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

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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 thoracetronic 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 $\sim$ 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

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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 thoracetron 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, thoracetrons, 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 thoracetronic fragments show similar distributions within the larger datasets (Fig. 4). Prosomae in aggregates range between 3.2–11.1 mm 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. Thoracetronic 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).

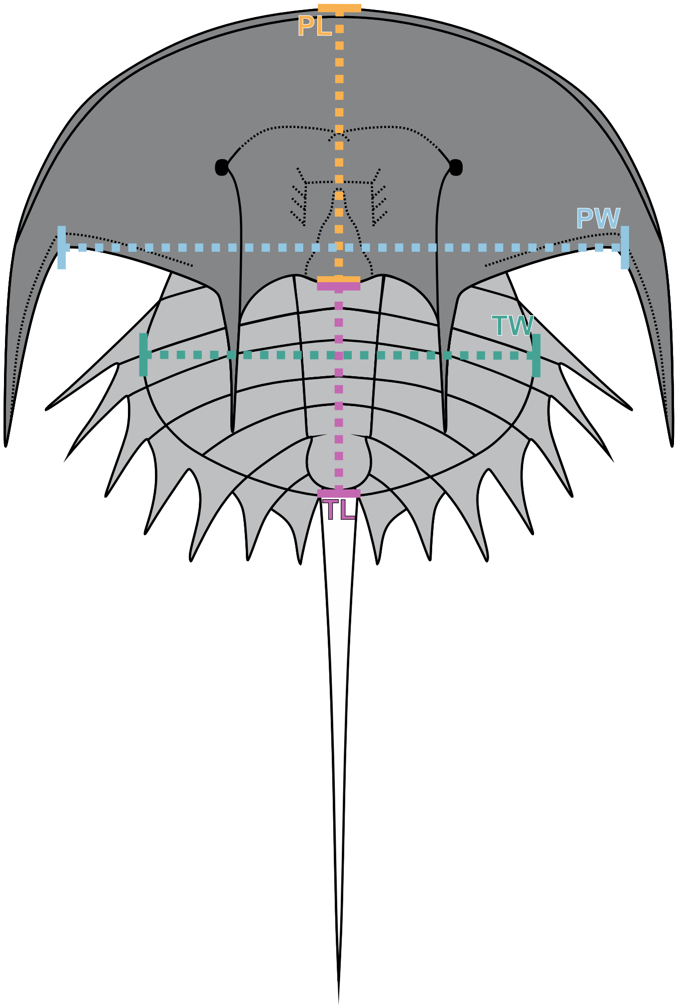

FIG. 1.—Diagram of measurements taken from *Euproops danae* exoskeletal sections. Abbreviations: PL = prosomal length; PW = prosomal width; TL = thoracetron length; TW = thoracetron width.

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 regurgitalite 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, thoracetron section, indeterminate material
LF 7283	48.5	45.8	Prosoma, thoracetron, telson
LF 7284	55.1	23.4	Prosoma, thoracetron, 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

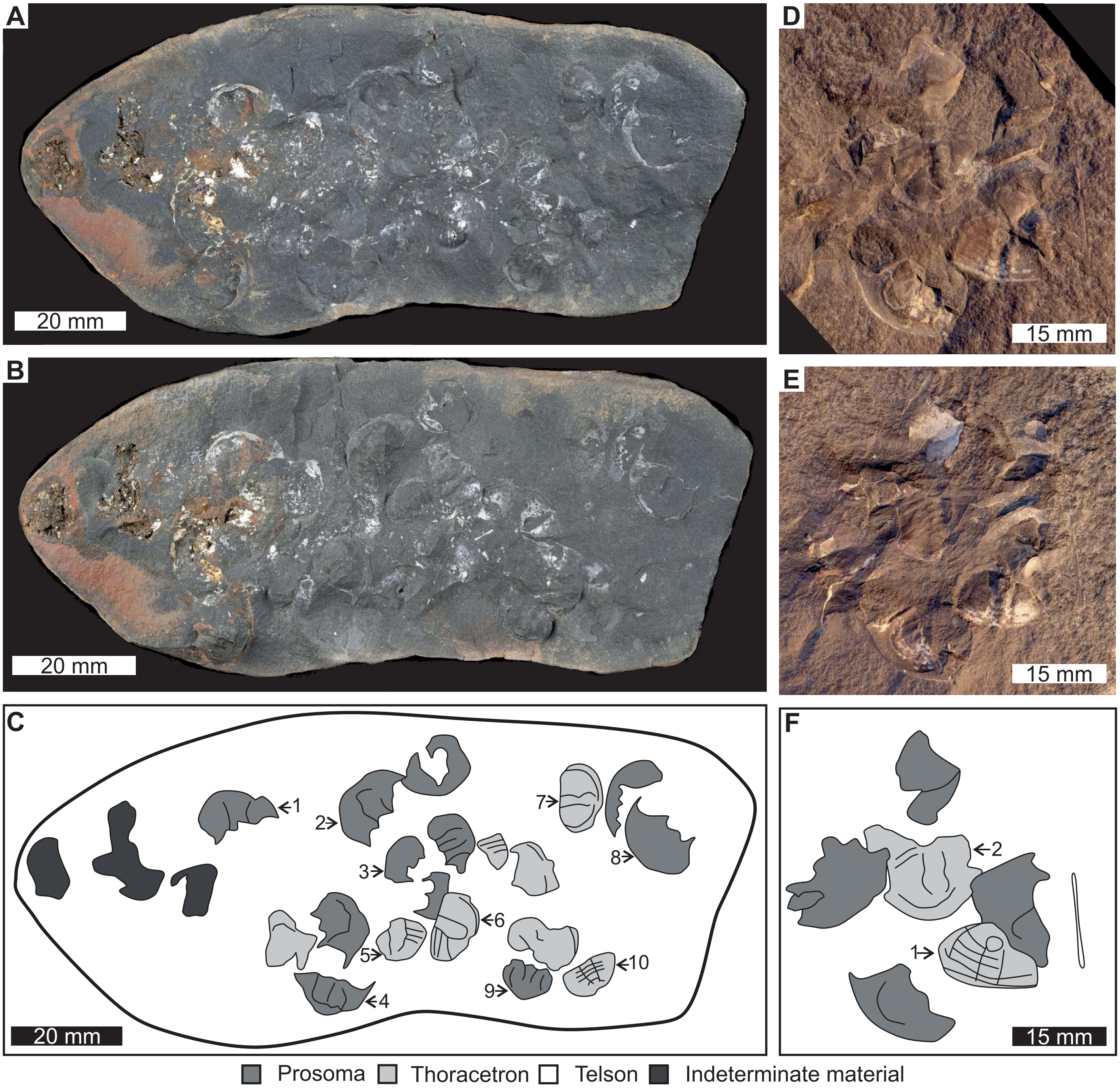

FIG. 2.—Xiphosurid-rich regurgitalites from the Mazon Creek *Lagerstätte*. **A–C**) Specimen from Pit 9; sample numbers (A, B), LF 7282 N, LF 7282 P, respectively. View C is a line drawing of A showing fragmented sections. **D–F**) Specimen from Pit 1; sample numbers (D, E): LF 7283 P, LF 7283 N. View 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.

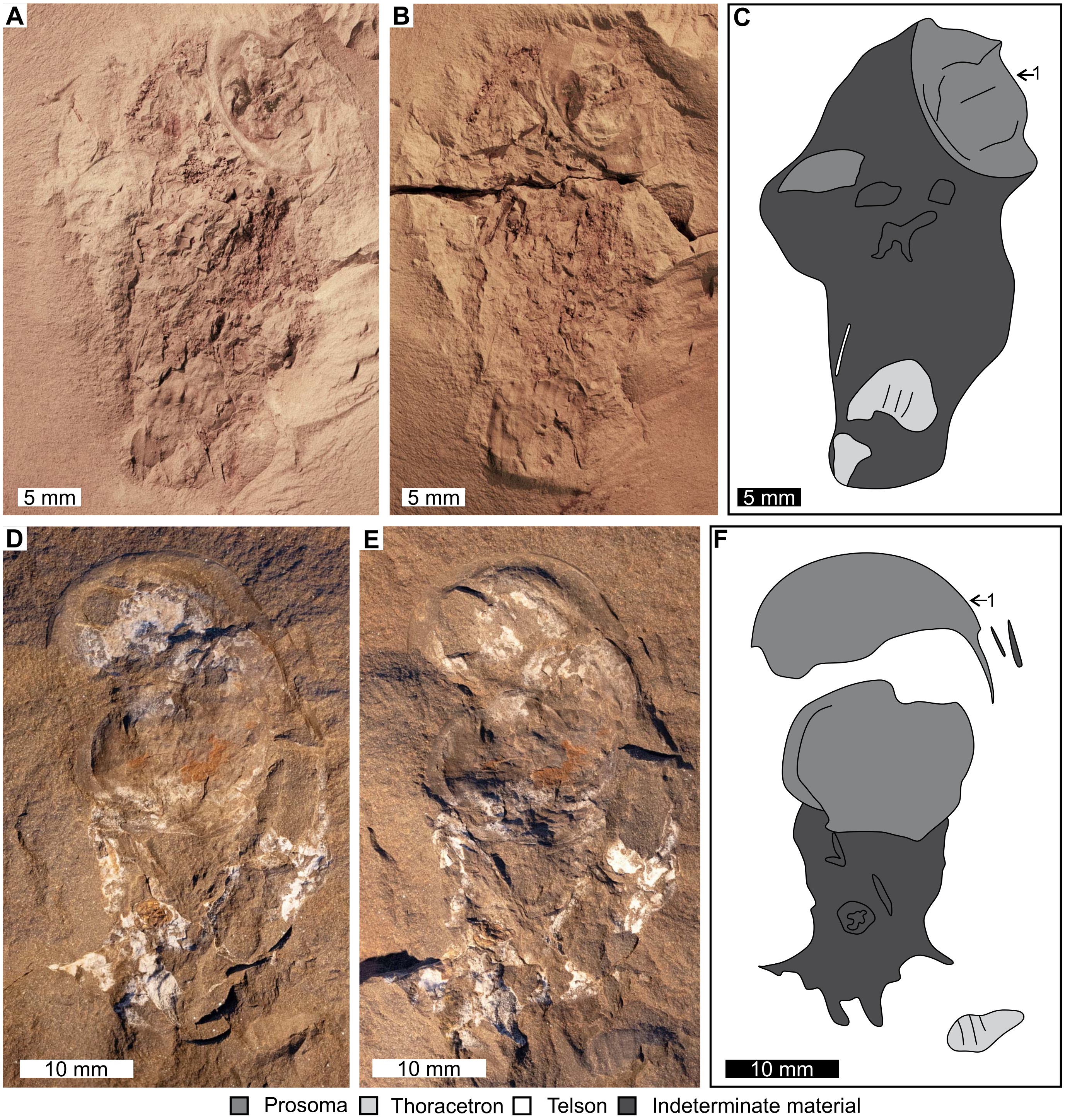

FIG. 3.—Additional xiphosurid-rich regurgitalites from the Mazon Creek Lagerstätte. **A–C**) Specimen from Morocco Mine, sample numbers (A, B): LF 7284 N, LF 7284 P, respectively. C is a line drawing of A showing fragments. **D–F**) Specimen from Pit 2; sample numbers (D, E): LF 7285 N, LF 7285 P, respectively. 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

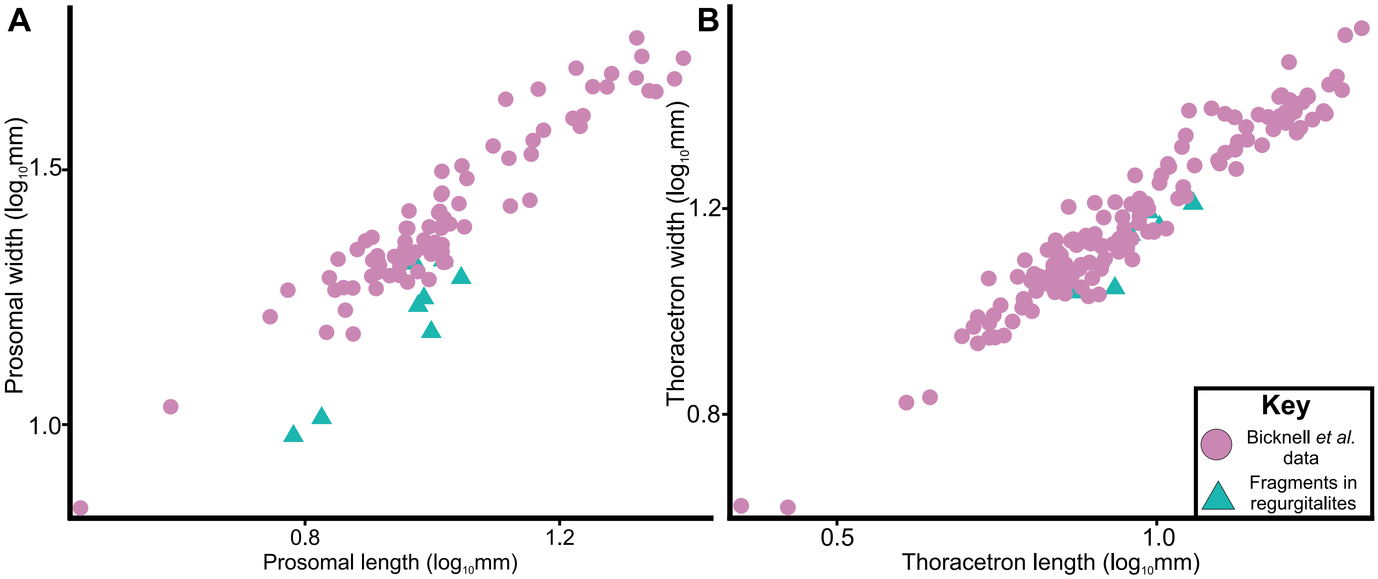

FIG. 4.—Measurements of Mazon Creek *Euproops danae* specimens from Bicknell et al. (2022b) and exoskeletal fragments within regurgitalites. Data are $\log_{10}$ normalized. **A**) Prosomal measurements. **B**) Thoracetronic measurements.

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; Brachaniec 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.

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SUPPLEMENTAL MATERIAL

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

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