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A unique example of the Late Cretaceous horseshoe crab *Tachypleus syriacus* preserves transitional bromalites

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ABSTRACT

Bromalites are the group of ichnofossils that record the consumption, processing, and elimination of material through digestive systems. Each main stage of processing has been ascribed to distinct bromalite subgroups, such as cololites, coprolites, and regurgitalites, with little evidence for transitions between these stages. To expand this limited record, we consider a fossil horseshoe crab—*Tachypleus syriacus*—from the Cenomanian Hjoula Lagerstätte (Sannine Formation, Lebanon) that showcases one such transition. The specimen illustrates a bromalite both within the animal's guts (cololite) and as expelled faecal matter (coprolite). This demonstrates a link between these two conditions for fossil chelicerates and highlights the level of exceptional preservation within the Hjoula Lagerstätte. Additionally, the specimen features prosomal nodules unique to limulids, suggesting new automorphic morphologies for *T. syriacus*.

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BROMALITES—the broad ichnofossil group that includes gut contents and prior gut contents—are useful fossils for understanding the diets and digestion processes of extinct animals (Knaust 2020). These traces have been categorized according to different stages of digestion (Hunt *et al.* 2012). Two groups that are especially useful within the arthropod fossil record are cololites and coprolites. Cololites (*sensu* Agassiz, 1833) are evidence of fossil digested food within the gastrointestinal tract posterior to the stomach (Kraft *et al.* 2023), while coprolites (*sensu* Buckland 1829) are fossil faecal material eliminated from the body (Häntzschel *et al.* 1968, Hunt *et al.* 2012). While coprolites can be linked to probable producers (Häntzschel *et al.* 1968, Kimmig & Strotz 2017, Kimmig & Pratt 2018), the majority of trace

makers are unknown. Furthermore, the fossil record linking the two trace fossil groups together is very limited. To date, there are rare unpublished examples of insects in amber showing this association, and one published roach in Cretaceous amber showing a bromalite traversing the anus (Hinkelman & Vršanská 2020). Here, we expand the record of these transitional trace fossils by examining a fossil horseshoe crab (Xiphosurida)—*Tachypleus syriacus* (Woodward, 1879)—from the Hjoula Lagerstätte of Lebanon that preserves a cololite transitioning into a coprolite.

Geological setting

The late Cenomanian Lebanese marine fossil-fish locality at Hjoula (Arabic: حججول) belongs to the Sannine Formation facies configuration (Nader *et al.* 2006) and is situated within the Byblos Governorate of Mount Lebanon in Central Lebanon. Precise palaeolatitude calculations (www.paleolatitude.org; van Hinsbergen *et al.* 2015) place the Hjoula limestone quarry at an average 14.36°N equatorial position within the 90-million-year age bracket. During

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the time of deposition, Lebanon formed part of the African platform at the northern frontiers of the Gondwana supercontinent (Philip *et al.* 1993). The fossiliferous rock units at Hjoula are recognized as a Konservat Lagerstätten producing rich assemblages of exceptionally well-preserved teleost fishes, cartilaginous fishes, cyclostomes, pterosaurs, and numerous invertebrate groups (Parry *et al.* 2015, Marramà *et al.* 2016, Bicknell *et al.* 2019a, Kellner *et al.* 2019, Miyashita *et al.* 2019, Klug *et al.* 2021). The laminated limestones of Hjoula were laid down under anoxic conditions in a confined, tectonically active carbonate basin (Hemleben 1977, Swinburne & Hemleben 1994, Wippich & Lehmann 2004).

Materials and methods

The *Tachypleus syriacus* fossil, AMNH-IF 141422, was found in 2020 at a quarry in Hjoula at 34°07'59.8" N 35°44'37.9" E. AMNH-IF 141422 was prepared and partially exposed using a pneumatic tool. Due to breakage along a calcite vein, the specimen has been repaired with a Paraloid B-72 adhesive solution. The viscosity of the adhesive was modified by adjusting the polymer concentration to 50% and dissolving in acetone solution (Koob 1986). The adhesive was applied systematically in intervals to restructure the void which contained the calcite vein. Measurements of AMNH-IF 141422 were made using digital calipers. However, due to the partly exposed nature of the carapace, measurements represent minimal (incomplete) values. Images of AMNH-IF 141422 were made under normal LED light using an Olympus E-M1MarkIII. For comparison, a fresh horseshoe crab scat was collected from a living *Limulus polyphemus* specimen in captivity.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA.

Results

AMNH-IF 141422 is a female *Tachypleus syriacus* individual (Lamsdell & McKenzie 2015) consisting of a partial prosoma that shows a doublure (92.9 mm long, 131.4 mm wide) and partial thoracetrone (34.6 mm long, 81.2 mm wide) (Fig. 1A). The gut is preserved as a mould and is a 18.22 mm long section (Fig. 1B). The posterior-most section of the gut shows marked relief, and is 12.13 mm long, 5.66 mm wide

anteriorly, tapering to 2.91 mm wide posteriorly. At the posterior-most point of the gut, an amorphous, sinuous structure is observed (Fig. 1B). This sinuous structure is 18.6 mm long, showing marked disaggregation distally from the body fossil. Shelly material is identified within the sinuous structure, although the exact nature of these fragments is indeterminate.

The prosomal rim is exceptionally preserved and shows unique taxonomic characteristics for *T. syriacus*. These are nodules along the rim proximal to the external margin (Fig. 1C). The nodules are 10.78–27.29 mm apart and more prevalent on the right side.

Discussion

The gut section along the thoracetrone midline in AMNH-IF 141422 is comparable to previously documented horseshoe crab cololites (Table 1). As such, we confidently consider this structure a cololite. Furthermore, the sinuous structure at the terminus of the bromolite, where the xiphosurid anus is located, is comparable to expelled modern horseshoe crab faeces (Bicknell *et al.* 2022a; compare Fig. 1B, D). We therefore conclude that this sinuous structure is a coprolite. Taken together, we propose that AMNH-IF 141422 represents a transitional horseshoe crab bromolite. Moreover, the coprolite shows evidence of shelly material (Fig. 1B), confirming the hypotheses that ancient xiphosurids had diets comparable to modern forms (Bicknell *et al.* 2019a), and processed shelly material using walking and pushing legs (Bicknell *et al.* 2018a, 2018b, 2021b).

The digestive tract of a horseshoe crab is a simple chitin-lined tube, subdivided into several regions (Botton *et al.* 2003). The oesophagus connects the mouth to the muscular proventriculus (gizzard), which is lined with thick ridges of chitin that macerate material. Distally, the food, often mixed with residual sediment and shell matter, is passed through the pyloric valve into the linear, non-convoluted intestine for enzymatic digestion and absorption. The faecal material is encased in mucus, and eliminated at the anus, located ventrally to the telson.

Horseshoe crabs feed on a variety of benthic organisms, such as molluscs, crustaceans, echinoderms and polychaetes (Botton 1984, Botton & Haskin 1984, Botton & Ropes 1989, Debnath *et al.* 1989, Chatterji *et al.* 1992, Razak *et al.* 2017). The consumption of ambient sediment particles is customary when the animals ingest their prey, and crushed shell debris and sediment are commonly found in the faecal material of extant limulids (Botton 1984). Thus,

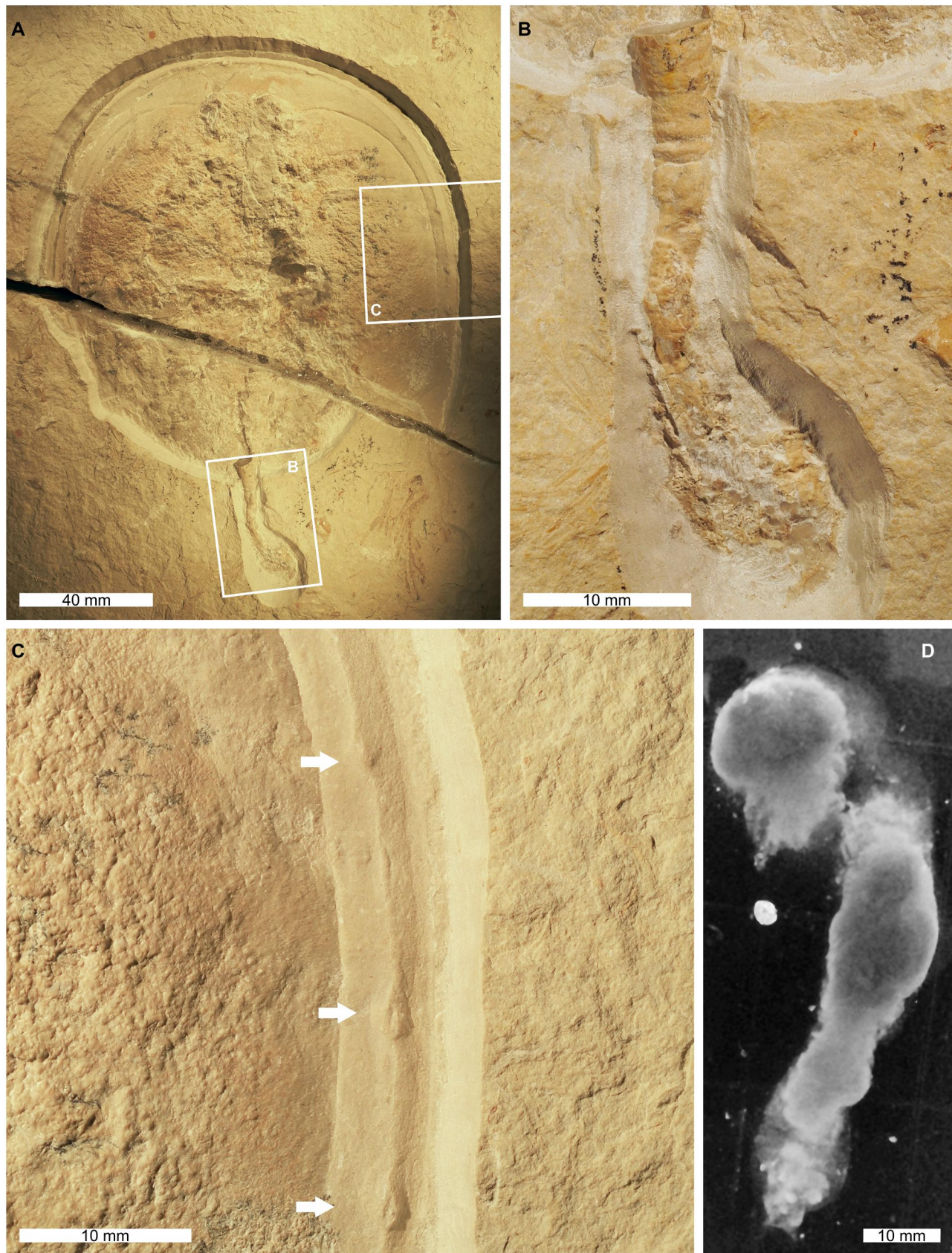


Fig. 1. Examined *Tachypleus syriacus* with a cololite transitioning to a coprolite and modern xiphosurid scat. **A,** Complete specimen, AMNH-IF 141422. **B,** Close up of cololite transitioning to coprolite. **C,** Close up of prosomal border showing nodules (white arrows). **D,** Example of modern xiphosurid scat, morphologically comparable to observed coprolite.

Table 1. Summary of previously documented xiphosuran cololites. Ordered by time period and higher taxonomic assignment following Bicknell & Pates (2020) and Lamsdell (2020).

| Taxon | Family | Formation | Age | Reference |
|---|-----------------|--|------------------------------|---|
| <i>Pickettia carteri</i> (Eller, 1940) | Kasibelinuridae | Cattaraugus Formation, Pennsylvania, USA | Late Devonian (Fammenian) | Bicknell <i>et al.</i> (2019b, fig. 1A, E) |
| <i>Paleolimulus mazonensis</i> Bicknell, Naugolnykh & McKenzie, 2022b | Paleolimulidae | Mazon Creek Konservat Lagerstätte, Carbondale Formation, Illinois, USA | Pennsylvanian (Moscovian) | Bicknell <i>et al.</i> (2022b, fig. 3C, D, 5C0) |
| <i>Tachypleus syriacus</i> | Limulidae | Sannine Formation, Lebanon | Late Cretaceous (Cenomanian) | Bicknell <i>et al.</i> (2019a, fig. 2, 3d) |
| <i>Tachypleus syriacus</i> | Limulidae | Sannine Formation, Lebanon | Late Cretaceous (Cenomanian) | This work |

we regard the shelly material and sediment in the observed bromalite as typical horseshoe crab feeding behaviour.

AMNH-IF 141422 expands the limited evidence of horseshoe crab cololites that range from the Late Devonian through to the Cenomanian (Table 1). At least four of these examples demonstrate cololites with relief compared to the fossil (Bicknell *et al.* 2019b, figs 1A, E; Bicknell *et al.* 2019a, figs 2, 3d; Fig. 1B). This relief suggests that the gut was likely infilled with sediment, reflecting the condition where modern horseshoe crabs consume and pass sediment through their gut while foraging (Botton & Haskin 1984, Carmichael *et al.* 2004). We can therefore infer that extinct horseshoe crabs may have consumed sediment as a byproduct of scavenging or predation. However, as we cannot confidently rule out post-mortem sediment infilling, we are tentative in this proposal.

Modern horseshoe crab faecal material decomposes quickly in the marine environment (Cuomo, pers. obs.). The preservation of horseshoe crab coprolites is therefore expected to be rare. Alternatively, these fossils have been documented in exceptional preservation conditions, but are not associated with xiphosurid body fossils. In either case, this area of research should be expanded to further understand these important ichnofossils.

Useful frameworks for documenting and interpreting vertebrate bromalites have been presented (Hunt *et al.* 2012, fig. 1; Prikryl *et al.* 2012; Hunt & Lucas 2021). These can also be applied to arthropod bromalites (Knaust, 2020; Bicknell *et al.* 2023, Bicknell *et al.* 2024). Despite this research, no term has been presented to describe transitional bromalites. Therefore, the trace fossil presented here is simultaneously a cololite proximally and a coprolite distally.

Prosomal nodules observed on AMNH-IF 141422 are unique within Limulidae (Bicknell *et al.* 2021a). Furthermore, they have not previously been noted on *Tachypleus syriacus* prosomae (Woodward 1879, Lamsdell & McKenzie 2015, Bicknell *et al.* 2019a). As such, these structures may represent a novel

autapomorphy for the species. The palaeobiological implications for these nodules are also interesting to consider. Nodules in Limulidae are commonly associated with dorsal spines, including in *T. syriacus* (see Lamsdell & McKenzie 2015). However, adult xiphosurids lack spines along the anterior and lateral prosomal margin (see Bicknell & Pates 2020, Lamsdell 2020). These nodules must therefore have had another use. One possibility is that they represent a sensory structure. Juvenile horseshoe crabs have sensory mechanoreceptors along the prosomal margin (Fornshell 2022). However, these structures are lost through ontogeny (Fornshell 2022). In *T. syriacus*, modified sensory mechanoreceptors may have been retained, producing these nodules, although it is impossible to state if these were functional or vestigial. Alternatively, these morphologies may be associated with the sexually dimorphic nature of the species (Lamsdell & McKenzie 2015). However, the exact use remains unknown.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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