and Waloszek, D., 2005, Immunohistochemical localization of neurotransmitters in the nervous system of larval *Limulus polyphemus* (Chelicerata, Xiphosura): Evidence for a conserved protocerebral architecture in Euarthropoda: *Arthropod Structure & Development*, v. 34, p. 327–342, <https://doi.org/10.1016/j.asd.2005.01.006>.
- Haug, C., and Rötzer, M.A.I.N., 2018, The ontogeny of the 300 million year old xiphosuran *Euproops danae* (Euchelicerata) and implications for resolving the *Euproops* species complex: *Development Genes and Evolution*, v. 228, p. 63–74, <https://doi.org/10.1007/s00427-018-0604-0>.
- Keller, W.D., 1988, Authigenic kaolinite and dickite associated with metal sulfides—Probable indicators of a regional thermal event: *Clays and Clay Minerals*, v. 36, p. 153–158, <https://doi.org/10.1346/CCMN.1988.0360209>.
- Lamsdell, J.C., 2016, Horseshoe crab phylogeny and independent colonizations of fresh water: Ecological invasion as a driver for morphological innovation: *Palaeontology*, v. 59, p. 181–194, <https://doi.org/10.1111/pala.12220>.
- Linnaeus, C., 1758, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*: Holmia, Laurentius Salvius, 824 p.
- McCoy, V.E., Young, R.T., and Briggs, D.E.G., 2015a, Factors controlling exceptional preservation in concretions: *Palaos*, v. 30, p. 272–280, <https://doi.org/10.2110/palo.2014.081>.
- McCoy, V.E., Young, R.T., and Briggs, D.E.G., 2015b, Sediment permeability and the preservation of soft-tissues in concretions: An experimental

- study: *Palaos*, v. 30, p. 608–612, <https://doi.org/10.2110/palo.2015.002>.
- McCoy, V.E., et al., 2016, The ‘Tully monster’ is a vertebrate: *Nature*, v. 532, p. 496–499, <https://doi.org/10.1038/nature16992>.
- Meek, F.B., and Worthen, A.H., 1865, Notice of some new types of organic remains from the Coal Measures of Illinois: *Proceedings of the Academy of Natural Sciences of Philadelphia*, v. 17, p. 41–48.
- Montagna, M., Haug, J.T., Strada, L., Haug, C., Felber, M., and Tintori, A., 2017, Central nervous system and muscular bundles preserved in a 240 million year old giant bristletail (Archaeognatha: Machilidae): *Scientific Reports*, v. 7, 46016, <https://doi.org/10.1038/srep46016>.
- Mozley, P.S., and Burns, S.J., 1993, Oxygen and carbon isotopic composition of marine carbonate concretions: An overview: *Journal of Sedimentary Research*, v. 63, p. 73–83, <https://doi.org/10.1306/D4267A91-2B26-11D7-8648000102C1865D>.
- Ortega-Hernández, J., Lerosey-Aubril, R., and Pates, S., 2019, Proclivity of nervous system preservation in Cambrian Burgess Shale-type deposits: *Proceedings of the Royal Society of London: B, Biological Sciences*, v. 286, 20192370, <https://doi.org/10.1098/rspb.2019.2370>.
- Raiswell, R., and Fisher, Q.J., 2000, Mudrock-hosted carbonate concretions: A review of growth mechanisms and their influence on chemical and isotopic composition: *Journal of the Geological Society*, v. 157, p. 239–251, <https://doi.org/10.1144/jgs.157.1.239>.
- Raymond, P.E., 1945, Xiphosura in the Langford collection: *Illinois State Museum Scientific Paper* 3, p. 4–10.
- Richardson, E.S., Jr., 1966, Wormlike fossil from the Pennsylvanian of Illinois: *Science*, v. 151, p. 75–76, <https://doi.org/10.1126/science.151.3706.75-a>.
- Saleh, F., Daley, A.C., Lefebvre, B., Pittet, B., and Perillat, J.-P., 2020, Biogenic iron preserves structures during fossilization: A hypothesis—Iron from decaying tissues may stabilize their morphology in the fossil record: *BioEssays*, v. 42, 1900243, <https://doi.org/10.1002/bies.201900243>.
- Sansom, R.S., 2016, Preservation and phylogeny of Cambrian ecdysozoans tested by experimental decay of *Priapulid*: *Scientific Reports*, v. 6, 32817, <https://doi.org/10.1038/srep32817>.
- Schmidt-Rhaesa, A., Harzsch, S., and Purschke, G., eds., 2015, *Structure and Evolution of Invertebrate Nervous Systems*: London, Oxford University Press, 748 p., <https://doi.org/10.1093/acprof:oso/9780199682201.001.0001>.
- Schweitzer, M.H., Zheng, W., Cleland, T.P., Goodwin, M.B., Boatman, E., Theil, E., Marcus, M.A., and Fakra, S.C., 2014, A role for iron and oxygen chemistry in preserving soft tissues, cells and molecules from deep time: *Proceedings of the Royal Society of London: B, Biological Sciences*, v. 281, 20132741, <https://doi.org/10.1098/rspb.2013.2741>.
- Sellés-Martínez, J., 1996, Concretion morphology, classification and genesis: *Earth-Science Reviews*, v. 41, p. 177–210, [https://doi.org/10.1016/S0012-8252\(96\)00022-0](https://doi.org/10.1016/S0012-8252(96)00022-0).
- Strausfeld, N.J., Ma, X., and Edgecombe, G.D., 2016, Fossils and the evolution of the arthropod brain: *Current Biology*, v. 26, p. R989–R1000, <https://doi.org/10.1016/j.cub.2016.09.012>.
- Tanaka, G., Hou, X., Ma, X., Edgecombe, G.D., and Strausfeld, N.J., 2013, Chelicerate neural ground pattern in a Cambrian great appendage arthropod: *Nature*, v. 502, p. 364–367, <https://doi.org/10.1038/nature12520>.
- Yoshida, H., Yamamoto, K., Ohe, T., Katsuta, N., Muramiya, Y., and Metcalfe, R., 2020, Diffusion controlled formation of spherical carbonate concretion in muddy sedimentary matrices: *Geochemical Journal*, v. 54, p. 233–242, <https://doi.org/10.2343/geochemj.2.0593>.
- Zacai, A., Vannier, J., and Lerosey-Aubril, R., 2016, Reconstructing the diet of a 505-million-year-old arthropod: *Sidneyia inexpectans* from the Burgess Shale fauna: *Arthropod Structure & Development*, v. 45, p. 200–220, <https://doi.org/10.1016/j.asd.2015.09.003>.

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