

Late Cretaceous marine arthropods relied on terrestrial organic matter as a food source: Geochemical evidence from the Coon Creek Lagerstätte in the Mississippi Embayment

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Abstract

The Upper Cretaceous Coon Creek Lagerstätte of Tennessee, USA, is known for its extremely well-preserved mollusks and decapod crustaceans. However, the depositional environment of this unit, particularly its distance to the shoreline, has long been equivocal. To better constrain the coastal proximity of the Coon Creek Formation, we carried out a multiproxy geochemical analysis of fossil decapod (crab, mud shrimp) cuticle and associated sediment from the type section. Elemental analysis and Raman spectroscopy confirmed the presence of kerogenized carbon in the crabs and mud shrimp; carbon isotope ($\delta^{13}\text{C}$) analysis of bulk decapod cuticle yielded similar mean $\delta^{13}\text{C}$ values for both taxa (-25.1% and -26% , respectively). Sedimentary biomarkers were composed of *n*-alkanes from C_{16} to C_{36} , with the short-chain *n*-alkanes dominating, as well as other biomarkers (pristane, phytane, hopanes). Raman spectra and biomarker thermal maturity indices suggest that the Coon Creek Formation sediments are immature, which supports retention of unaltered, biogenic isotopic signals in the fossil organic carbon remains. Using our isotopic results and published calcium carbonate $\delta^{13}\text{C}$ values, we modeled carbon isotope values of carbon sources in the Coon Creek Formation, including potential marine (phytoplankton) and terrestrial (plant) dietary sources. Coon Creek Formation decapod $\delta^{13}\text{C}$ values fall closer to those estimated for terrigenous plants than marine phytoplankton, indicating that these organisms were feeding primarily on terrigenous organic matter. From this model, we infer that the Coon Creek Formation experienced significant terrigenous organic matter input via a freshwater source and thus was deposited in a shallow, nearshore marine environment proximal to the shoreline. This study helps refine the paleoecology of nearshore settings in the Mississippi Embayment during the global climatic shift in the late Campanian–early Maastrichtian and demonstrates for the first time that organic $\delta^{13}\text{C}$ signatures in exceptionally preserved fossil marine arthropods are a viable proxy for use in paleoenvironmental reconstructions.

1 | INTRODUCTION

The Late Cretaceous represents a time of dramatic climatic and environmental perturbations (Norris & Bice, 2002). Following the Cretaceous Thermal Maximum, there was a global shift toward intense global cooling in the mid-Campanian that continued through

the earliest Maastrichtian (Huber, Norris, & Macleod, 2002; Tabor et al., 2016). Although the climatic trend during this interval is well-established, its potential impact on nearshore marine biota is not fully known. North American epicontinental seas were zones of high diversity during the Late Cretaceous (Lagomarcino & Miller, 2012) and thus represent ideal sites for characterizing ecological changes in

shallow marine settings. However, paleoecological analyses in these settings have been restricted by poor understanding of depositional environments in the inland and marginal nearshore regions of the continent. The inland Western Interior Seaway has undergone extensive geochemical analysis (e.g., Cochran, Landman, Turekian, Michard, & Schrag, 2003; Coulson, Kohn, & Barrick, 2011), but paleoenvironmental interpretations remain equivocal because of unusual water column stratification. The Mississippi Embayment represents the southeastern margin of the Western Interior Seaway, but it was formed under largely normal marine conditions (Russell & Parks, 1975) and has the potential to provide environmental data for nearshore marine settings during the late Campanian–early Maastrichtian. However, critical details, such as proximity to the shoreline, remain uncertain in some biologically rich units in the embayment, which limits our understanding of environmental dynamics and their potential influence on shallow marine biota in this region.

One such unit is the Coon Creek Formation of western Tennessee and northern Mississippi (Figure 1). The type section, near Enville, Tennessee, has long been recognized as a site of exceptional fossil preservation (Lagerstätte) and yields some of the best preserved late Mesozoic molluscan and decapod remains in the world (Bishop, 1983, 1986; Bishop & Williams, 2005; Ebersole, 2009; Gibson & Dunagan, 2003; Moore, 1974; Wade, 1926). The shells of molluscan fauna are typically pristine, retaining their original aragonitic composition, and fully articulated crab exoskeletons are common (Bishop, 1983, 2016; Lowenstam & Epstein, 1954; Weiner, Lowenstam, & Hood, 1976; Zakharov et al., 2006; Zakharov, Tanabe, Safronov, Popov, & Smyshlyayeva, 2014). Despite the extensive faunal studies, the depositional setting of the Coon Creek Lagerstätte remains unresolved: interpreted environments vary widely, from terrestrially dominated to open marine, and inferred paleodepth is poorly constrained, with estimates ranging from ~10 to 200 m (Ebersole, 2009; Landman, Kennedy, Cobban, & Larson, 2010; Stringer, 2016).

The lack of agreement among Coon Creek environment studies may result from challenges in applying traditional methods to this particular system. Biogeochemical analyses of preserved organic remains have not yet been used in this setting but could potentially provide additional information for inferring the paleoenvironment (Briggs & Summons, 2014). For example, recent studies have shown that stable isotope analysis of organic fossil remains, such as arthropod cuticle, and entombing sediments from marine settings can be used to characterize burial conditions and the chemotaphonomy of organic matter, and even organismal paleoecology (Melendez, Grice, & Schwark, 2013; Melendez, Grice, Trinajstić et al., 2013; Plet et al., 2016).

In the Coon Creek Formation, decapod cuticle, and specifically chitin, represents a possible substrate for biogeochemical analysis. Chitin is a structural biopolymer found in numerous phyla, including within the exoskeletons of all modern arthropods (Muzzarelli, 1977). This biomolecule is second only to cellulose in terms of abundance in the modern global ecosphere, but generally rare in the fossil record (Cody et al., 2011; Ehrlich et al., 2013; Flannery, Stott, Briggs, & Evershed, 2001; Gupta, Tetlie, Briggs, & Pancost, 2007; Schimmelman et al., 1986; Stankiewicz, Briggs, Evershed, & Duncan, 1997; Stankiewicz, Briggs, Evershed, Flannery, & Wuttke, 1997; Weaver et al., 2011). This is because, under normal marine conditions, chitin is rapidly degraded and mineralized (usually within days to weeks), limiting its potential for long-term preservation (Allison, 1990; Boyer, 1994; Gooday, 1990; Kirchman & White, 1999; Perga, 2011; Poulicek, Gail, & Goffinet, 1998; Poulicek & Jeuniaux, 1991; Seki, 1966; Seki & Taga, 1963b; Sturz & Robinson, 1986). However, when chitin is preserved, it has the potential to provide isotopic signatures that can be used for paleoecological and paleoenvironmental reconstruction (Miller, Fritz, & Morgan, 1988; Schimmelman et al., 1986). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values in the α -chitin polymorph in arthropod exoskeletal cuticle reflect diet and trophic level (Schimmelman & Deniro, 1986b), while oxygen ($\delta^{18}\text{O}$) and hydrogen ($\delta^2\text{H}$) isotopes can be used as

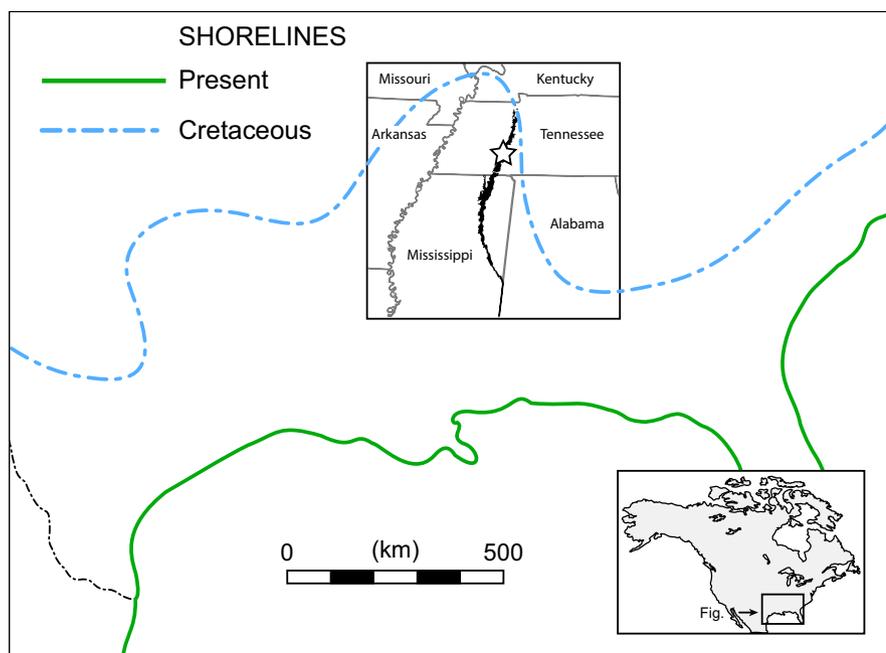


FIGURE 1 Regional map for the Mississippi Embayment and study area. Black area represents surface exposures of the Upper Cretaceous Coon Creek Formation; star marks the type section, near Enville, Tennessee, where all specimens were obtained for this study. Map modified from NOAA (2004) and Ebersole (2009)

temperature and salinity proxies (Miller et al., 1988; Nielson & Bowen, 2010; Schimmelmann & Deniro, 1986c; Wang, O'Brien, Jenson, Francis, & Wooller, 2009). In a marine setting, dietary $\delta^{13}\text{C}$ values can also provide information on relative terrigenous organic matter input and thus distance to shore (Schimmelmann & Deniro, 1986b).

To date, the use of stable isotope signatures in arthropod remains for paleoecological and paleoenvironmental reconstruction has largely been limited to Holocene-age subfossils from terrestrially dominated aquatic settings (Hodgins, Thorpe, Coope, & Hedges, 2006; Hood-Nowotny & Knols, 2007; Perga, 2010; Verbruggen, Heiri, Reichart, Blaga, & Lotter, 2011; Wang et al., 2009; Wooller, Wang, & Axford, 2008; but see Schweizer, Wooller, Toporski, Fogel, & Steele, 2006; Schweizer, Steele, Toporski, & Fogel, 2007). The use of these signatures within marine environments in deep time has not been previously investigated. Nevertheless, if fossil chitin is present in the Coon Creek Lagerstätte, it has the potential to provide information about this enigmatic setting. In this study, we investigated the viability of biogenic stable isotope signatures in fossil chitin and their ability to track input of terrestrial organic matter to the Coon Creek Formation by performing: (i) bulk stable carbon isotope analysis and Raman spectroscopy of fossil decapod cuticle, (ii) biomarker composition analysis of associated sediment, and (iii) compound-specific stable isotope analysis of sedimentary *n*-alkanes. Using new and previously published $\delta^{13}\text{C}$ values, we develop a model of the Coon Creek Lagerstätte carbon isotope system, from which the diet of the decapod fauna is inferred and the shoreline proximity of the Coon Creek Formation is assessed.

2 | GEOLOGY AND PALEONTOLOGY

The Upper Cretaceous (upper Campanian or lower Maastrichtian) Coon Creek Formation is exposed from west-central Tennessee through eastern Mississippi, within the northern to northeastern end of the Mississippi Embayment, USA (Gibson & Dunagan, 2003; Figure 1). The Coon Creek beds were originally designated as a member of the Ripley Formation by Wade (1926), but Hardeman, Miller, and Swingle (1966) later elevated the unit to formation rank in Tennessee where it is bounded by the underlying Demopolis Chalk and overlying McNairy Sand formations. The Coon Creek Formation is informally subdivided into lower and upper members based on lithofacies (Russell & Parks, 1975). At the type section in Enville, Tennessee, where only the lower member is exposed, the sediment is primarily composed of massively bedded and lightly cemented, fine-medium grained dark gray to green micaceous and glauconitic clayey sand or silts, with interbedded sideritic, phosphatic, and calcitic concretions, and fossil assemblages (Gibson & Dunagan, 2003; Moore, 1974; Rhenberg, 2007; Russell & Parks, 1975). Fossils occur throughout the type section, but the most fossil-rich and diverse Lagerstätte beds occur at the base of the exposure (Wade, 1926).

Various index fossil and isotope data suggest either a late Campanian or early Maastrichtian age for the Coon Creek Formation. The presence of the oyster *Exogyra costata* was traditionally used to assign an early Maastrichtian age to units in the Gulf Coastal Plain

(Stephenson, 1933), including the Coon Creek Formation. This taxon has since been found in upper Campanian units elsewhere, however, and is now considered to be of limited use as an index species in this region (Ebersole, 2009). Palynological studies across the upper Campanian–lower Maastrichtian boundary have dated the Coon Creek Formation as late Campanian based on angiosperm pollen (e.g., Tschudy, 1975; Wolfe, 1976), but the presence of certain palynomorph taxa (e.g., *Holkopollenites chemardensis*, *Cordosphaeridium*) may suggest that an early Maastrichtian age is more appropriate (Baghai-Riding, Kelley, & Swann, 2016). Ammonite zonation at the type section constrains the age of the lower half of the formation to the latest Campanian, and specifically to 72–71.5 Myr (Larson, 2012, 2016). However, carbon isotope stratigraphic dating places the Campanian–Maastrichtian boundary age at 72.1 ± 0.1 Ma (Voigt, Gale, Jung, & Jenkyns, 2012), which would appear to suggest that either the lower Coon Creek Formation should be placed in the early Maastrichtian or that the age range estimated from ammonite zonation is incorrect.

The Coon Creek Formation contains a wide range of invertebrate and vertebrate taxa, including an extremely abundant and well-preserved molluscan fauna (Brister & Young, 2007; Cobban & Kennedy, 1994; Ebersole, 2009; Gibson & Dunagan, 2003; Landman et al., 2010; Larson, 2012, 2016; Rhenberg, 2007; Wade, 1926) and one of the best records of Late Cretaceous decapods presently known (Bishop, 1983, 1986, 2016; for recent studies on other Coon Creek fauna, see Ehret, Harrell, & Ebersole, 2016). The decapod assemblage includes brachyuran crabs, lobsters and crayfish, and mud shrimp (Bishop, 1983, 2003; Brister & Young, 2007; Moore, 1974; Wade, 1926), and is taxonomically similar to decapod assemblages from correlative units elsewhere in North America (Bishop, 2016; Kornecki, 2014; Moore, 1974). Moving south from Tennessee to Mississippi, the Coon Creek Lagerstätte beds are absent, and the molluscan assemblage becomes increasingly depauperate and poorly preserved, but well-preserved decapod remains are still found in abundance (Bishop, 1983, 2016; Ebersole, 2009; Kornecki, 2014).

Coon Creek crabs occur in thin, laterally extensive layers throughout the lower nine meters of the exposure at the type section in Tennessee, but crab-bearing horizons, including those that produce whole animals, are more abundant within the primary Lagerstätte bed at the base of the exposure (Ebersole, 2016; Moore, 1974; M. A. Gibson, pers. comm., 2017). Whole, fully articulated crabs—some in life position—are common, as are disarticulated carapaces and isolated appendages. Mud shrimp are almost entirely preserved as isolated clawed appendages and appear to be closely associated with crab-bearing beds in the Coon Creek Formation of Mississippi (Bishop, 2016); however, they are rarely found in situ at the type section in Tennessee, limiting identification of their source horizon. Based on associated matrix, mud shrimp float specimens are thought to originate in one of the two fossiliferous beds at the base of the type section (M.A. Gibson, pers. comm., 2017). The presence of small concretions around some mud shrimp may indicate that specimens originated from a concretion-bearing horizon approximately one meter above the primary Lagerstätte bed, where crabs are less prolific (Gibson & Dunagan, 2003). If any stratigraphic separation between the crab and mud shrimp-bearing facies is present,

however, it appears to be very minor; the two fossiliferous beds at the base of the type section grade into each other and are often sedimentologically indistinguishable (Gibson & Dunagan, 2003).

2.1 | Depositional setting

The depositional setting of the Coon Creek Formation has long been subject to debate. Past interpretations include a deep to shallow mixing zone, marine shelf, shallow and low-energy nearshore marine environment, the front of a delta platform, freshwater marsh, and hypersaline estuary (Lobegeier & Lusk, 2008; Moore, 1974; Pryor, 1960; Russell & Parks, 1975; Self, 2003; Wade, 1926). Recent studies of the Coon Creek fauna (e.g., Ehret et al., 2016) largely agree that the unit was a marine-dominated setting. Likewise, isotope geochemistry studies of the Coon Creek molluskan fauna consistently support a marine-dominated interpretation (Keller et al., 2006; Lowenstam & Epstein, 1954; Weiner et al., 1976; Zakharov et al., 2006, 2014). Although terrestrial plants occur in the formation, they are locally rare and of limited diversity (Berry, 1925; Dilcher, 2016).

Yet despite a growing consensus on a marine depositional setting for the Coon Creek Formation, paleodepth and distance to shore remain unclear; estimates vary widely based on paleoecological interpretations. Analysis of the Coon Creek bony fish fauna only provides limited depth constraint (shallower than outer shelf, i.e., <200 m; Stringer, 2016), and the interpreted ecology of the ammonite fauna suggests a depth of <100 m (Landman, Cobban, & Larson, 2012). In contrast, comparison of the extant component of the formation's bivalve fauna to that of modern nearshore marine settings provides strong evidence that the unit was deposited at a very shallow depth (<10 m; Ebersole, 2009, 2016). Similarly, Moore (1974) and Bishop (2016) suggested that Coon Creek crabs inhabited an intertidal zone.

2.2 | Taphonomy

Well-preserved Coon Creek Formation mollusks and crustaceans are found both free in the matrix and in concretions (Bishop, 1983, 2016; Ebersole, 2016; Kornecki, 2014; Sohl, 1960). Mollusks often retain their original iridescence, and geochemical analyses of various non-concretionary molluskan taxa indicate that their original aragonitic composition is preserved (Lowenstam & Epstein, 1954; Weiner et al., 1976; Zakharov et al., 2006, 2014). Bishop (1986) suggested that, qualitatively, non-concretionary Coon Creek crustaceans were virtually unaltered, and at least one crab specimen has been found with visible color markings (Kesling & Reimann, 1957). However, subsequent geochemical analyses of the decapods have shown that exoskeletal organic remains are kerogenized, have reduced organic carbon and nitrogen content, and contain evidence for phosphatization (Kornecki, 2014; Schimmelman, Krause, & Deniro, 1988). Evidence for silica and aluminum replacement of the outer cuticle was also noted on some Coon Creek decapod specimens, but this was attributed to surficial weathering of phosphatized remains into clay (Kornecki, 2014).

In contrast to the extensive studies of the Coon Creek fauna, there has been relatively little investigation of the environmental controls on

the Lagerstätte's formation (Ebersole, 2016; Gibson & Dunagan, 2003). Russell and Parks (1975) and Ebersole (2009) noted the presence of relict cross-bedded sand lenses from the overlying McNairy Formation at several Coon Creek Formation localities. Ebersole (2016) concluded that these lenses are evidence that the Coon Creek Lagerstätte was deposited behind protective back-bars or barrier islands. Sedimentary evidence for cyclic storm-driven sedimentation is found in the Coon Creek Formation in both Tennessee and Mississippi (Self, 2003). However, in the latter region there is no evidence for barrier structures, and preservation of the molluskan fauna is significantly reduced (Bishop, 1983; Kornecki, 2014). S. E. Ebersole (pers. comm., 2014) suggested that the effects of storm currents were reduced in the Lagerstätte beds in Tennessee because of their position behind a protective barrier, and that this increased faunal preservation potential there.

Sedimentation rate and rapid internment are also thought to have played a significant role in the preservation of the largely unaltered Coon Creek Lagerstätte fauna (Gibson & Dunagan, 2003; Moore, 1974). Mollusk shells, decapod exoskeletons, and burrows in the Coon Creek Lagerstätte beds lack any evidence for compaction (Gibson & Dunagan, 2003). The absence of distortion has been taken to indicate that organisms were buried rapidly, underwent little post-burial exhumation or disturbance, and were not subsequently subjected to extensive post-Cretaceous sedimentary overburden (Cushing, Boswell, & Hosman, 1964; Gibson & Dunagan, 2003; Moore, 1974).

Following burial, Coon Creek sediment composition appears to have played a role in long-term preservation of fossil remains. Kaolinite and illite are low-swell/expansion clays (Moore & Reynolds, 1989), and large amounts of both clay types have been noted in Coon Creek Formation sediments (Ebersole, 2016; Kornecki, 2014). In Tennessee, these clays comprise, on average, 30% of the total sediment composition (~15% illite, ~15% kaolinite; Ebersole, 2016). At the Blue Springs locality in Mississippi, clays comprise up to ~48% of the total sediment composition (Kornecki, 2014). S. E. Ebersole (pers. comm., 2014) suggested that the low expansion-contraction quality of these clays after burial and deposition in a low-energy back-bar setting were the two primary drivers of the excellent preservation in the Coon Creek Lagerstätte beds in Tennessee. This hypothesis is supported in part by recent experiments that show that decay of soft and non-mineralized tissues and decay bacteria growth are reduced in illite and kaolinite, compared to other sediments (McMahon, Anderson, Saupe, & Briggs, 2016; Wilson & Butterfield, 2014).

3 | MATERIALS AND METHODS

All specimens and sediment sampled in this study come from the lower member of the Coon Creek Formation type section adjacent to the Coon Creek Science Center, 1.6 km south of Enville, Tennessee (35°20'10.8"N/88°25'50.4"W). Specimens were either collected in situ at the type locality or obtained from the Pink Palace Museum (Memphis, Tennessee) and the Geier Collections and Research Center (Cincinnati, Ohio) collections. We sampled the two most common decapod taxa from the formation in Tennessee: the brachyuran crab, *Avitelmessus*

grapsoides (Kesling & Reimann, 1957), and the mud shrimp, *Mesostylus* (= *Protocallianassa*) *mortoni* (Schweitzer & Feldmann, 2012; Figure 2). Only non-concretionary specimens were sampled. For mud shrimp, we sampled chelipeds (clawed appendages) and isolated chelae (claws), which are the most common body parts found at the type section. Chelipeds and chelae are also the most common body parts for crabs in the Coon Creek Formation, but some specimens occur partially or fully articulated; hence, we sampled a combination of crab appendages and carapaces from several individuals for stable isotope analyses (see Table 1).

3.1 | Raman spectroscopy

Single specimens of a Coon Creek brachyuran crab and mud shrimp chelae were analyzed at the University of Cincinnati, using a Horiba T64000 Raman spectrometer (Horiba, Inc., Edison, NJ, USA) in single mode with 244-nm laser excitation from a Coherent FreD C Ar+ laser. Sample spots on sediment-free fossil surfaces were located using an attached Olympus BX41 microscope and analyzed with a 40× UV objective (NA = 0.50). The laser was focused to a spot size of ~2 μm and had a power at the sample surface of <1 mW. To avoid alteration of the fossils, spectra were collected in a manner similar to those described by Czaja, Kudryavtsev, and Schopf (2006). Areas were mapped using a 9 × 7-point grid with a spacing of 5 μm, and each point was analyzed for 1 s (two 0.5 s acquisitions were averaged per point). All 63 resulting spectra from each grid were inspected to ensure homogeneity and averaged to increase the signal-to-noise ratio. Sample areas were imaged before and after each analysis, and no evidence of alteration by the laser was detected. Data were

collected and processed using the software program LabSpec (v.5; Horiba, Inc.).

3.2 | Elemental and stable isotope analysis of specimens

3.2.1 | Bulk stable isotope analysis

Fossil decapod samples were prepared following a modified version of the protocol described by Bierstedt, Artur Stankiewicz, Briggs, and Evershed (1998). Specimens were manually liberated from sediment matrix, ground to a fine powder using a mortar and pestle, ultrasonicated in solvent (CH₂Cl₂; four times × 10 min) to remove organic lipids and contaminants, and air-dried. Dried specimens were demineralized using 0.5N HCl, which was gradually added to samples in a 50-ml centrifuge tube until bubbling ceased (15–60 min). Specimens were then rinsed to neutrality with ultrapure water and lyophilized before several milliliters of HCl was reapplied to confirm that all carbonates were removed. Specimens were again rinsed to neutrality with ultrapure water and lyophilized a final time. Coarse, commercially prepared (demineralized) chitin (TCI America) derived from crabs and shrimp was also ball-milled into a very fine, homogenized powder and solvent-rinsed, ultrasonicated, and lyophilized.

Following demineralization and prior to analysis, samples of the prepared fossil material and commercial chitin were weighed according to expected total organic carbon (weight%; TOC) and total organic nitrogen (weight%; TON) composition; this weight was based on published values (Flannery et al., 2001; Schimmelmann, 2011; Schimmelmann et al., 1988) and test samples. For TOC and δ¹³C values, target masses for fossil and modern chitin samples were similar, 1.2 and 1 mg, respectively. For TON, the target masses were ~10–30 mg for fossil samples and 1 mg for commercial chitin, the difference being due to the large difference in weight% C:N ratios between modern isolated chitin (~7:1) compared to fossil decapod remains (>25:1; Schimmelmann & Deniro, 1986a; Schimmelmann et al., 1988). Obtained TOC and TON values were then used to calculate C:N ratios for fossil and commercial chitin samples. The C:N ratio is a useful metric for identifying preservation or loss of organic matter in fossil arthropod exoskeletal material as these values can be compared to those from modern taxa (e.g., Schimmelmann et al., 1988).

All samples were analyzed on a Costech Elemental Analyzer connected to a Thermo Fisher Delta V IRMS via a ConFlo IV in the Stable Isotope Laboratory at the University of Cincinnati. Following analysis, δ¹³C values were calculated using conventional δ notation in per mil (‰) relative to a universal standard (Vienna Pee Dee Belemnite [VPDB]):

$$\delta X_{\text{sample}} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1,000$$

where X is ¹³C, and R is the corresponding ¹³C/¹²C ratio following the guidelines of Coplen et al. (2006) and Coplen (2011). Based on repeated measurements of laboratory standards, analytical precision and accuracy for δ¹³C were ±0.44‰ (1σ, n = 32) and ±0.05‰



FIGURE 2 Photographs of decapods from the Coon Creek Formation of Tennessee. Upper Panel: *Avitelmessus grapsoides*; scale bar = 5 cm. Lower Panel: Partial cheliped (clawed appendage) from *Mesostylus mortoni*; scale bar = 1 cm

($n = 32$), respectively. Minor variability ($\pm 0.2\%$) has been observed in exoskeletal $\delta^{13}\text{C}$ values among body sections of individual modern decapods (Schimmelmann & Deniro, 1986c). For specimens where a combination of cheliped and carapace was sampled, TOC, TON, and $\delta^{13}\text{C}$ values were averaged prior to data analysis. All statistical analyses of decapod isotopic results were performed in the R programming language (R Core Team, 2015).

3.2.2 | Biomarker and compound-specific stable isotope analysis of sediment

To analyze the biomarker composition of sediment from the Coon Creek Lagerstätte, sediment was collected from a non-weathered exposure at the type locality and ground to a powder. Biomarkers were extracted from a single sample of sediment (~ 30 g) using an accelerated solvent extractor (Dionex ASE 350). We used 5:1 (v/v) dichloromethane/methanol with three extraction cycles at 10.34 MPa (1,400 psi) and 100°C. The total lipid extract was purified via asphaltene precipitation and separated into apolar and polar fractions on alumina with 9:1 (v/v) hexanes/dichloromethane and 1:1 dichloromethane/methanol, respectively. The apolar fraction was further separated into saturated and unsaturated fractions on 5% Ag-impregnated silica gel (w/w) with hexanes and ethyl acetate, respectively. Biomarkers were analyzed at the University of Cincinnati on an Agilent 7890A gas chromatograph (GC) and Agilent 5975C quadrupole mass spectrometer and flame ionization detector. Biomarker concentrations are normalized to the grams of sediment extracted (ng/g).

Compound-specific $\delta^{13}\text{C}$ values of the isolated n -alkanes were determined by GC-combustion (C)-IRMS. Samples were analyzed on a Thermo Trace GC Ultra coupled via an IsoLink combustion furnace and Conflo IV open split interfaced to a Thermo Electron Delta V Advantage IRMS. GC conditions were similar to those described earlier. Isotopic abundances were determined relative to a reference gas calibrated with Mix A (Arndt Schimmelmann, Indiana University) and sample size dependency (linearity) monitored with Mix B. Isotopic precision and accuracy, which were determined with co-injected internal standards (n -C₃₈ and n -C₄₁ alkanes) during the course of analyses, are $\pm 0.3\%$ (1σ , $n = 138$) and $\pm 0.2\%$ ($n = 138$), respectively.

Several environmental indices were calculated using the n -alkane composition of Coon Creek sedimentary matrix. The carbon preference index (CPI; Bray & Evans, 1961) is widely used to determine the thermal maturity of source sediments and was calculated from the ratio of straight-chain and odd-numbered n -alkanes in the sediment using the revised calculation of Marzi, Torkelson, and Olson (1993). Maturity was also determined with the homohopane maturity index for the isomerism at C-22 (Peters, Walters, & Moldowan, 2005). The 22S and 22R isomer abundances were measured from 17a, 21b-homohopane (C₃₁) using the m/z 191, 205, and 426 chromatograms. Homohopane maturity indices were calculated using the 22S/(22S + 22R) ratio for each ion to rule out effects from co-elution of closely eluting compounds. In addition, we measured the pristane/phytane ratio, which is often used as an indicator of redox conditions in the depositional environment (Didyk,

Simoneit, Brassell, & Eglinton, 1978; but see Volkman & Maxwell, 1986; ten Haven, De Leeuw, Rullkotter, & Damste, 1987). Ratio values < 1 and > 3 are indicative of reducing or oxidizing environments, respectively.

All statistical analyses for biomarker and non-decapod isotopic results in this section and the following section were performed using JMP Pro 12.1 (SAS, Cary, NC, USA). Where noted, error propagation was completed using the Monte Carlo method to estimate uncertainties. The Monte Carlo simulation was completed assuming normal distributions of the input variables with 5,000 iterations. This was sufficient iterations for the simulation mean to differ from the exact solution by $< 0.05\%$ and for the standard error of the mean to be $< 0.1\%$.

3.3 | Calculation of carbon sources and fluxes in the Coon Creek environment

To assess the degree to which organic $\delta^{13}\text{C}$ values obtained from Coon Creek decapods reflected a marine versus terrestrially derived diet, $\delta^{13}\text{C}$ values of the local environment as well as sources in the Late Cretaceous carbon cycle were first identified. Respective terrestrial and marine carbon sources within the Coon Creek Formation were determined from: (i) terrestrial $\delta^{13}\text{C}$ values calculated from measured terrestrial leaf waxes (long-chain n -alkanes), and (ii) $\delta^{13}\text{C}$ values for marine phytoplankton and atmospheric CO₂ ($\delta^{13}\text{C}_{\text{atm}}$), which were estimated from previously published isotope values for calcium carbonate in Coon Creek mollusks and Upper Cretaceous foraminifera (Barral, Gomez, Legendre, & Lécuyer, 2017; Keller et al., 2006; Zakharov et al., 2006, 2014). In the following section, we describe the approach used to calculate these carbon sources in the Coon Creek paleoenvironment.

3.3.1 | Calculating terrestrial plant $\delta^{13}\text{C}$ values

To calculate $\delta^{13}\text{C}$ values for terrestrial plants, the $\delta^{13}\text{C}$ values for leaf waxes n -C₂₉ and n -C₃₁ alkanes were converted to leaf $\delta^{13}\text{C}$ values following Diefendorf, Freeman, Wing, Currano, and Mueller (2015). The fractionation factor between n -alkane and leaf is dependent on plant type. The regional conifer families that were present in the Late Cretaceous are not known to produce significant amounts of n -alkanes compared to co-occurring angiosperms (Diefendorf, Freeman, Wing, & Graham, 2011; Diefendorf, Leslie, & Wing, 2015). Therefore, we use angiosperm fractionation factors of $-5.2 \pm 2.4\%$ and $-5.6 \pm 2.5\%$ for n -C₂₉ and n -C₃₁ alkanes, respectively (Diefendorf & Freimuth, 2017).

3.3.2 | Estimating marine phytoplankton $\delta^{13}\text{C}$ values

We were not able to isolate definitive marine biomarkers in Coon Creek sediment and therefore could not directly measure the $\delta^{13}\text{C}$ value of marine phytoplankton (e.g., Freeman & Hayes, 1992). Instead, we estimated marine phytoplankton $\delta^{13}\text{C}$ values using independent estimates of $\delta^{13}\text{C}_{\text{atm}}$ from benthic foraminifera, which we converted to calcite $\delta^{13}\text{C}$ values using the approach of Hayes, Strauss, and Kaufman (1999). This approach has the advantage that

we can check our estimated $\delta^{13}\text{C}_{\text{calcite}}$ values against $\delta^{13}\text{C}$ values of clams (aragonite) collected at the Coon Creek Formation type section (e.g., Keller et al., 2006). Atmospheric $\delta^{13}\text{C}$ is best-estimated using compilations of benthic marine foraminifera (Tippie, Meyers, & Pagani, 2010). Recently, Barral et al. (2017) compiled $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for Cretaceous benthic marine foraminifera; we averaged their reported data for 70 to 72 Ma, which yielded a $\delta^{13}\text{C}_{\text{atm}}$ value of $-6.4 \pm 0.5\text{‰}$ (1σ , $n = 445$).

To estimate $\delta^{13}\text{C}$ values for marine phytoplankton, we first estimated $\delta^{13}\text{C}_{\text{calcite}}$ values from $\delta^{13}\text{C}_{\text{atm}}$ (determined above) by rearranging the equations in Tippie et al. (2010). Our estimated Coon Creek water temperature of $20.1 \pm 0.6^\circ\text{C}$ is based on the mean of previously reported values of $19.2 \pm 2.3^\circ\text{C}$ and $17.7 \pm 2.3^\circ\text{C}$, estimated from bivalves (Zakharov et al., 2006, 2014), and $23.5 \pm 2.2^\circ\text{C}$, estimated from various non-belemnite mollusks (Lowenstam & Epstein, 1954). Marine phytoplankton $\delta^{13}\text{C}$ values were then determined using the recognized carbon isotope fractionation factors between sedimentary TOC and calcite (ϵ_{TOC}), and between TOC and biomass (Δ_2), as reported in Hayes et al. (1999). For the Late Cretaceous, we used the closest reported ϵ_{TOC} values of $-28.4 \pm 0.5\text{‰}$ at 69 Ma and note that these values are very similar ($\sim 1\text{‰}$) throughout the Late Cretaceous. For Δ_2 , the recommended value of 1.5‰ was used, and we assigned an error to this term of 0.5‰ (see Discussion in Hayes et al., 1999). With this approach, we estimate that marine phytoplankton $\delta^{13}\text{C}$ values were -30.5‰ with a Monte Carlo assigned uncertainty of 1.0‰ .

3.3.3 | Comparing measured clam $\delta^{13}\text{C}_{\text{aragonite}}$ values to those estimated from $\delta^{13}\text{C}_{\text{atm}}$

We compared aragonitic $\delta^{13}\text{C}$ values that were estimated for the Coon Creek Formation using the $\delta^{13}\text{C}_{\text{atm}}$ values from Barral et al. (2017) with a published $\delta^{13}\text{C}$ value for a clam (Keller et al., 2006). This provides a test of the reported $\delta^{13}\text{C}_{\text{atm}}$ values from Barral et al. (2017) and $\delta^{13}\text{C}_{\text{calcite}}$ values that were assumed in calculating phytoplankton $\delta^{13}\text{C}$ values. For this test, we used the same approach as in the previous subsection and then converted $\delta^{13}\text{C}_{\text{calcite}}$ values to $\delta^{13}\text{C}_{\text{aragonite}}$ values using the aragonite–calcite fractionation factor ($\epsilon = 1.7 \pm 0.4$) from Romanek, Grossman, and Morse (1992). This resulted in an estimated $\delta^{13}\text{C}_{\text{aragonite}}$ value of $1.1 \pm 0.9\text{‰}$, which is very similar to the published $\delta^{13}\text{C}$ value ($1.3 \pm 0.5\text{‰}$) for the clam *Crassatellites vadosus* that was collected at the Coon Creek Formation type section (Keller et al., 2006). Because we find strong agreement between measured and calculated aragonite $\delta^{13}\text{C}$ values, this would suggest that C in the atmosphere–marine system was in isotopic equilibrium.

4 | RESULTS

4.1 | Raman spectroscopy

The results of the Raman spectroscopy of Coon Creek crab and mud shrimp specimens are presented in Figure 3. Raman spectra of the Coon Creek decapod cuticle reveal broad first-order vibrational bands centered at $1,368\text{ cm}^{-1}$ and $1,608\text{ cm}^{-1}$, which are characteristic of

carbonaceous (kerogenous) material, and are typically designated as D (disordered) and G (ordered) bands, respectively. This is in agreement with Schimmelmann et al. (1988) who documented kerogen in Coon Creek crabs. The spectra also reveal a sharp peak characteristic of calcium phosphate (963 cm^{-1}) and a smaller peak characteristic of calcium carbonate ($\sim 1,080\text{ cm}^{-1}$). We note that we did not use the intensity ratio or spectral separation distance of the D and G bands (e.g., R1, Beysac, Goffé, Chopin, & Rouzaud, 2002; R_0 , Kelemen & Fang, 2001) to determine kerogen temperature and maturation; the spectra reported here were measured with UV excitation, whereas these maturity metrics are calibrated based on Raman spectra measured with visible excitation.

4.2 | Bulk stable isotope analysis

TOC, TON, and C:N values for all specimen samples are presented in Table 1, and TOC and TON values are plotted in Figure 4. TOC and TON values for the Coon Creek fossil specimens are low compared to those of the commercial chitin and indicate depletion of organic content in the fossil cuticle. Likewise, the C:N ratios for both fossil taxa are much higher than those observed in the modern chitin ($6.6 \pm 0.2\text{‰}$), indicating disproportionate loss of nitrogen. These results are comparable to the low TOC and high C:N values in Coon Creek fossil decapod cuticle previously reported by Schimmelmann et al. (1988). Carbon isotope values for all analyzed fossil specimens are presented in Table 1 and Figure 5. Mean $\delta^{13}\text{C}$ values for the crabs and mud shrimp are statistically indistinguishable (Mann–Whitney, $p > .05$). There is also no significant relationship between $\delta^{13}\text{C}$ and TOC values for either the crabs (Pearson's $n = 13$, $r^2 = .06$, $p = .42$) or mud shrimp ($n = 8$, $r^2 = .15$, $p = .35$).

4.3 | Biomarker composition and compound-specific isotope values of sediment

Biomarker abundances and compound-specific $\delta^{13}\text{C}$ values for sediment *n*-alkanes are presented in Table 2. Partial chromatograms for biomarkers in Coon Creek sediments are presented in Figure 6. Short-chain alkanes (C_{17} – C_{20}) dominate and have a mean $\delta^{13}\text{C}$ value of $-30.1 \pm 0.2\text{‰}$. The less abundant long-chain *n*-alkanes (C_{29} – C_{33}), which are common in terrestrial plants, yield a $\delta^{13}\text{C}$ value similar to short-chain alkanes ($-30.8\text{‰} \pm 0.5\text{‰}$).

Thermal maturity of the Coon Creek Formation was determined using the values obtained from the CPI (1.37) and homohopane thermal maturity index (0.12). These values are both indicative of low thermal maturity (e.g., Peters et al., 2005). For the pristane/phytane ratio, we obtained an intermediate value of 1.8, which does not allow for conclusive assignment of redox conditions during Coon Creek sedimentation.

5 | DISCUSSION

Raman spectroscopy and total organic carbon results indicate that the Coon Creek decapods retain organic carbon. Below, we first discuss the potential for these fossils to yield biogenic stable isotope signatures that can be used as paleoenvironmental proxies, and fossil composition

Sample	Body section	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)	TOC (wt%)	TON (wt%)	C:N (wt%)
Avitelmessus_1	Cheliped	-25.5	8.4	0.3	24.5
Avitelmessus_2	Cheliped	-26.0	8.3	0.3	25.9
Avitelmessus_3	Cheliped	-25.4	13.2	0.2	85.4
Avitelmessus_4a	Cheliped	-24.1	6.4	0.2	41.5
Avitelmessus_4b	Cheliped	-24.4	6.3	0.2	39.9
Avitelmessus_5a	Cheliped	-24.2	4.7	0.2	32.8
Avitelmessus_5b	Carapace	-25.2	3.8	0.3	25.4
Avitelmessus_6a	Cheliped	-25.9	4.4	0.3	15.3
Avitelmessus_6b	Carapace	-25.5	4.9	0.3	18.6
Avitelmessus_7	Cheliped	-24.9	3.8	n.d.	n.d.
Avitelmessus_8	Cheliped	-25.4	7.0	n.d.	n.d.
Avitelmessus_9	Cheliped	-25.5	6.0	n.d.	n.d.
Avitelmessus_10	Cheliped	-24.4	5.1	n.d.	n.d.
<i>Mean ± 1σ</i>		-25.1 ± 0.6	6.9 ± 2.7	0.3 ± 0.1	37.1 ± 24.9
Mesostylus_1	Cheliped	-27.8	8.5	0.3	32.8
Mesostylus_2	Cheliped	-26.9	2.6	n.d.	n.d.
Mesostylus_3	Cheliped	-25.4	6.7	0.3	23.8
Mesostylus_4	Cheliped	-25.9	1.7	0.1	25.2
Mesostylus_5	Cheliped	-26.2	1.9	0.1	29.4
Mesostylus_6	Cheliped	-25.5	9.3	0.3	30.5
Mesostylus_7	Cheliped	-24.7	10.1	0.4	27.7
Mesostylus_8	Cheliped	-25.2	12.3	0.4	29.8
<i>Mean ± 1σ</i>		-26.0 ± 1.0	6.6 ± 4.1	0.3 ± 0.1	28.5 ± 3.1
Chitin_1	n.d.	-21.4	43.4	6.2	7.0
Chitin_2	n.d.	-21.4	43.0	6.5	6.6
Chitin_3	n.d.	-21.4	42.2	6.7	6.3
Chitin_4	n.d.	-21.5	41.7	6.6	6.4
Chitin_5	n.d.	-21.4	42.4	6.5	6.6
Chitin_6	n.d.	-21.4	42.2	6.4	6.6
Chitin_7	n.d.	-21.4	41.9	6.5	6.4
Chitin_8	n.d.	-21.4	n.d.	6.6	n.d.
<i>Mean ± 1σ</i>		21.4 ± 0.04	42.4 ± 0.6	6.5 ± 0.2	6.6 ± 0.2

"n.d." indicates values not determined or detected.

When more than one body section from an individual crab was sampled, the sample ID is denoted with an "a" or "b" suffix.

Mean $\delta^{13}\text{C}$, TOC, and TON values for *Avitelmessus* ($n = 10$) were calculated using the individual mean values from crabs where more than one body section was sampled (e.g., *Avitelmessus_4*).

and taphonomy. We then integrate isotopic data from the decapods and sedimentary n -alkanes with estimated $\delta^{13}\text{C}$ values for marine phytoplankton, terrestrial plants, and atmospheric CO_2 to assess the (i) diet of the Coon Creek decapods and the (ii) degree of terrigenous input into the northern Mississippi Embayment during the Late Cretaceous.

5.1 | Composition and taphonomy of fossil cuticle

The depleted TOC and TON, and high C:N values obtained from the fossil decapods indicate that some degradation of the organic component of the cuticle, including chitin, took place either before

or after burial. Experimental degradation studies on arthropod cuticle in aquatic settings have shown that a number of environmental factors (e.g., temperature, pH, salinity, oxygenation) can influence the rate of bulk chitin mass loss and depletion of exoskeletal TOC and TON (Allison, 1990; Boyer, 1994; Gooday, Prosser, Hillman, & Cross, 1991; Perga, 2011; Poulicek & Jeuniaux, 1991; Schimmelman et al., 1986; Seki, 1966; Seki & Taga, 1963a,b; Zobell & Rittenberg, 1938). In normal marine systems, degradation rates appear to be lowest when chitin is interred within fine-grained sediments under anoxic conditions. Our obtained pristane/phytane ratio is ambiguous in regard to redox conditions in the Coon Creek

TABLE 1 Taxonomic, anatomical, isotopic, and elemental data for decapods from the Coon Creek Formation type section (Enville, Tennessee)

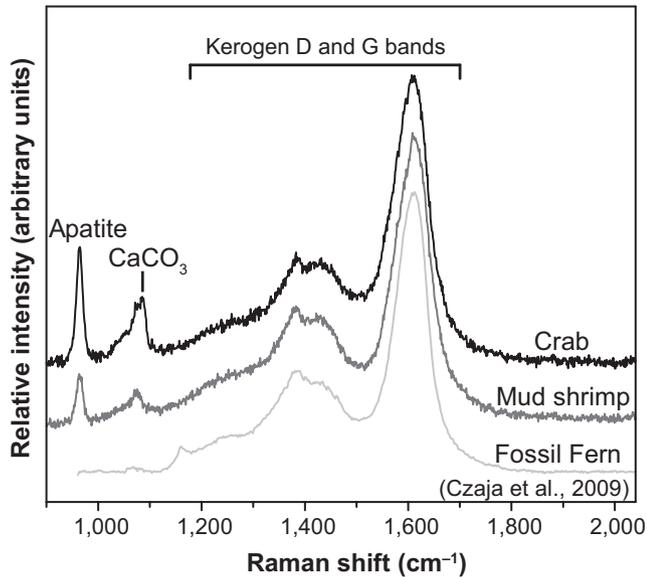


FIGURE 3 Raman spectra for a brachyuran crab (*Avitelmessus*) and mud shrimp (*Mesostylus*) from the Coon Creek Formation type Section (Enville, Tennessee). Spectra represent the average of three spot analyses from different locations on each specimen. The kerogen “D” and “G” bands indicate the presence of disordered and more ordered carbonaceous material, respectively. The lowermost spectrum is for an Eocene-age fern from the Clarno Formation, Oregon, USA (Czaja et al., 2009)

Formation, but local anoxia is evidenced by glauconitic sediments, phosphatic concretions, and very rare pyrite nodules (Bishop, 1983; Sohl, 1960; M. A. Gibson, pers. comm., 2017). The excellent preservation of many Coon Creek specimens (some fully articulated) has also been inferred to be the result of anoxia in the subsurface following periods of rapid sedimentation (Gibson & Dunagan, 2003). Subsurface anoxia would have reduced the potential for exoskeletal disruption and disarticulation via biostratinomic processes and post-burial bioturbation (see Bishop, 1986). In the context of a

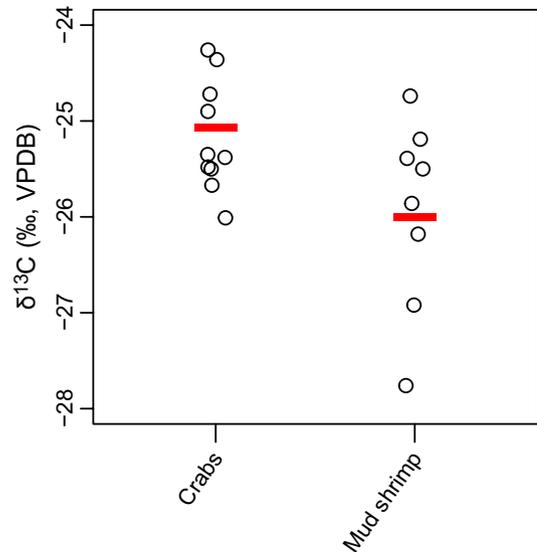


FIGURE 5 Carbon isotope ($\delta^{13}\text{C}$) values for crabs (*Avitelmessus*, $n = 10$) and mud shrimp (*Mesostylus*, $n = 8$) from the Coon Creek Formation type section (Enville, Tennessee). Data points are offset on the x-axis for visual clarity; taxon means are indicated by red bars. Mean values are reported for crabs where more than one body section was sampled

back-bar environment interpretation of the Coon Creek Formation (Ebersole, 2016), it is plausible that reduced circulation and water stagnation due to barriers further promoted periods of dysoxia or anoxia in Coon Creek sediments. In any case, anoxic conditions following burial most likely increased the preservation potential for non-mineralized tissues in the decapods. Burial in anoxic sediments containing kaolinite and illite clays would have also facilitated long-term preservation in two ways: (i) the fine grain size of the clays has been shown to inhibit organismal decay (Wilson & Butterfield, 2014) and impede the growth of bacteria that cause decay (McMahon et al., 2016); and (ii) the low-swell properties of

FIGURE 4 Results from elemental analysis of decapods from the Coon Creek Formation type section (Enville, Tennessee) and commercial chitin. (a) Total organic carbon (TOC) for commercial chitin ($n = 7$), fossil crabs (*Avitelmessus*, $n = 10$), and fossil mud shrimp (*Mesostylus*, $n = 8$). (b) Total organic nitrogen (TON) for commercial chitin ($n = 8$), fossil crabs ($n = 9$), and fossil mud shrimp ($n = 7$). Data points are offset on the x-axis for visual clarity; taxon means are indicated by red bars. Mean values are reported for crabs where more than one body section was sampled

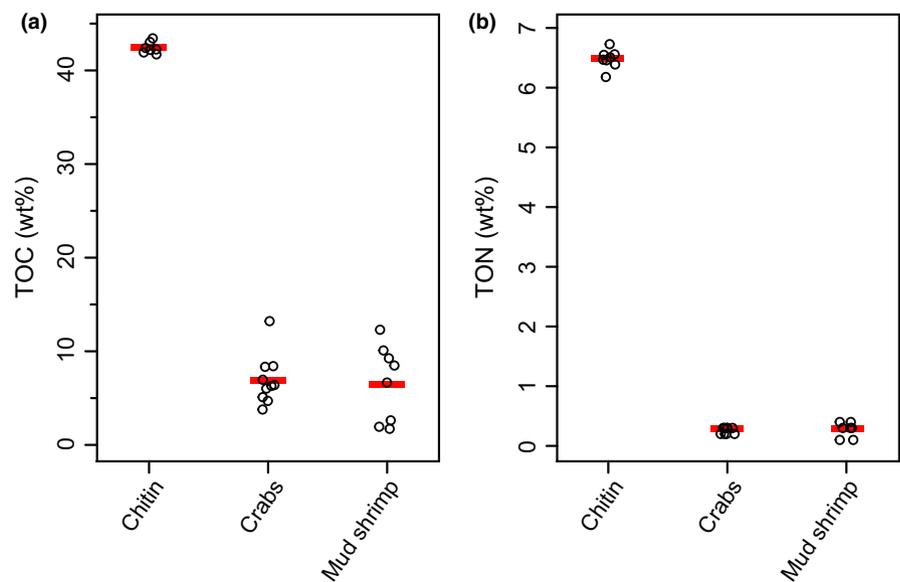


TABLE 2 Results from GC-MS and GC-C-IRMS analysis of *n*-alkanes in Coon Creek Formation sediment (type section, Enville, Tennessee)

<i>n</i> -Alkanes	ng/g	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)
C ₁₆	4.4	-30.2
C ₁₇	37.7	-30.0
C ₁₈	75.6	-30.0
C ₁₉	60.5	-30.3
C ₂₀	30.4	-30.3
C ₂₁	22.5	-30.3
C ₂₂	25.7	-30.1
C ₂₃	18.1	n.d.
C ₂₄	8.9	-29.9
C ₂₅	4.2	-29.8
C ₂₆	2.6	-30.1
C ₂₇	2.6	-30.6
C ₂₈	1.8	-31.8
C ₂₉	2.7	-31.5
C ₃₀	1.3	-30.7
C ₃₁	2.2	-30.6
C ₃₂	0.7	n.d.
C ₃₃	0.7	-30.4
C ₃₄	0.2	n.d.
C ₃₅	0.2	n.d.
C ₃₆	0.1	n.d.

"n.d." indicates *n*-Alkane $\delta^{13}\text{C}$ values not determined when below our limit of quantitation or when co-eluting with other compounds.

n-Alkane $\delta^{13}\text{C}$ precision and accuracy are $\pm 0.3\%$ (1σ) and $\pm 0.2\%$, respectively.

the clays would have allowed little to no mechanical disaggregation, and limited chemical dissolution by groundwater (S. E. Ebersole, pers. comm., 2014; Ebersole, 2016).

The calcium phosphate and calcium carbonate minerals in the fossil exoskeletons revealed by Raman spectroscopy are somewhat uninformative with respect to diagenetic alteration following burial because they could represent either the original biomineralized component of the cuticle (Boßelmann, Romano, Fabritius, Raabe, & Eppe, 2007) or products of microbially driven diagenetic alteration (Briggs & Kear, 1994; or some combination thereof). However, the structure of the kerogenized organic carbon in the decapod specimens does provide insight into diagenetic conditions. The height ratios and overall shape of the two carbonaceous bands (D, G) in the Raman spectra of the Coon Creek specimens are nearly identical to those measured using UV excitation in a kerogenized fossil fern preserved in chert in the Eocene Clarno Formation of Oregon, USA (Czaja, Kudryavtsev, Cody, & Schopf, 2009; Figure 5). Visible and UV Raman spectroscopy, optical microscopy, and fluorescence imaging of the kerogen in this fern confirmed that it is of very low organic thermal maturity (Czaja et al., 2009; Kudryavtsev, Schopf, Agresti, & Wdowiak, 2001; Shi, Schopf, & Kudryavtsev, 2013), and thus, we infer

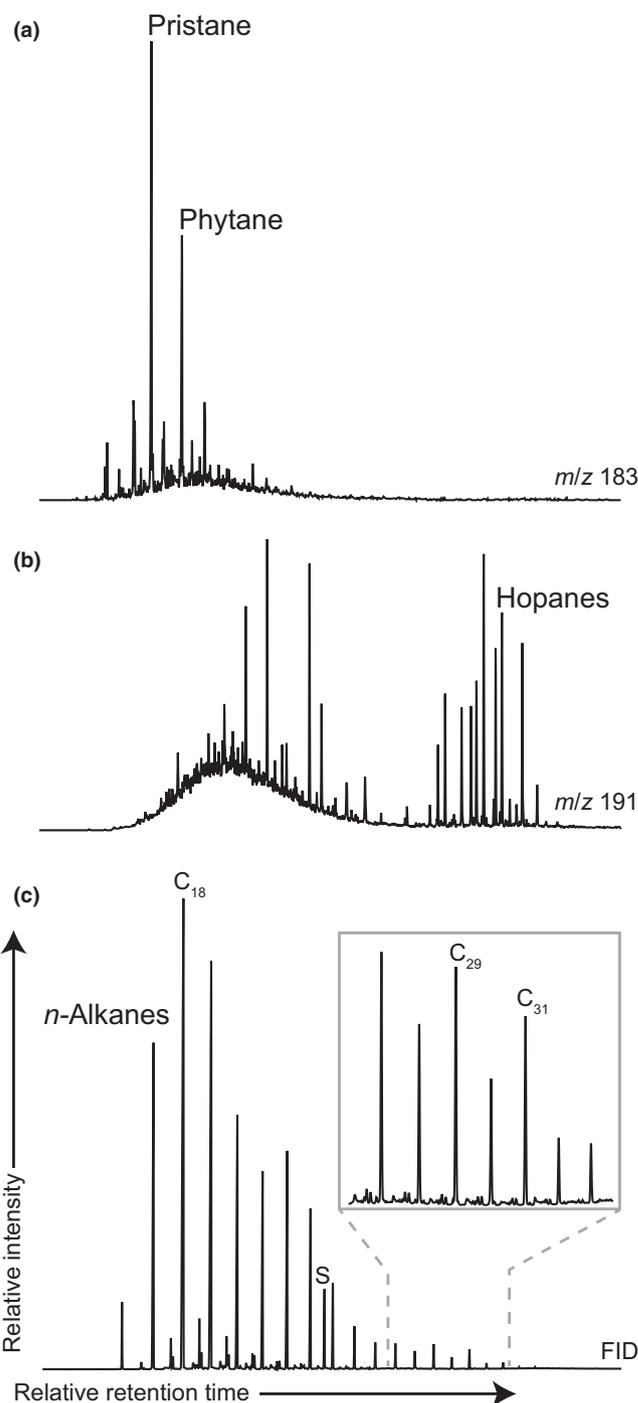


FIGURE 6 Partial gas chromatography–mass spectrometry and flame ionization chromatograms for sediment from the Coon Creek Formation type section (Enville, Tennessee). The selected ion chromatogram for (a) m/z 183 and (b) m/z 191 for the saturated branched and cyclic fraction (following urea adduction), showing pristane, phytane, and the hopanes. (c) Flame ionization chromatogram for the saturated *n*-alkyl fraction with *n*-alkane chain lengths indicated. The internal standard (1-1' binaphthyl) is indicated with an "S"

similar low-grade thermal maturity for the Coon Creek decapods. The CPI and homohopane maturity index values obtained in the present study also provide support for sediment immaturity and a low-grade

thermal regime following deposition of Coon Creek sediments. These indices values are consistent with regional post-Cretaceous volcanic and tectonic quiescence (Cox & Van Arsdale, 2002), and a relatively shallow burial depth for this unit (Cushing et al., 1964).

5.1.1 | Preservational pathway

Given the kerogenized nature of the Coon Creek decapods, it is important to consider the possible pathways for their diagenetic alteration as it relates to potential influences on their stable isotope signatures. A number of fossil and experimental diagenesis studies have examined the preservational pathway through which arthropod chitin, or compositionally similar carbonaceous tissue (e.g., plant cellulose), becomes altered or kerogenized (Cody et al., 2011; Gupta, Briggs, Collinson, Evershed, Michels, Jack et al., 2007; Gupta, Briggs, Collinson, Evershed, Michels, Pancost, 2007; Gupta, Cody, Tetlie, Briggs, & Summons, 2009; Gupta, Michels, Briggs, Evershed, & Pancost, 2006; Schimmelmann et al., 1988; for reviews, see Gupta, 2011; Gupta & Summons, 2011). Gupta, Briggs, Collinson, Evershed, Michels, Jack et al. (2007), Gupta, Briggs, Collinson, Evershed, Michels, Pancost (2007) and Gupta, Tetlie, Briggs, & Pancost (2007) and subsequent authors concluded that in situ polymerization is the biomolecular process that facilitates long-term preservation of chitinous remains. In this process, exoskeletal chitin becomes more aliphatic (and recalcitrant) over time due to diagenetic transformation and incorporation of cuticle lipids into the fossil macromolecule. Critically, this process does not rely on (or result from) the introduction of organic components from external sources (e.g., sediment); thus, remnants of the original elemental composition of the cuticle chitin are retained (Cody et al., 2011). We infer here that a similar polymerization process facilitated preservation of the chitinous portion of Coon Creek decapod cuticle following burial.

Artificial diagenesis and experimental degradation of chitinous remains also indicate that carbon isotopes of the organic content of decapod cuticle are relatively stable through time. For example, Schimmelmann et al. (1986) found no significant changes to $\delta^{13}\text{C}$ values in different crab taxa following subjugation to artificial heating and biodegradation in both normoxic and anoxic sediments. Moreover, these authors found that $\delta^{13}\text{C}$ values for subfossil crab remains (<1,400 ka) and related modern taxa from an analogous habitat were similar, which suggests that $\delta^{13}\text{C}$ values from well-preserved chitinous remains can be used for paleoecological and paleoenvironmental reconstruction. Similarly, Perga (2011) observed only a ~1% enrichment in ^{13}C during decay experiments on non-biomineralized *Daphnia* exoskeletons buried in anoxic lake sediments. Given that Coon Creek decapods were probably buried in anoxic sediments and kerogenized under a low-grade diagenetic regime similar to that tested by Schimmelmann et al. (1986), we consider it unlikely that the $\delta^{13}\text{C}$ signatures obtained from Coon Creek decapods have been significantly altered. Likewise, low thermal maturity in the Coon Creek Formation suggests minimal alteration of the *n*-alkane $\delta^{13}\text{C}$ values obtained from our sediment samples (Diefendorf & Freimuth, 2017).

Along with the polymerization process described above, anaerobic decay and microbially driven mineralization of soft and non-mineralized tissues have been shown to play a critical role in tissue preservation (Briggs, 2003). Under anoxic conditions, bacterial sulfate reduction is one of the most common forms of organic mineralization. Evidence for anaerobic metabolism in the Coon Creek Formation includes local concretions in some beds and the presence of calcium phosphate, phosphorous, and sulfur in the decapod cuticle (Ebersole, 2016; Kornecki, 2014; this study).

Sulfate-reducing bacteria have been shown to metabolize chitin and its hydrolysis products (Boyer, 1986; Seki, 1965). Experiments indicate that during chitinolysis, the biomass of common sulfate-reducing bacteria typically becomes depleted in ^{13}C relative to the organic substrates (Kaplan & Rittenberg, 1964; Londry & Des Marais, 2003), in which case any residual substrate must become enriched in ^{13}C . Therefore, it is possible that anaerobic bacterial mineralization of chitin in the Coon Creek decapod exoskeletons altered it in a way that would obscure the original biogenic $\delta^{13}\text{C}$ signal recorded in the residual organic remains (i.e., kerogen). There are several reasons why we believe this unlikely, however. First, specimens chosen for this study occurred free in the sediment. We were careful to avoid specimens in concretions, which would be the most likely zones of elevated sulfate reduction and $\delta^{13}\text{C}$ fractionation (Bishop, 2007; Plet et al., 2016). We also note that in a recent study of a Devonian concretionary crustacean from a carbonate-dominated reef setting, in which sulfurization is thought to have played a large role in organic preservation, compound-specific $\delta^{13}\text{C}$ values from organic remains were nevertheless considered biogenic (Melendez, Grice, & Schwark, 2013; Melendez, Grice, Trinajstić et al., 2013). Second, no macroscopic evidence for sulfide mineral precipitation (e.g., pyrite) was noted in tested specimens, and pyrite is very rare in the Coon Creek Formation in general (M.A. Gibson, pers. comm., 2017). Where sulfur has been observed in Coon Creek organisms, it only occurs in trace amounts (Kornecki, 2014) and thus sulfate reduction appears to be both rare and highly localized. Third, obtained decapod $\delta^{13}\text{C}$ values show no statistical correlation with TOC values, and our $\delta^{13}\text{C}$ values are also generally more depleted than those obtained from typical modern marine decapods (e.g., Schimmelmann & Deniro, 1986b). This does not support the above hypothesis that organic residues have higher $\delta^{13}\text{C}$ values following decay. In the unlikely event that reducing bacteria increased decapod $\delta^{13}\text{C}$ values during chitinolytic decay, we conclude that the change would have been <2‰ (e.g., Londry & Des Marais, 2003; Perga, 2011). In this case, such an isotopic shift would not influence our interpretation of decapod $\delta^{13}\text{C}$ values within the larger carbon isotope system (see next section).

5.1.2 | Decapod taphonomy

The degree of organismal biomineralization is traditionally known to control long-term preservation potential. Decapod exoskeletal cuticle comprises a chitin-protein complex ultrastructure impregnated with varying amounts of precipitated mineral salts, including calcium carbonate, phosphate, and magnesium, and the degree of

mineralization varies within an individual's exoskeleton and among taxa (Amato, Waugh, Feldmann, & Schweitzer, 2008; Boßelmann et al., 2007; Waugh, Feldmann, Schroeder, & Mutel, 2006). For example, the exoskeletons of modern brachyuran crabs (e.g., *Callinectes*) tend to be heavily calcified, particularly in their chelae. Mud shrimp (Callianassidae) exoskeletons are mineralized to a lesser degree, but their chelipeds are much more heavily mineralized than the rest of the exoskeleton (Amato et al., 2008; Bishop & Williams, 2005).

We know of no studies that have examined the influence of differential biomineralization on preservation of the organic component of the decapod exoskeleton. However, numerous experimental studies have shown that the degree of mineralization can influence the likelihood of macrostructural preservation of individual body parts, and particularly chelipeds (e.g., Krause, Parsons-Hubbard, & Walker, 2011; Mutel, Waugh, Feldmann, & Parsons-Hubbard, 2008; Plotnick, Baumiller, & Wetmore, 1988; Plotnick, Mccarroll, & Powell, 1990; Stempien, 2005). These experimental findings align with those from taphonomic studies on fossil decapods. For example, in assessments of fossil mud shrimp taphonomy, Bishop (1986) and Bishop and Williams (2005) noted that chelipeds and their elements are the most abundant component within fossil decapod assemblages. These authors suggested that this was due to a higher degree of mineralization and recalcitrance compared to the rest of the body. Although Coon Creek crab specimens are typically unabraded and many are fully articulated, isolated appendages of both crabs and mud shrimp were the most commonly preserved body section observed in collections, suggesting the presence of a taphonomic bias toward more mineralized parts. The preponderance of isolated chelipeds from both crabs and mud shrimp in the Coon Creek Formation may also be attributed to exhumation during storms, infaunal scavenging, or intermittent periods of slower sedimentation, during which time carcasses or molts became disarticulated, leaving only more recalcitrant chelipeds to be subsequently buried permanently (e.g., Bishop, 1986). This observation is supported by qualitative assessments of sub-Recent faunal assemblages, which show that isolated mud shrimp chelae are often the most prevalent body parts in shallow, nearshore marine sediments (K. M. Feser, pers. comm., 2014).

Because of its protective qualities, Bishop and Williams (2005) suggested that the infaunal burrow habitat of mud shrimp should increase the preservation potential of their whole body. While some partial mud shrimp body fossils have been found in the Coon Creek Formation of Mississippi (Bishop & Williams, 2005), the scarcity of body remains in this unit ultimately suggests either that exhumation and scavenging, as described above, or some other factor limited the preservation of non-cheliped body parts. Increased sediment oxygenation in modern mud shrimp burrow systems has been shown to foster unique microbial communities (Kinoshita, Wada, Kogure, & Furota, 2008) and increase organic matter turnover in sediments (Kristensen, 2000). The small concretionary growths found only at the base of some Coon Creek mud shrimp chelipeds examined during this study suggest the presence of micro-chemoclines in the subsurface and variable microbial decay processes acting on the soft tissues following disarticulation of carcasses (for discussion on

decapod-bearing concretions and their geochemistry, see Feldmann et al., 2012). Such microbial variability and sediment oxygenation may have ultimately limited the in situ preservation potential of the poorly mineralized mud shrimp bodies under normal marine conditions. It is possible that enhanced microbial decay also promoted increased metabolic fractionation of cuticle chitin by microbes, resulting in the slight depletion of ^{13}C seen in some mud shrimp samples compared to others (Figure 4); however, if this occurred, the net effect was small (see previous section).

5.2 | Paleocology and paleoenvironment of the Coon Creek Formation

Our assessment of the Coon Creek Formation preservational pathway in the previous section does not suggest significant diagenetic or microbial alteration of biogenic $\delta^{13}\text{C}$ signatures from decapods or the sediment. Therefore, we conclude that organic $\delta^{13}\text{C}$ values in the decapods can be used to infer both paleocology and paleoenvironment.

5.2.1 | Coon Creek decapod paleocology

The $\delta^{13}\text{C}$ signature of decapod cuticle chitin has a near 1:1 relationship with the $\delta^{13}\text{C}$ signature of the animal's diet ($\pm 1\%$), and thus, in nearshore marine systems, exoskeletal chitin $\delta^{13}\text{C}$ values will reflect the relative input of marine organic and terrigenous organic matter into the organism's diet (Schimmelmann & Deniro, 1986b). In modern marginal marine trophic systems, brachyurans (e.g., *Callinectes*) tend to be generalists, whereas mud shrimp (e.g., *Callianassa*) tend to be detritivores (Dworschak, 1987; Laughlin, 1982). However, both taxa regularly feed on terrestrial plant remains, particularly the mud shrimp. Assuming that the Coon Creek decapods behaved similarly, the carbon isotope signature of their fossil cuticle can be used as a paleoenvironmental proxy for terrigenous input (Schimmelmann et al., 1986).

In our isotopic reconstruction of the Coon Creek system, potential marine and terrigenous dietary sources are represented by marine phytoplankton and terrestrial plant material, respectively (Figure 7). On average, Coon Creek decapod $\delta^{13}\text{C}$ values ($-25.5 \pm 0.9\%$) are closer to the calculated values for angiosperms ($n\text{-C}_{29}$, $-26.4 \pm 2.3\%$; $n\text{-C}_{31}$, $-25.2 \pm 2.6\%$) than phytoplankton ($-30.5 \pm 1.0\%$), indicating that the Coon Creek decapod diet included more terrestrial organic matter than marine. Although both decapod taxa in our study are extinct, comparison to modern related taxa that occupy similar niches provides general support for this dietary inference (Dworschak, 1987; Laughlin, 1982).

The similarity in $\delta^{13}\text{C}$ values for the decapod taxa, as well as previous interpretations of Coon Creek decapod ecology and the likeness of the Coon Creek at the type section to other localities, allow us to make further inferences about the Coon Creek decapod community and their diet. Moore (1974) noted that the diverse age and sex distribution of the crabs in the formation were indicative of an established community in a shallow-water setting. Moore, and later Bishop (2016), suggested that the crab *Avitelmessus grapsoideus* was a mobile epifaunal organism that frequented the low salinity, intertidal zone of the Coon Creek Formation. Bishop (2016) further suggested that

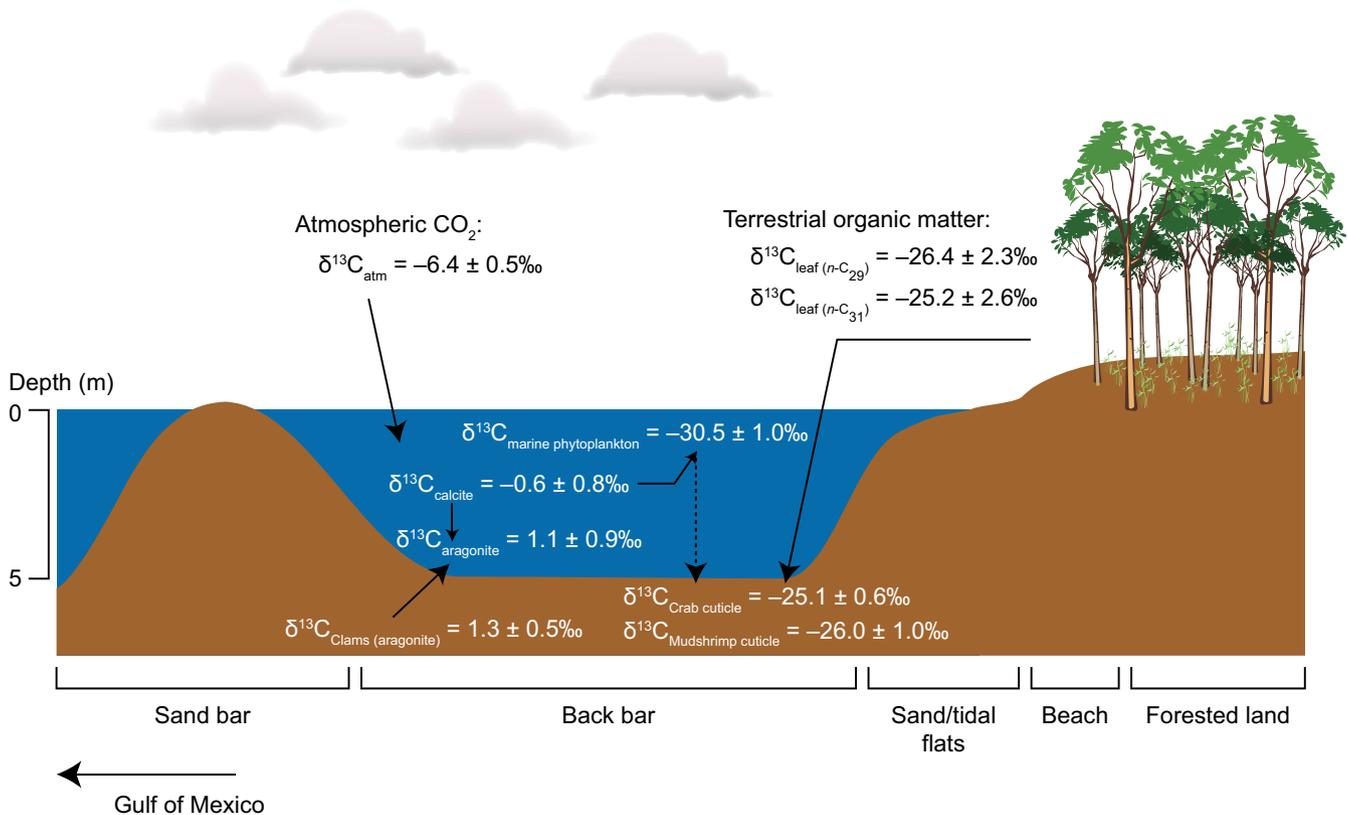


FIGURE 7 Carbon isotope systematics and interpreted environment of the Coon Creek Formation. Calcite and phytoplankton $\delta^{13}\text{C}$ values were estimated from reported atmospheric $\delta^{13}\text{C}$ CO_2 values (Barral et al., 2017). Estimated water temperature and measured aragonite $\delta^{13}\text{C}$ values are very similar, suggesting that our estimated calcite $\delta^{13}\text{C}$ values are robust. Terrestrial organic matter $\delta^{13}\text{C}$ values were estimated from measured long-chain n -alkanes (C_{29} , C_{31}) after accounting for fractionation between n -alkanes and leaf tissue. See text for a complete description of values

the crabs fed on soft-bodied flora and fauna that were not likely to be preserved in the fossil record (e.g., worms, algae). Conversely, the mud shrimp *Mesostylus mortoni* was probably an infaunal organism that remained within a single burrow for life and fed on detritus, as is common for modern mud shrimp (Bishop, 2016; Moore, 1974). Our isotopic data and inference of a terrestrially influenced diet for the decapods broadly support these authors' nearshore, shallow-water interpretations for the Coon Creek Formation, even if they do not allow for further inference of the specific depositional environment or depth (see next section). A very shallow, nearshore habitat interpretation would help explain the rarity of plant remains in the formation. Modern burrowing mud shrimp cause the release and oxidation of significant amounts of nutrients and organic detritus from sediments in nearshore settings (D'Andrea & Dewitt, 2009) and it is plausible that similar behavior by Coon Creek mud shrimp reduced or removed macroscopic terrestrial organic matter from the local sedimentary record, thus limiting its preservation potential. A possible modern environmental analog can be found in the Delaware Bay, USA. Here, terrestrial plant material is regularly flushed into tidal flat sediments, but is then degraded quickly, leaving little presence in accreting sediments (Fonjweng & Pfefferkorn, 2001). Burrowing organisms such as fiddler crabs excavate the sediment and rapidly turn over organic matter washed into the system. Mud shrimp probably filled a similar niche in the Coon Creek Formation environment.

Fluctuating environmental conditions in a nearshore marine setting could also explain the variable abundance of crab remains in certain beds in the Coon Creek Formation in Tennessee. Rapid crab population growth and subsequent declines have previously been used to explain the assemblages of well-preserved Coon Creek decapods in Mississippi and contemporaneous units in South Dakota (Bishop, 1986, 2016). Bishop suggested that, in these settings, increased nutrient load or food resources initiated a sudden population growth of *Dakoticancer* (another common Late Cretaceous brachyuran crab). Subsequent taphonomic feedback between the declining crab population and phosphate concentrating benthic organisms (e.g., worms) and microbes then drove their eventual preservation. Similar sporadic and small-scale changes in water chemistry may have caused crab populations in the Coon Creek Formation of Tennessee to experience comparable expansions and crashes. Excess nutrient load in the embayment would have promoted eutrophication and subsequent hypoxic conditions on the seafloor that were inimical to the crabs. In an effort to escape nearshore hypoxia or stagnation, the crab population may have mass migrated into less hostile settings. This type of migratory behavior is seen today in the Chesapeake Bay, USA, and other nearshore estuarine settings, where nutrient runoff in the water column causes anoxic events that drive mass migrations and mortalities of crabs in shallow habitats (termed "crab jubilees," Eggleston, Bell, & Amavisca, 2005; Loesch, 1960). If such perturbations resulted

in localized concentrations of Coon Creek decapods and increased decapod mortality rates, this could explain the variable abundance of decapod remains throughout the formation. Alternatively, if fully articulated specimens of *A. grapsoides* represent molts instead of carcasses, this might suggest that the crabs occasionally came together in these settings to molt *en masse*, a behavior which is seen in modern brachyurans (Stone, 1999). In either scenario, a mobile, epifaunal lifestyle for *A. grapsoides* would explain the localized concentrations of crab remains in the Coon Creek Formation type section and the inconsistent association with *M. mortoni*, both locally and regionally (e.g., Bishop, 1983).

5.2.2 | Revised Coon Creek Formation depositional environment

If Coon Creek decapods regularly consumed terrestrial foods, this would require a consistent influx of terrigenous organic matter into the environment. Here, we discuss lines of evidence relating to a terrestrial organic matter source and its depositional pathway, and implications for the environmental interpretation.

The terrestrial plant and pollen record in the Coon Creek Formation indicates that it was deposited proximal to a wooded, mainland environment (Baghai-Riding et al., 2016; Dilcher, 2016; Moore, 1974). Further evidence for distance to this terrestrial source is limited, however. Baghai-Riding et al. (2016) noted the presence of well-preserved pteridophyte and bryophyte spores at Coon Creek localities in Mississippi, which they argued provided evidence for close proximity to land and freshwater input, via either flooding or a channel. Given that exposures of the Coon Creek Formation in Mississippi probably represent a more offshore setting than to the north (Ebersole, 2016), Baghai-Riding et al.'s (2016) interpretation would, by extension, suggest more regular freshwater input into the Coon Creek Formation of Tennessee. In contrast, the rarity of terrestrial plant matter in the formation led Dilcher (2016) to argue for wind as the primary transport mechanism for terrestrial plant matter into the unit. In light of the terrestrial $\delta^{13}\text{C}$ signal recorded by the Coon Creek mud shrimp in the present study, we suggest that this paucity could be the result of burrowing organisms rapidly removing macroscopic organic matter from the system, as discussed above.

Terrigenous input into the Coon Creek ecosystem is also supported by the *n*-alkane composition of the sediment. Short-chain alkanes (e.g., C_{17} – C_{20}) dominate, suggesting a greater supply of marine-dominated organic matter. However, long-chain *n*-alkanes, representative of potential terrestrial plant material, are also present, albeit in smaller concentrations. This biomarker distribution is consistent with deposition in a nearshore marine environment (e.g., Peters et al., 2005) and supports interpretations of the Coon Creek Formation as nearshore and relatively shallow (e.g., Bishop, 2016; Ebersole, 2016; Moore, 1974).

Conversely, previously published $\delta^{18}\text{O}$ values for Coon Creek mollusks indicate normal marine (euhaline) conditions with little evidence for recorded freshwater input (Keller et al., 2006; Lowenstam & Epstein, 1954; Weiner et al., 1976; Zakharov et al., 2006, 2014). However, if the Coon Creek Formation was deposited in a very shallow,

circulation-restricted back-bar environment, as suggested by Ebersole (2016), it is possible that elevated molluscan $\delta^{18}\text{O}$ values do not reflect actual paleosalinity and instead are the result of evaporative enrichment and overprinting in an environment that was originally brackish (e.g., Hendry & Kalin, 1997). The lack of samples from beyond the type section prevents testing of this hypothesis in the present study, but this question warrants future investigation.

Within the broader stratigraphic patterns in the Mississippi Embayment, decapod $\delta^{13}\text{C}$ values support a nearshore position for the lower member of the Coon Creek Formation. This unit was deposited during a time of significant eustatic change and represents a highstand deposit for one of several global transgressions that occurred during the late Campanian–Maastrichtian (Hancock, 1993; Mancini, Puckett, & Tew, 1996). The influx of terrestrial organic matter recorded by the decapod $\delta^{13}\text{C}$ values, in conjunction with the siliciclastic-dominated Coon Creek sediment, provide evidence for increased terrigenous sediment deposition in the embayment as the rate of sea-level rise slowed. A nearshore marine position experiencing higher rates of siliciclastic deposition would also explain the occasionally rapid burial of the Coon Creek fauna and ultimately the exceptional preservation in the Lagerstätte beds.

In summary, fossil decapod $\delta^{13}\text{C}$ values, which provide unambiguous evidence for terrigenous input, together with the sediment biomarker composition data and the paleontological evidence described above, indicate to us that the Coon Creek Formation was deposited close to shore and most likely in a shallow environment that was proximal to a freshwater source. Although we cannot further constrain the Coon Creek Formation to a specific depositional setting or depth, such as a back-bar environment (Ebersole, 2016) or subtidal–intertidal zone (Bishop, 2016), our isotopic results do not refute these studies, and they can be used to bolster future interpretations of the depositional environment based upon sedimentology. Our decapod carbon isotope data add to previous inorganic isotopic analyses of molluscan fauna and foraminifera in this region (Keller et al., 2006; Lowenstam & Epstein, 1954; Sessa et al., 2015; Weiner et al., 1976; Zakharov et al., 2006, 2014) and with these studies provide a basic framework for understanding carbon cycling in the nearshore of the Late Cretaceous Mississippi Embayment. The presence of biogenic isotope results in Coon Creek decapods suggests that unaltered biogenic organic isotopic signals are also probably preserved in associated bivalves and ammonites, and thus these taxa may represent viable substrates for future isotope analyses.

6 | CONCLUSION

This study confirms that carbon isotope signatures of well-preserved chitinous remains are a viable proxy for paleoecological and paleoenvironmental reconstructions in marine settings. Within the modeled carbon isotope systematics of the Coon Creek Formation, decapod $\delta^{13}\text{C}$ values are considered biogenic. These values indicate that brachyuran crabs and mud shrimp both had diets primarily comprised of terrestrial rather than marine organic matter and that there was a regular freshwater

influx into the embayment. Our results provide strong geochemical support for recent interpretations of the Coon Creek Formation as a shallow, nearshore marine setting and, in doing so, help constrain the problematic environment of the northern Mississippi Embayment during the late Campanian–early Maastrichtian. Along with recent multiproxy isotope studies of Upper Cretaceous taxa in this region (e.g., Sessa et al., 2015), the combined organismal and sedimentary geochemical analysis presented here is a promising approach for understanding ecological responses to major climatic shifts in the Mississippi Embayment during the Late Cretaceous. More broadly, the increasingly regular discoveries of unaltered or vestigial chitin of geologic age suggest that biogenic isotopic signals from fossil arthropods have the potential to refine our understanding of a wide range of environments and foraging ecologies of organisms in deep time.

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