

MAZON CREEK BROMALITES EVIDENCE A SPECIALIZED, XIPHOSURID-RICH DIET FOR PENNSYLVANIAN PREDATORS

RUSSELL D. C. BICKNELL,^{1,2,3} JULIEN KIMMIG,^{4,5} ANDREW YOUNG,⁶ BRUCE LAUER,³ RENÉ LAUER,³ AND VICTORIA E. MCCOY^{3,7}

¹Division of Paleontology, American Museum of Natural History, New York City, New York 10024, USA

²Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2351, Australia

³Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois 60189, USA

⁴Paläontologie und Evolutionsforschung, Abteilung Geowissenschaften, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe 76133, Germany

⁵The Harold Hamm School of Geology & Geological Engineering, University of North Dakota, Grand Forks, North Dakota 58202, USA

⁶The David and Sandra Douglass Collection, Evanston, Illinois 60202, USA

⁷Department of Geosciences, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53211, USA

email: rbicknell@amnh.org

ABSTRACT: The Mazon Creek Konservat-Lagerstätte is a globally significant Pennsylvanian (late Carboniferous) fossil assemblage characterized by exceptional soft-tissue preservation in siderite concretions. Coprolites documented from this site have provided crucial insights into trophic interactions within a Pennsylvanian deltaic environment but have not been widely studied. To expand the limited record in the literature of Mazon Creek bromalites, we investigate four shelly specimens, considered regurgitalites, with high concentrations of fragmented xiphosurid (*Euproops danae*) exoskeletal elements, indicating a specialized, durophagous diet. The sizes of prosomal and thoracetrone fragments within regurgitalites reveal a constrained prey size range, suggesting either prey size selection by the predator or differential survival of larger individuals. These findings highlight successful predation on xiphosurids within the late Carboniferous and provide direct evidence of their position within benthic food webs. This study underscores the utility of bromalites in informing paleoecological reconstructions and contributes to a broader understanding of trophic structures within late Carboniferous deltaic ecosystems.

INTRODUCTION

The Mazon Creek fossil assemblage is a world-class Konservat-Lagerstätte (*sensu* Kimmig and Schiffbauer 2024) that presents insight into a Pennsylvanian (late Carboniferous) deltaic environment (Johnson and Richardson 1968; Schram 1979; Shabica and Hay 1997; Clements et al. 2019; Burke et al. 2024). Mazon Creek siderite concretions exceptionally preserve invertebrates, vertebrates, and plants from this paleoecosystem (see Baird et al. 1986; Shabica and Hay 1997; Clements et al. 2019; Burke et al. 2024 for reviews). Soft-bodied preservation common in the Mazon Creek fossil assemblage has uncovered data on the ontogeny, morphology, and taxonomy of > 465 plant and > 350 animal species (Clements et al. 2019; Burke et al. 2024), as well as rare anatomical information (e.g., neural systems and muscles) for vertebrate (Bardack 1979; Mann and Gee 2019; McCoy et al. 2023) and invertebrate (Tetlie and Dunlop 2008; Bicknell et al. 2021; Plotnick et al. 2023) groups. This combination has resulted in the Mazon Creek Lagerstätte being subject to detailed taphonomic, geological, and paleontological examination.

Aggregations containing fragmented animal parts record predation or scavenging in the fossil record and are useful for reconstructing trophic interactions in deep time (Knaust 2020). Shell-rich aggregations, commonly considered bromalites, often reflect shell-crushing (durophagous) activity and can have a higher preservation potential than their producers (Vannier and Chen 2005). Shelly bromalites rich in arthropod fragments illustrate the position of arthropods as prey in the fossil record (Habgood et al. 2003; Northwood 2005; Qvarnström et al. 2016). Shelly, arthropod-rich bromalites from Paleozoic deposits require exceptional preservation, and are, therefore, rare. The majority of Paleozoic shelly bromalites are Cambrian-aged (Mikuláš 1995; Nedin 1999; Vannier and Chen 2005;

English and Babcock 2010; Daley et al. 2013; Kulkarni and Panchang 2015; Kimmig and Strotz 2017; Bicknell and Paterson 2018; Kimmig and Pratt 2018; Bicknell et al. 2022a), with rare Ordovician (Briggs et al. 2015; Bicknell et al. 2024), Silurian (Caster and Kjellesvig-Waering 1964; Bicknell et al. 2023), and Devonian (Habgood et al. 2003; Zatoń and Rakociński 2014) examples. Limited evidence for Carboniferous, arthropod-rich bromalites has also been presented (Fisher 1979). These bromalites originate from the Mazon Creek Konservat-Lagerstätte and contain horseshoe crab (*Euproops danae*) and millipede fragments (Fisher 1979). Despite the paleoecological implications of this material, such specimens have not been considered in detail. To address this, we present four new records of *Euproops*-rich bromalites from the Mazon Creek Lagerstätte, explore the origins of this material, its possible producers, and outline indications for limitations on prey size.

GEOLOGICAL CONTEXT

The siderite concretions that contain Mazon Creek fossils are hosted in the lower 3–8 meters of the ~ 25-meter-thick Francis Creek Shale (Clements et al. 2019). During the Pennsylvanian (late Carboniferous), the Mazon Creek area was a nearshore coal swamp with a large river system periodically carrying heavy sediment loads into the sea (Clements et al. 2019).

Sea-level rise during an interglacial period expanded areas for deposition, eventually blanketing the lower elevations in silty sediments. These deposits created a nearshore delta spanning both brackish and marine ecosystems and entombing most of its inhabitants (Clements et al. 2019). The peat below the sediments ultimately became coal and, above it, the sediment became shale that holds the concretions preserving both plants and animals. Today, Mazon

Creek fossils are found in localities throughout northeastern Illinois, but primarily in spoil piles from former coal strip mining operations. These pit mines are numbered (Burke et al. 2024), or named, and tend to span the paleoshoreline, from nearshore brackish water habitats to nearshore marine habitats. The localities closest to the paleoshoreline preserve the Braidwood assemblage, which includes abundant and diverse allochthonous plants, rare but diverse allochthonous terrestrial/freshwater animals, and an abundant, low-diversity, *in situ* brackish water fauna (Shabica and Hay 1997; Clements et al. 2019; Burke et al. 2024). The localities more distal to the paleoshoreline preserve the Essex fauna: an abundant, diverse, autochthonous nearshore marine fauna, as well as some allochthonous elements of the Braidwood assemblage (Shabica and Hay 1997; Clements et al. 2019; Burke et al. 2024). The fossils investigated in this paper come from Pits 1, 2, and 9, and the Morocco Mine, all of which represent the brackish water habitat of the Braidwood fauna assemblage.

METHODS

The shelly aggregates considered here are permanently housed in the Lauer Foundation for Paleontology, Science and Education in Wheaton, Illinois, and have been assigned LF specimen numbers. The mission of the Lauer Foundation is to curate its fossil collections to provide the scientific community and other museums with permanent access for the purposes of scientific research, education, and exhibition. Permanent access to type and figured specimens, as well as specimens listed or cited in publications together with other scientifically important specimens is guaranteed. LF 7282, LF 7283, and LF 7284 were originally collected by Dave Douglass in the late 1960s to mid-1970s and housed in the David and Sandra Douglass Collection before being generously donated to the Lauer Foundation for Paleontology, Science and Education to make them available for this research. LF 7282 was collected in the Dresden Lakes area, Illinois, from the Pit 9 Northern Mine of the Northern Illinois Coal Corporation. LF 7283 was collected in Coal City, Illinois, from the Pit 1 Northern Mine of the Northern Illinois Coal Corporation. LF 7284 was collected in Morris, Illinois, from the Morocco Mine of the Morris Coal and Mining Company. The fourth specimen in this study, LF 7285, was collected by AY (circa 2012) and donated to the Lauer Foundation for Paleontology, Science and Education for this study. This specimen was collected in Wilmington, Illinois, from the Pit 2 Northern Mine of the Northern Illinois Coal Corporation.

Specimens were photographed using a Nikon Z9 mirrorless camera with a 60 mm Nikkor macro lens and a Nikon FTZ II adapter. Visible light images were taken using a BDS halogen twin goose neck microscope lamp. All images were captured using Nikon Capture 2 then rendered as focus stacked images using Heliconfocus software.

Prosomal and thoracetrone widths and lengths (Fig. 1) of *Euproops danae* fragments within the aggregates were collated from photographs using ImageJ (v.1.52a) (Schneider et al. 2012). These data were combined with the *E. danae* measurements in Bicknell et al. (2022b) to compare fragment sizes to a dataset of 182 specimens. All measurements were $\log_{10}$ normalized (Online Supplemental File 1) prior to plotting to adjust for size variation.

RESULTS

Four shelly aggregates are documented as parts and counterparts (Table 1, Figs. 2, 3). Aggregates range in size from 46.3–155.4 mm long and 23.4–60.3 mm wide (Table 1) and elongate to almost quadrate in morphology. The aggregates include randomly arranged, fragmentary *Euproops danae* prosomae, thoracetrone, and telsons. Three aggregates also include indeterminate, highly fragmented material, including bivalve shell bits and unidentifiable arthropod shards with no describable exoskeletal sections (Figs. 2A, 3A, 3D). The aggregates contain little to no groundmass.

Prosomal and thoracetrone fragments show similar distributions within the larger datasets (Fig. 4). Prosomae in aggregates range between 3.2–11.1 mm

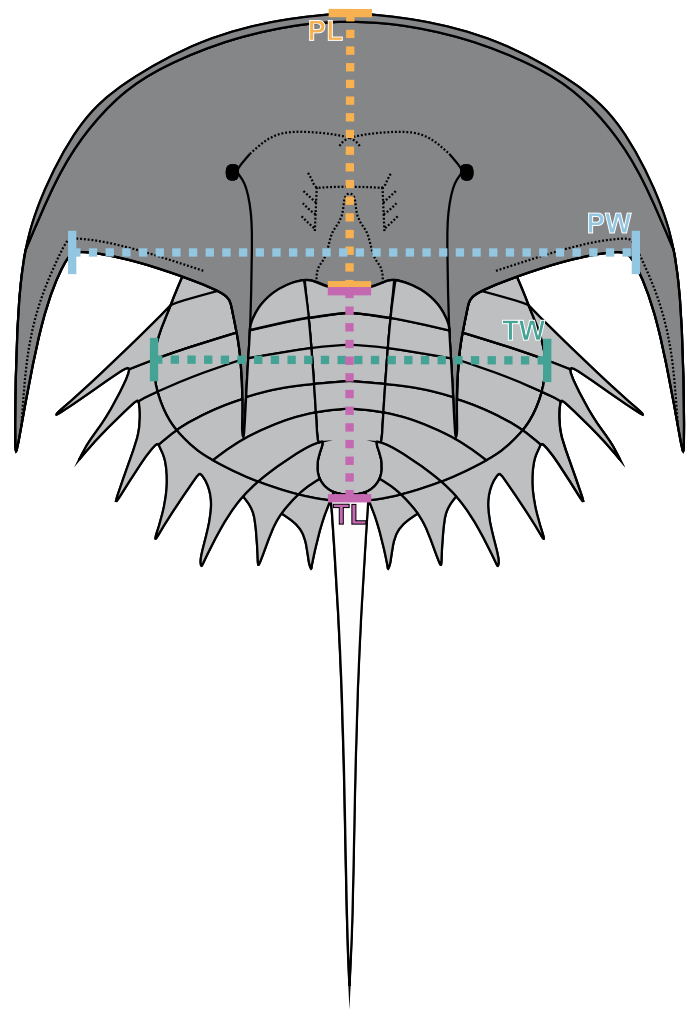


Fig. 1.—Diagram of measurements taken from *Euproops danae* exoskeletal sections. Abbreviations: PL = prosomal length; PW = prosomal width; TL = thoracetrone length; TW = thoracetrone width.

long and 9.5–21.0 mm wide and are generally located within most common *Euproops danae* size class in Bicknell et al. (2022b) (Fig. 4A). Two fragments are less wide than expected given their length. This offset reflects the fragmentary nature of sections, as opposed to a biological signal. Thoracetrone fragments range between 7.4–11.4 mm long and 10.9–16.2 mm wide (Fig. 4B) and are located within the most common *E. danae* size class in Bicknell et al. (2022b).

DISCUSSION

The specimens documented here are morphologically comparable to other Paleozoic shelly aggregates (Briggs et al. 2015; Kimmig and Strotz 2017; Hawkins et al. 2018; Kimmig and Pratt 2018; Knaust 2020; Bicknell et al. 2024). While most arthropod-rich aggregates from this era contain trilobite or bivalved arthropod fragments (Vannier and Chen 2005; Daley et al. 2013; Kimmig and Pratt 2016, 2018; Pratt and Kimmig 2019), aggregates containing softer exoskeletal fragments have been reported (Brett 2003; Briggs et al. 2015; Pratt and Kimmig 2019; Yang et al. 2021). Despite distinctions in contents, there is limited ichnofossil taxonomy differentiating these trace fossils when produced by invertebrates (see Knaust 2020 and Hunt and Lucas 2021 for reviews). However, there are two accepted vertebrate regurgitate ichnotaxa (Hunt and Lucas 2025a) and at least 56 valid vertebrate

TABLE 1.—Measurements and contents of regurgitalites examined herein.

Specimen	Length (mm)	Maximum width (mm)	Material contained within
LF 7282	155.4	60.3	Prosoma, thoracetrons, indeterminate material
LF 7285	46.3	23.4	Prosoma, thoracetreron section, indeterminate material
LF 7283	48.5	45.8	Prosoma, thoracetreron, telson
LF 7284	55.1	23.4	Prosoma, thoracetreron, telson, indeterminate material

coprolite ichnotaxa (Hunt and Lucas 2021, 2025b). For ecologic and taphonomic information, specimens are compared to other shelly aggregations (e.g., Häntzschel et al. 1968; Hunt et al. 2012; Salamon et al. 2014; Shen et al. 2014; Zatoń and Rakociński 2014; Brachaniec et al. 2016; Knaust 2020; Hunt and Lucas 2021, 2025b). The Mazon Creek aggregations have loosely connected, fragmented arthropod sections preserved, similar to trilobite-rich aggregations in shales and carbonates. The fragmented horseshoe crab sections are therefore interpreted as incompletely digested prey (Hawkins et al. 2018). The disarticulated, but associated, xiphosurid exoskeletal sections are also similar to other

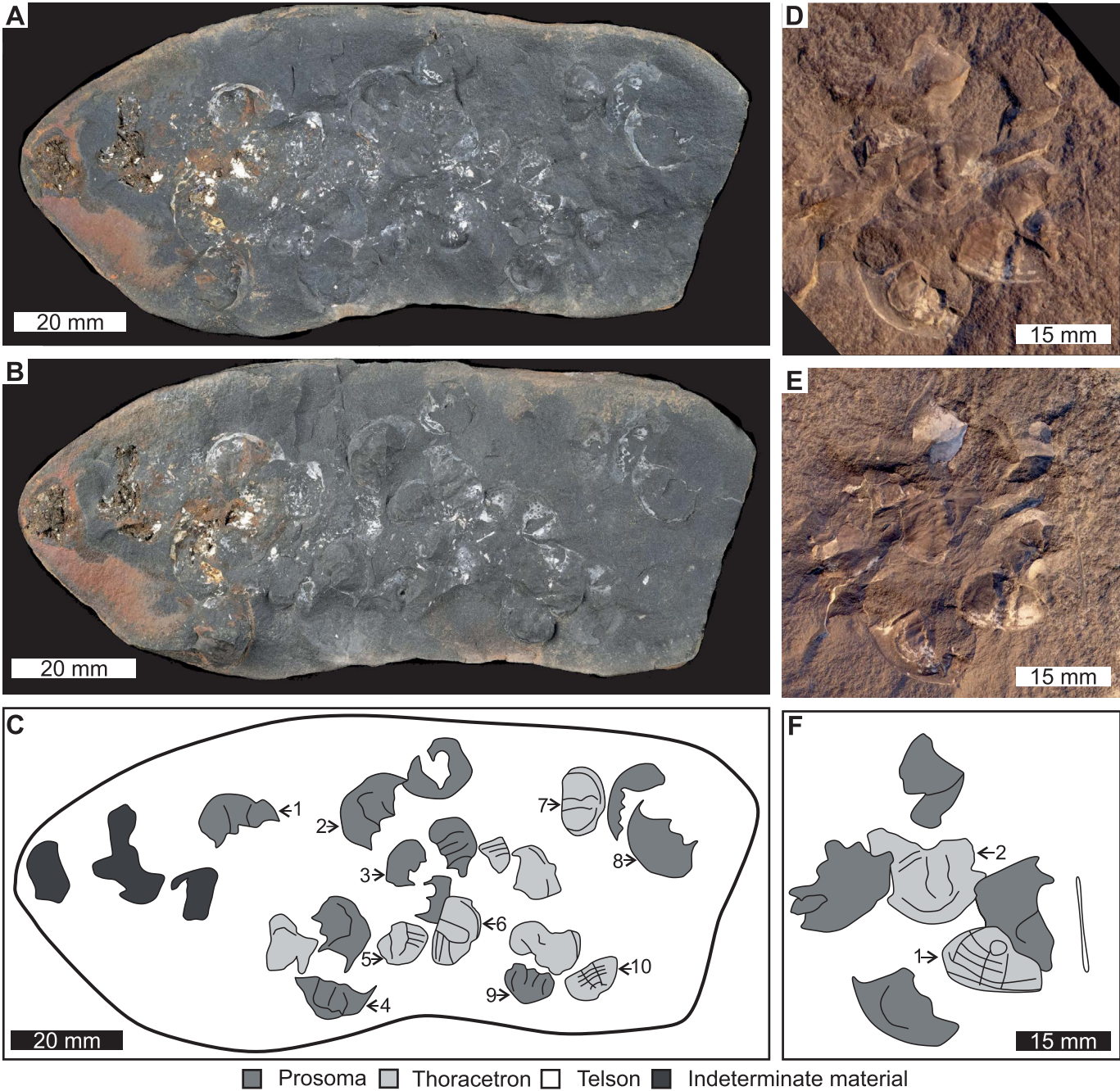


FIG. 2.—Xiphosurid-rich regurgitalites from the Mazon Creek Lagerstätte. A–C) Specimen from Pit 9; sample numbers (A, B), LF 7282 N, LF 7282 P, respectively. View C is a line drawing of A showing fragmented sections. D–F) Specimen from Pit 1; sample numbers (D, E): LF 7283 P, LF 7283 N. View F is a line drawing of D showing fragments. Numbers in C and F denote fragments measured and included in Online Supplemental File 1. Views B and E are reflected to align with A and D, respectively.

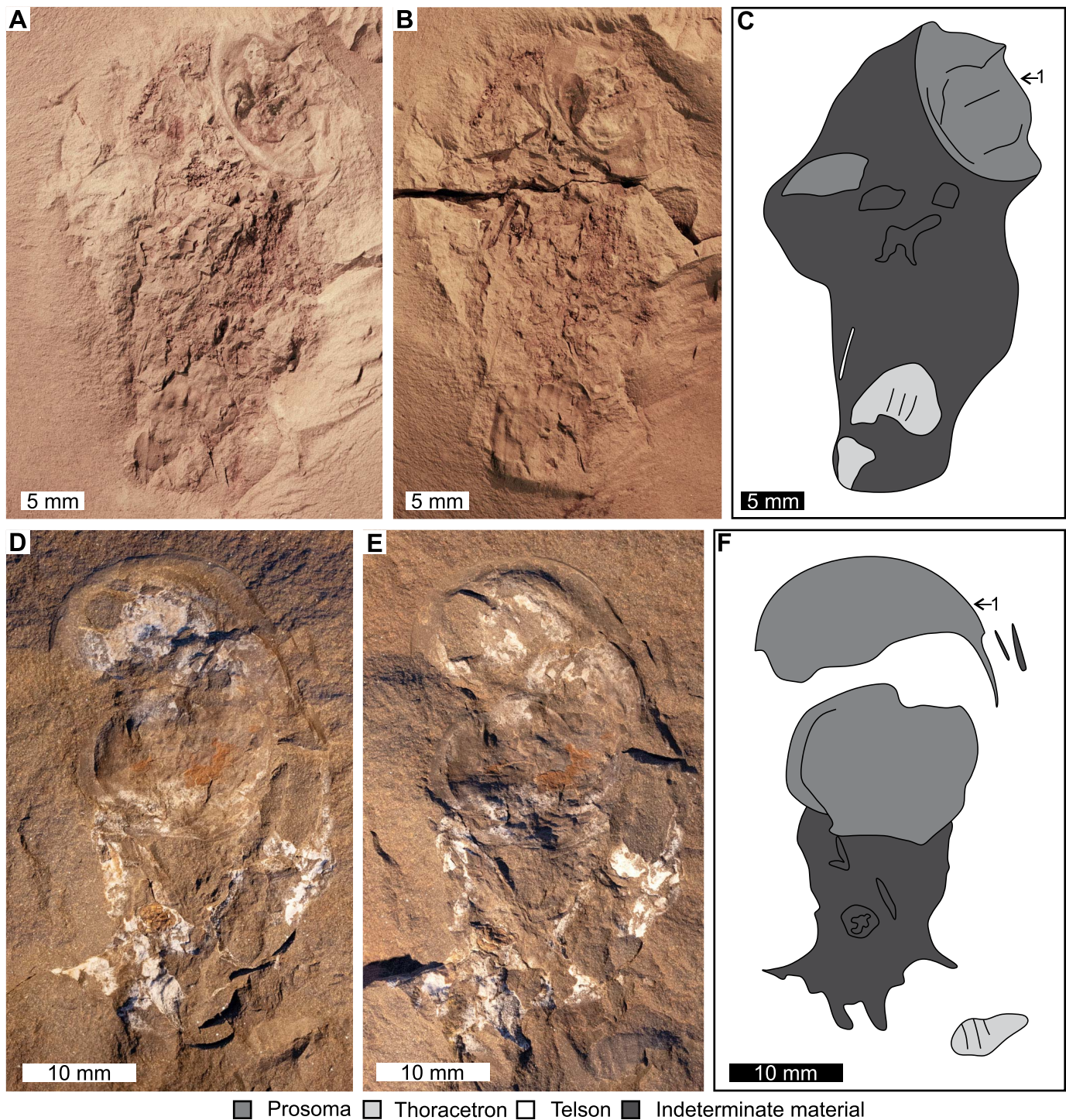


FIG. 3.—Additional xiphosurid-rich regurgitalites from the Mazon Creek Lagerstätte. A–C) Specimen from Morocco Mine, sample numbers (A, B): LF 7284 N, LF 7284 P, respectively. C is a line drawing of A showing fragments. D–F) Specimen from Pit 2; sample numbers (D, E): LF 7285 N, LF 7285 P, respectively. View F is a line drawing of D showing fragments. Numbers in C and F denote fragments measured and included in Online Supplemental File 1. Views B and E are reflected to align with A and D, respectively.

xiphosurid-rich aggregations from the Mazon Creek fossil assemblage (Fisher 1979). We therefore suggest following Fisher (1979), that these represent coprolites or regurgitalites.

Differentiating coprolites (fossilized feces) and regurgitalites (fossilized regurgitated stomach contents) is often difficult and no rigorous method of distinguishing regurgitalites from coprolites has been established (Vannier and Chen 2005; Hunt et al. 2012; Gordon et al. 2020; Hunt and Lucas 2021).

Much of the discussion on differentiating between coprolites and regurgitalites, the two forms of exterior bromalites, is based in vertebrate ichnology, and many criteria have been proposed: for example, corrosion of bones in bromalites, presence and absence of phosphatic residue, degree of fragment digestion, size of hard parts, or presence and absence of soft-tissues (e.g., Gordon et al. 2020; Hunt and Lucas 2021, 2025b). A characteristic that has been used to distinguish between coprolites and regurgitalites of invertebrates is specimen

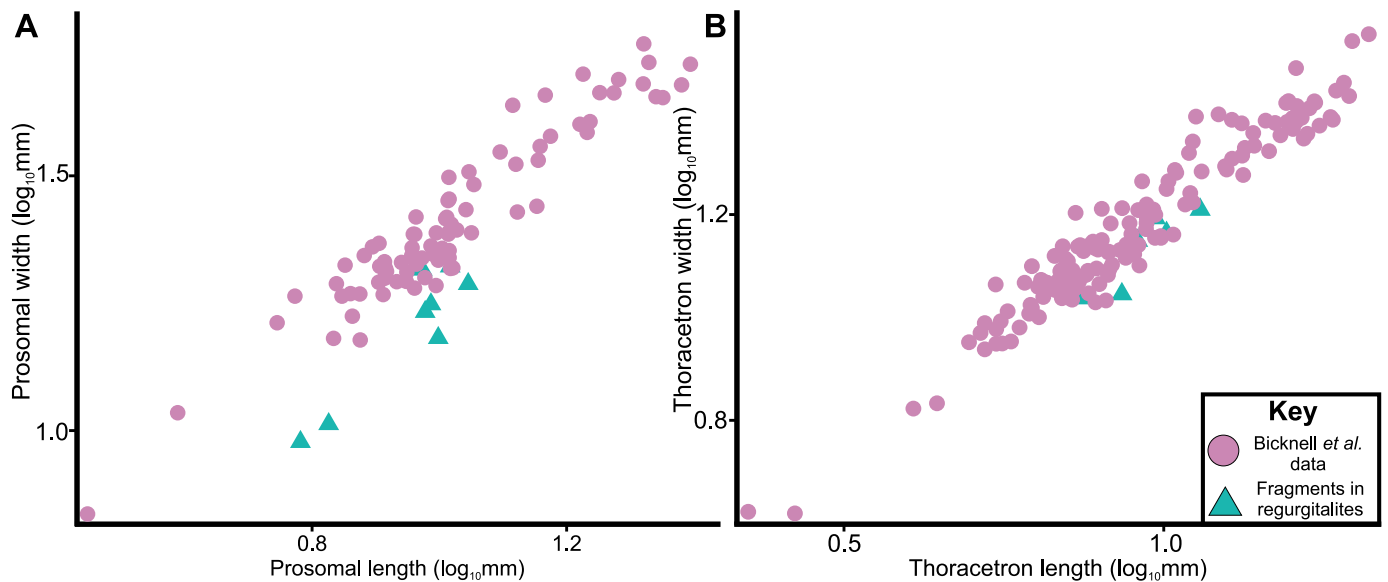


FIG. 4.—Measurements of Mazon Creek *Euproops danae* specimens from Bicknell et al. (2022b) and exoskeletal fragments within regurgitalites. Data are log₁₀ normalized. A) Prosomal measurements. B) Thoracetrone measurements.

compaction and morphology. Invertebrate coprolites are usually well-defined in shape, whereas regurgitalites are typically poorly formed and the components are diffused or dispersed (Vannier and Chen 2005; Brachanec et al. 2016; Kimmig and Pratt 2018; Hunt and Lucas 2021, 2025b). Based on these criteria, the herein presented Mazon Creek specimens most likely represent regurgitalites, as they preserve little groundmass, no phosphatic matrix, and relatively identifiable shelly fragments. Some specimens are compact, the arthropod pieces are not widely dispersed, and do not preserve soft tissues. As such, the coprolite hypothesis cannot be completely disregarded. Nonetheless, for the reasons listed above, we suggest that these bromalites represent regurgitalites rather than coprolites. However, as the specimens herein described are not comparable to the two named regurgitalites ichnotaxa, the specimens are left in open nomenclature.

Euproops danae fossils are commonly found in Braidwood (brackish water) localities, and only rarely in Essex (marine) localities (Shabica and Hay 1997; Haug and Rötzer 2018; Bicknell and Pates 2020; Bicknell et al. 2022c). This distribution suggests that *E. danae* within the Essex fauna are washout specimens, and that *E. danae* is part of the brackish water/terrestrial Braidwood fauna rather than the marine Essex fauna (Bicknell et al. 2022c). *Euproops danae*, solemyid bivalves, and syncarid shrimp dominate the Braidwood fauna, and are generally considered to reflect an *in situ* brackish water fauna (Shabica and Hay 1997), with additional elements of allochthonous freshwater and terrestrial animals. It has been suggested that *E. danae* may have engaged in subaerial activity (Fisher 1979), but purely terrestrial animals tend to be extremely rare in the Braidwood fauna, suggesting *E. danae* was not terrestrial (Shabica and Hay 1997). The four *Euproops*-rich regurgitalite specimens were also found in Braidwood localities. This suggests that the regurgitalite-producer inhabited these brackish water habitats and fed on the abundant *E. danae* that lived there. These regurgitalite specimens also corroborated exceptionally rare evidence of *E. danae* with failed injuries (Bicknell et al. 2018, 2022d). Therefore, the regurgitalite-producer would most likely be found among the Braidwood fauna.

The only arthropod represented in Mazon Creek Braidwood localities robust enough to successfully prey upon *Euproops danae*, and large enough to produce these regurgitalites, is *Arthropleura*. This myriapod is represented in the Mazon Creek fauna by, at most, fragmentary exoskeletal elements (Wittry 2012). *Arthropleura* was traditionally considered to be terrestrial, but more recent evidence, including stalked eyes (Lhéritier et al. 2024) and

both subaerial and subaqueous trackways (Davies et al. 2022), suggests a semi-aquatic lifestyle which could allow it to encounter *E. danae*. However, the overall *Arthropleura* anatomy is most consistent with detritivory (Lhéritier et al. 2024), making it unlikely to be the producer of *Euproops*-rich regurgitalites, regardless of habitat. Although there were large Carboniferous eurypterids, these generally lived in freshwater rather than brackish conditions, and all Mazon Creek eurypterid fossils represent individuals too small to produce these regurgitalites (Wittry 2012; Hunt and Lucas 2021, 2025; Ruebenstahl et al. 2024). The few bromalites that have been attributed to eurypterids are usually unstructured and have been reported to include fragments of conodonts, brachiopods, phyllocarids, trilobites, eurypterids, and other small arthropods, such as ostracods (e.g., Caster and Kjellesvig-Waering 1964; Turner 1999; Hawkins et al. 2018; Hunt and Lucas 2021, 2025a; Bicknell et al. 2023).

Tetrapods are extremely rare in the Mazon Creek fossil array, with estimates of one tetrapod per 100,000 fossiliferous concretions (Shabica and Hay 1997). Moreover, there is no direct evidence, such as fossils of isolated teeth or scales, of tetrapods large enough to produce these regurgitalites in the Mazon Creek fossil assemblage. However, many tetrapods are represented as larvae (Mann and Gee 2019). As such, despite a lack of fossil evidence for large tetrapods, an adult form may have been the regurgitalite-producer.

Most fish preserved in the Braidwood fauna are too small to have produced these regurgitalites, although the presence of larger fish living at the site is indicated through fragmentary remains (Wittry 2012). Evidence for large fish primarily includes bromalites (often with an uncertain producer), isolated teeth, and isolated scales, although there are rarer examples of preserved bone, fin spines, and skin fragments (Wittry 2012). The most common, large vertebrate teeth in the Braidwood fauna are the robust and sharply pointed teeth of the freshwater shark *Orthacanthus* (Wittry 2012). However, the *Euproops danae* pieces in these regurgitalites do not show any puncture marks, scrapes, or scratches from sharp teeth, suggesting the regurgitalite-producer had crushing, rather than sharp, teeth. Additional common, large vertebrate remains in the Braidwood fauna include isolated scales (upwards to 8 cm in length) attributable to lungfish or other unidentified lobe-finned fish (Bardack 1979), and large lungfish are represented in the Braidwood fauna by isolated *Ctenodus cristatus* tooth plates (Bardack 1979). These tooth plates have large, flat surfaces with radiating ridges and small cusps. The exact function of *C. cristatus* tooth plates is unclear, but the tooth plates of

some *Ctenodus* species are likely specialized for crushing hard prey (Sharp and Clack 2013). Relatively large, durophagous lungfish, which may have left behind isolated scales and crushing *C. cristatus* teeth, are the most likely producers of the *Euproops*-rich regurgitalites found in the Mazon Creek area.

Most vertebrates, including lungfish, can regurgitate difficult-to-digest elements of their diet through vomiting or stomach eversion (Hunt and Lucas, 2021). These difficult-to-digest elements often include mechanically dangerous hard parts such as large or sharp bones and exoskeleton elements (Hunt and Lucas 2021). Lungfish have commonly been durophages from the Early Devonian to the present day, and many of the characteristic features of their feeding apparatus are attributable to durophagy (Bemis 1986; Cui et al. 2022). The earliest, Devonian lungfish were likely obligate durophages, although extant lungfish will feed on a broader range of prey items (Pardo et al. 2014). Hard-shelled prey items of Australian lungfish (*Neoceratodus forsteri*) today include gastropods, bivalves, and crustaceans, which are part of a broad omnivorous diet (Kemp 1986; Tao et al. 2020). In contrast, adult South Africa lungfish (*Lepidosiren paradoxa*) feed largely on bivalves, although younger individuals eat a broader diet (Bemis and Lauder 1986). The marbled lungfish (*Protopterus aethiopicus*) primarily eats fish (Mlewa and Green 2005).

The size distribution of xiphosurid fragments within the regurgitalites examined here suggests consumed prey were within similar size classes. The predator, possibly lungfish, may therefore have been limited to eating these and smaller-sized xiphosurids. Alternatively, larger *Euproops danae* may have survived attacks, as evidenced by rare, injured *E. danae* (Bicknell et al. 2018, 2022d).

In modern systems, horseshoe crabs are not commonly documented prey items. While juvenile individuals are eaten by fishes (Shuster 1982; Botton et al. 2003), adult forms are targeted by a more limited range of animals. Adult *Limulus polyphemus* have been documented as prey for large vertebrates, such as alligators, leopard sharks, and loggerhead turtles (Reid and Bonde 1990; Keinath 2003; Bicknell et al. 2018; Lamsdell 2019); gulls target inverted individuals (Botton and Loveland 1989; Bicknell et al. 2022d); and gastropod mollusks drill holes through the carapace. *Tachypleus gigas* has been consumed by long-tailed macaques and domestic pigs (Ang 2016; Pati and Dash 2016; Lamsdell 2019), with house crows attacking overturned individuals (Debnath and Choudhury 1988). The regurgitalites considered here demonstrate that horseshoe crabs have been key dietary components for predators over the xiphosurid evolutionary history and may have been more commonly consumed as prey items during the Carboniferous.

ACKNOWLEDGMENTS

This research was funded by a MAT Program Postdoctoral Fellowship (to R.D.C.B.). We highlight LF 7282, LF 7283, and LF 7284 were originally housed within the David and Sandra Douglass Collection, who made them available to us for preliminary investigation. The specimens were then donated to the Lauer Foundation for Paleontology, Science and Education in Wheaton, Illinois, to place them into a publishable repository (see <https://www.lauerfoundationpse.org/>). We thank Michele Micetich for sharing with us her vast knowledge of the mining history of the Mazon Creek area. Finally, we thank Adrian Hunt and an anonymous reviewer for their insightful comments.

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: <https://www.sepm.org/supplemental-materials>.

REFERENCES

ANG, A., 2016, Long-tailed Macaque feeding on horseshoe crab *Tachypleus gigas* at Tanjung Piai, Johor, Peninsular Malaysia: South-East Asia Vertebrate Record, v. 28, p. 51–52.

- 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: PALAIOS, v. 1, p. 271–285.
- BARDACK, D., 1979, Fishes of the Mazon Creek fauna, in M.H. Nitecki (ed.), Mazon Creek Fossils: Academic Press, New York, p. 501–528.
- BEMIS, W.E., 1986, Feeding systems of living *Dipnoi*: anatomy and function: Journal of Morphology v. 190.S1, p. 249–275.
- BEMIS, W.E. AND LAUDER, G.V., 1986, Morphology and function of the feeding apparatus of the lungfish, *Lepidosiren paradoxa* (Dipnoi): Journal of Morphology, v. 187, p. 81–108.
- BICKNELL, R.D.C., BRUTHANSOVÁ, J., AND KIMMIG, J., 2024, Shelly coprolites record durophagous predation in the Late Ordovician Bohdalec Formation (Katian; Prague Basin, Czech Republic): Geobios, v. 82, p. 1–11.
- BICKNELL, R.D.C., HOLMES, J.D., PATES, S., GARCÍA-BELLIDO, D.C., AND PATERSON, J.R., 2022a, Cambrian carnage: trilobite predator-prey interactions in the Emu Bay Shale of South Australia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 591, p. 110877.
- BICKNELL, R.D.C., KIMMIG, J., BUDD, G.E., LEGG, D.A., BADER, K.S., HAUG, C., KAISER, D., LAIBL, L., TASHMAN, J.N., AND CAMPIONE, N.E., 2022b, Habitat and developmental constraints drove 330 million years of horseshoe crab evolution: Biological Journal of the Linnean Society, v. 136, p. 155–172.
- BICKNELL, R.D.C., NAUGOLNYKH, S.V., AND MCKENZIE, S.C., 2022c, On *Paleolimulus* from the Mazon Creek Konservat-Lagerstätte: Comptes Rendus Palevol, v. 21, p. 303–322.
- BICKNELL, R.D.C., ORTEGA-HERNÁNDEZ, J., EDGEcombe, G.D., GAINES, R.R., AND PATERSON, J.R., 2021, Central nervous system of a 310-million-year-old horseshoe crab: expanding the taphonomic window for nervous system preservation: Geology, v. 49, p. 1381–1385.
- BICKNELL, R.D.C. AND PATERSON, J.R., 2018, Reappraising the early evidence of durophagy and drilling predation in the fossil record: implications for escalation and the Cambrian Explosion: Biological Reviews, v. 93, p. 754–784.
- 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, p. 98.
- BICKNELL, R.D.C., PATES, S., AND BOTTON, M.L., 2018, Abnormal xiphosurids, with possible application to Cambrian trilobites: Palaeontologia Electronica, v. 21, p. 1–17.
- BICKNELL, R.D.C., PATES, S., KAISER, D., ZAKRZEWSKI, S., AND BOTTON, M.L., 2022d, Applying records of extant and extinct horseshoe crab abnormalities to xiphosurid conservation, in J.T. Tanacredi, M.L. Botton, P.K.S. Shin, Y. Iwasaki, S.G. Cheung, K.Y. Kwan, and J.H. Mattei (eds.), International Horseshoe Crab Conservation and Research Efforts: 2007–2020, Conservation of Horseshoe Crabs Species Globally: Springer, Cham, Switzerland, p. 85–104.
- BICKNELL, R.D.C., SMITH, P.M., AND KIMMIG, J., 2023, Novel coprolitic records from the Silurian (Pridoli) Wallace Shale of New South Wales: Alcheringa, v. 47, p. 24–30.
- BOTTOM, M.L. AND LOVELAND, R.E., 1989, Reproductive risk: high mortality associated with spawning by horseshoe crabs (*Limulus polyphemus*) in Delaware Bay, USA: Marine Biology, v. 101, p. 143–151.
- BOTTOM, M.L., SHUSTER, C.N., JR., AND KEINATH, J.A., 2003, Horseshoe crabs in a food web: who eats whom?, in C.N. Shuster, Jr., R.B. Barlow, and H.J. Brockmann (eds.), The American Horseshoe Crab: Harvard University Press, Cambridge, p. 133–153.
- BRACHANIEC, T., LEKO, K., AND WIECZOREK, A., 2016, Regurgitalite from the Silurian of Holy Cross Mountains, southern Poland: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 280, p. 331–334.
- BRETT, C.E., 2003, Durophagous predation in Paleozoic marine benthic assemblages, in P.H. Kelley, M. Kowalewski, and H.J. Hansen (eds.), Predator-Prey Interactions in the Fossil Record: Springer, Boston, MA, p. 401–432.
- BURGESS, D.E.G., LIU, H.P., MCKAY, R.M., AND WITZKE, B.J., 2015, Bivalved arthropods from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA: Journal of Paleontology, v. 89, p. 991–1006.
- BURKE, P.J.C., MAYER, P.S., AND MCCOY, V.E., 2024, Mazon Creek fossils brought to you by coal, concretions and collectors: Geological Society, London, Special Publications, v. 543, p. SP543–2022.
- CASTER, K.E. AND KJELLESVIG-WAERING, E.N., 1964, Upper Ordovician eurypterids of Ohio: Palaeontographia Americana, v. 3, p. 301–358.
- 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.
- CUI, X., FRIEDMAN, M., QIAO, T., YU, Y., AND ZHU, M., 2022, The rapid evolution of lungfish durophagy: Nature Communications, v. 13, p. 2390.
- DALEY, A.C., PATERSON, J.R., EDGEcombe, G.D., GARCÍA-BELLIDO, D.C., AND JAGO, J.B., 2013, New anatomical information on *Anomalocaris* from the Cambrian Emu Bay Shale of South Australia and a reassessment of its inferred predatory habits: Palaeontology, v. 56, p. 971–990.
- DAVIES, N.S., GARWOOD, R.J., McMAHON, W.J., SCHNEIDER, J.W., AND SHILLITO, A.P., 2022, The largest arthropod in Earth history: insights from newly discovered *Arthropleura* remains (Serpukhovian Stainmore Formation, Northumberland, England): Journal of the Geological Society, v. 179, p. jgs2021–115.
- DEBNATH, R. AND CHOUDHURY, A., 1988, Predation of Indian horseshoe crab *Tachypleus gigas* by *Corvus splendens*: Tropical Ecology, v. 29, p. 86–89.
- ENGLISH, A.M. AND BABCOCK, L.E., 2010, Census of the Indian Springs Lagerstätte, Poleta Formation (Cambrian), western Nevada, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 295, p. 236–244.

- FISHER, D.C., 1979, Evidence for subaerial activity of *Euproops danae* (Merostomata, Xiphosurida), in M.H. Nitecki (ed.), *Mazon Creek Fossils*: Elsevier, New York, p. 379–447.
- GORDON, C.M., ROACH, B.T., PARKER, W.G., AND BRIGGS, D.E.G., 2020, Distinguishing regurgitalites and coprolites: a case study using a Triassic bromalite with soft tissue of the pseudosuchian archosaur *Revueltosaurus*: *PALAIOS*, v. 35, p. 111–121.
- HABGOOD, K.S., HASS, H., AND KERR, H., 2003, Evidence for an early terrestrial food web: coprolites from the Early Devonian Rhynie chert: *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, v. 94, p. 371–389.
- HANTZSCHEL, W., EL-BAZ, F., AND AMSTUTZ, G.C., 1968, *Coprolites an Annotated Bibliography*: Geological Society of America, Boulder, 132 p.
- 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.
- HAWKINS, A.D., LIU, H.P., BRIGGS, D.E.G., MUSCENTE, A.D., MCKAY, R.M., WITZKE, B.J., AND XIAO, S., 2018, Taphonomy and biological affinity of three-dimensionally phosphatized bromalites from the Middle Ordovician Winneshiek Lagerstätte, northeastern Iowa, USA: *PALAIOS*, v. 33, p. 1–15.
- HUNT, A.P. AND LUCAS, S.G., 2021, The ichnology of vertebrate consumption: dentalites, gastroliths and bromalites: *New Mexico Museum of Natural History and Science Bulletin*, v. 87, p. 1–215.
- HUNT, A.P. AND LUCAS, S.G., 2025a, Coprolites, in S.G. Lucas, A.P. Hunt and H. Klein (eds.), *Vertebrate Ichnology: Fish Ichnology, Consumption, Burrows and Reproduction, Geoconservation*: Elsevier, New York, p. 1–24.
- HUNT, A.P. AND LUCAS, S.G., 2025b, Regurgitalites, in S.G. Lucas, A.P. Hunt, and H. Klein (eds.), *Vertebrate Ichnology: Fish Ichnology, Consumption, Burrows and Reproduction, Geoconservation*: Elsevier, New York, p. 1–97.
- HUNT, A.P., MILÁN, J., LUCAS, S.G., AND SPIELMANN, J.A., 2012, Vertebrate coprolite studies: status and prospectus: *New Mexico Museum of Natural History and Science Bulletin*, v. 57, p. 5–24.
- JOHNSON, R.G. AND RICHARDSON, E.S., JR., 1968, Pennsylvanian invertebrates of the Mazon Creek area, Illinois, The Essex fauna and medusae: *Fieldiana, Geology, New Series*, p. 109–115.
- KEINATH, J.A., 2003, Predation of horseshoe crabs by loggerhead sea turtles, in C.N. Shuster, Jr., R.B. Barlow, and H.J. Brockmann (eds.), *The American Horseshoe Crab*: Harvard University Press, Cambridge, p. 152–153.
- KEMP, A., 1986, The biology of the Australian lungfish, *Neoceratodus forsteri* (Krefft 1870): *Journal of Morphology*, v. 190, p. 181–198.
- KIMMIG, J. AND PRATT, B.R., 2016, Taphonomy of the middle Cambrian (Drumian) Ravens Throat River Lagerstätte, Rockslide Formation, Mackenzie Mountains, Northwest Territories, Canada: *Lethaia*, v. 49, p. 150–169.
- KIMMIG, J. AND PRATT, B.R., 2018, Coprolites in the Ravens Throat River Lagerstätte of Northwestern Canada: implications for the middle Cambrian food web: *PALAIOS*, v. 33, p. 125–140.
- KIMMIG, J. AND SCHIFFBAUER, J.D., 2024, A modern definition of Fossil-Lagerstätten: *Trends in Ecology and Evolution*, v. 39, p. 621–624.
- KIMMIG, J. AND STROTZ, L.C., 2017, Coprolites in mid-Cambrian (Series 2-3) Burgess Shale-type deposits of Nevada and Utah and their ecological implications: *Bulletin of Geosciences*, v. 92, p. 297–309.
- KNAUST, D., 2020, Invertebrate coprolites and cololites revised: *Papers in Palaeontology*, v. 6, p. 385–423.
- KULKARNI, K.G. AND PANCHANG, R., 2015, New insights into polychaete traces and fecal pellets: another complex ichnotaxon?: *PLoS ONE*, v. 10, e0139933.
- LAMSDALL, J.C., 2019, Evolutionary history of the dynamic horseshoe crab: *International Water Studies*, v. 21, p. 1–15.
- LHÉRITIER, M., EDGEcombe, G.D., GARWOOD, R.J., BUISSON, A., GERBE, A., KOCH, N.M., VANNIER, J., ESCARGUEL, G., ADRIEN, J., AND FERNANDEZ, V., 2024, Head anatomy and phylogenomics show the Carboniferous giant *Arthropleura* belonged to a millipede-centipede group: *Science Advances*, v. 10, eadp6362.
- MANN, A. AND GEE, B.M., 2019, Lissamphibian-like toepads in an exceptionally preserved amphibiform from Mazon Creek: *Journal of Vertebrate Paleontology*, v. 39, e1727490.
- MCCOY, V.E., WITTRY, J., SADABADI, H., AND MAYER, P., 2023, A reappraisal of *Nemavermes mackeei* from the Mazon Creek fossil site expands Carboniferous cyclostome diversity: *Journal of Paleontology*, v. 97, p. 1116–1132.
- MÍKULÁŠ, R., 1995, Trace fossils from the Paseky Shale (early Cambrian, Czech Republic): *Journal of the Czech Geological Society*, v. 40, p. 37–44.
- MLEWA, C. M. AND GREEN, J. M., 2005, Biology of the marbled lungfish, *Protopterus aethiopicus* Heckel, in Lake Baringo, Kenya. *African Journal of Ecology*, v. 42, p. 338–345.
- NEDIN, C., 1999, *Anomalocaris* predation on nonmineralized and mineralized trilobites: *Geology*, v. 27, p. 987–990.
- NORTHWOOD, C., 2005, Early Triassic coprolites from Australia and their palaeobiological significance: *Palaeontology*, v. 48, p. 49–68.
- PARDO, J.D., HUTTENLOCKER, A.K., AND SMALL, B.J., 2014, An exceptionally preserved transitional lungfish from the Lower Permian of Nebraska, USA, and the origin of modern lungfishes: *PLoS ONE*, v. 9, e108542.
- PATI, S. AND DASH, B.P., 2016, Horseshoe crab (*Tachyplesus gigas*) as prey of domestic pig (*Sus domesticus*) in Khandaia estuary, Balasore, Odisha, India: *Zoo's Print*, v. 31, p. 14–15.
- PLOTNICK, R.E., YOUNG, G.A., AND HAGADORN, J.W., 2023, An abundant sea anemone from the Carboniferous Mazon Creek Lagerstätte, USA: *Papers in Palaeontology*, v. 9, e1479.
- PRATT, B.R. AND KIMMIG, J., 2019, Extensive bioturbation in a middle Cambrian Burgess Shale-type fossil Lagerstätte in northwestern Canada: *Geology*, v. 47, p. 231–234.
- QVARNSTRÖM, M., NIEDZWIEDZKI, G., AND ŽIGAITĖ, Ž., 2016, Vertebrate coprolites (fossil faeces): an underexplored Konservat-Lagerstätte: *Earth-Science Reviews*, v. 162, p. 44–57.
- REID, J.P. AND BONDE, R.K., 1990, *Alligator mississippiensis* (American alligator) diet: *Herpetological Review*, v. 21, p. 59.
- RUEBENSTALH, A., MONGIARDINO KOCH, N., LAMSDALL, J.C., AND BRIGGS, D.E.G., 2024, Convergent evolution of giant size in eurypterids: *Proceedings of the Royal Society B*, v. 291, e20241184.
- SALAMON, M.A., GORZELAK, P., NIEDZWIEDZKI, R., TRZĘSIK, D., AND BAUMILLER, T.K., 2014, Trends in shell fragmentation as evidence of mid-Paleozoic changes in marine predation: *Paleobiology*, v. 40, p. 14–23.
- SCHNEIDER, C.A., RASBAND, W.S., AND ELICEIRI, K.W., 2012, NIH Image to ImageJ: 25 years of image analysis: *Nature Methods*, v. 9, p. 671–675.
- SCHRAM, F.R., 1979, The Mazon Creek biotas in the context of a Carboniferous faunal continuum, in M.H. Nitecki (ed.), *Mazon Creek Fossils*: Academic Press, New York, p. 159–190.
- SHABICA, C.W. AND HAY, A.A., 1997, *The Fossil Fauna of Mazon Creek*: Northeastern Illinois University, Chicago.
- SHARP, E.L. AND CLACK, J.A., 2013, A review of the Carboniferous lungfish genus *Ctenodus* Agassiz, 1838 from the United Kingdom, with new data from an articulated specimen of *Ctenodus interruptus* Barkas, 1869: *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, v. 104, p. 169–204.
- SHEN, C., PRATT, B.R., AND ZHANG, X.-G., 2014, Phosphatized coprolites from the middle Cambrian (Stage 5) Duyun fauna of China: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 410, p. 104–112.
- SHUSTER, C.N., JR., 1982, A pictorial review of the natural history and ecology of the horseshoe crab *Limulus polyphemus*, with reference to other Limulidae: *Progress in Clinical and Biological Research*, v. 81, p. 1–52.
- TAO, J., KENNARD, M.J., ROBERTS, D.T., FRY, B., KAINZ, M.J., CHEN, Y., AND BUNN, S.E., 2020, Quality and contribution of food sources to Australian lungfish evaluated using fatty acids and stable isotopes: *Aquatic Sciences*, v. 82, p. 1–11.
- TETLIE, O.E. AND DUNLOP, J.A., 2008, *Geralinura carbonaria* (Arachnida; Uropygi) from Mazon Creek, Illinois, USA, and the origin of subchelate pedipalps in whip scorpions: *Journal of Paleontology*, v. 82, p. 299–312.
- TURNER, S., 1999, The importance of coprolite events: *Ichthyolith Issues*, v. 20, p. 37–38.
- VANNIER, J. AND CHEN, J., 2005, Early Cambrian food chain: new evidence from fossil aggregates in the Maotianshan Shale biota, SW China: *PALAIOS*, v. 20, p. 3–26.
- WITTRY, J., 2012, *The Mazon Creek Fossil Fauna*: Earth Science Club of Northern Illinois, Downers Grove, Illinois, 202 p.
- YANG, X., KIMMIG, J., ZHAI, D., LIU, Y., KIMMIG, S.R., AND PENG, S., 2021, A juvenile-rich palaeocommunity of the lower Cambrian Chengjiang biota sheds light on palaeo-boom or palaeo-bust environments: *Nature Ecology and Evolution*, v. 5, p. 1082–1090.
- ZATOŃ, M. AND RAKOCIŃSKI, M., 2014, Coprolite evidence for carnivorous predation in a Late Devonian pelagic environment of southern Laurussia: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 394, p. 1–11.

Received 25 March 2025; accepted 10 June 2025.