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The Shallow Benthic Invertebrate Recovery from the End-Cretaceous Mass Extinction across the Gulf Coastal Plain

Ronan B. Beltracchi
San Jose State University

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THE SHALLOW BENTHIC INVERTEBRATE RECOVERY FROM THE END-CRETACEOUS MASS EXTINCTION ACROSS THE GULF COASTAL PLAIN

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by

Ronan B. Beltracchi

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CRETACEOUS MASS EXTINCTION ACROSS THE GULF COASTAL PLAIN

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Ronan B. Beltracchi

APPROVED FOR THE DEPARTMENT OF GEOLOGY

SAN JOSÉ STATE UNIVERSITY

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Carlie Pietsch, Ph.D.   Department of Geology

Ryan Portner, Ph.D.   Department of Geology

Scott Shaffer, Ph.D.   Department of Biological Sciences

ABSTRACT

THE SHALLOW BENTHIC INVERTEBRATE RECOVERY FROM THE END-
CRETACEOUS MASS EXTINCTION ACROSS THE GULF COASTAL PLAIN

by Ronan B. Beltracchi

The Gulf Coastal Plain, in the southeastern United States, contains several sites with well-preserved fossil assemblages from the Cretaceous- Paleogene boundary (K/Pg). Changes in benthic macroinvertebrate assemblages after mass extinction events commonly include reduction in body size of surviving organisms and preferential survival based on ecospace occupation. This study examines patterns of functional ecology and body size change in mollusk fossils from bulk samples collected throughout the post-extinction recovery interval at a well-studied boundary site from Darting Minnow Creek in Brazos, Texas USA and a recently described K/Pg boundary section on the Ouachita River in Malvern, Arkansas USA. The proportional abundance of mollusk ecological life modes at Malvern, AR shows a shift from an assemblage dominated by immobile, epifaunal suspension feeding oysters in the first 1.5 meters of the Paleogene to a community composed of mobile, infaunal, suspension and deposit-feeding bivalves. The change from a disaster assemblage to a recovery assemblage is consistent with previous community ecology studies documenting the recovery from the end-Cretaceous mass extinction. The shift in functional ecology is matched by a significant increase in bivalve body size and is interpreted as an increase in the available energy from primary productivity at this site. The disappearance of oysters suggests additional changes to the substrate, sedimentation, and/or freshwater input. Across the U.S. Gulf Coastal Plain, both sites show evidence of multiple stages in the recovery of diversity, ecological complexity, and body size of the benthic mollusk community in the aftermath of the K/Pg.

ACKNOWLEDGMENTS

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INTRODUCTION

The study of mass extinction events contributes to improved knowledge of Earth history, as well as a finer understanding of ecosystems and their potential responses to extreme stressors. The Cretaceous-Paleogene boundary (K/Pg), 66 million years ago, is marked by the disappearance of about 40% of living genera including non-avian dinosaurs, large marine reptiles, ammonoids, and inoceramid bivalves (Russell, 1979). In the aftermath of the extinction, mammals diversified in the terrestrial realm, and the Modern Fauna (e.g., bivalves, gastropods, echinoids, crustaceans, bony fish, and sharks) dominated the oceans (Raup and Sepkoski, 1982; McGhee et al., 2013). Bivalves experienced an increase in speciation rates that has continued throughout the Cenozoic (Krug et al., 2009), and ray-finned bony fishes rose to ecological dominance over chondrichthyan sharks (Sibert and Norris, 2015).

The Gulf Coastal Plain (GCP), in the southeastern United States, records shallow marine sedimentation from the Late Cretaceous through the Modern and has long been a focus of the study of benthic marine macrofossils (Cannon, 1922; Wade, 1926; Stephenson, 1955; Sohl, 1964; Palmer and Brann, 1966; Toulmin, 1977; Sohl and Koch, 1983; Hansen et al., 1987; Hansen et al., 1993, Hansen et al., 2004, Sessa et al., 2009; Hart et al., 2012; Sessa et al., 2012; Larina et al., 2016; Ivany et al., 2018; Foster et al., 2020). The present study aims to contribute to an understanding of spatial variation in the recovery by comparing two GCP sites: the Brazos River tributary of Darting Minnow Creek in Falls County, Texas, (herein Brazos, TX) and the Ouachita River channel in Hot Spring County, near the town of Malvern, Arkansas (herein Malvern, AR). Both sites have stratigraphic exposure of the K/Pg boundary and the early Danian. The Brazos, TX site has been studied extensively in the

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literature (Hansen et al., 1993; Sessa et al., 2009; Hart et al., 2012; Foster et al., 2020) (Fig. 1). Benthic macroinvertebrate studies have also been performed at K/Pg sites on the eastern part of the shelf, in Alabama and Georgia (Toulmin, 1977) (Fig. 1), and many of these data sets, as well as several from the Brazos River region, are available in the Paleobiological Database (PBDB). These can serve as a comparative basis for the Malvern, AR site, which has only been evaluated for fossil vertebrate material (Becker et al., 2006; Becker et al., 2010) and biostratigraphic study of Cretaceous ammonites (Larina et al., 2016) and Danian dinoflagellates (Dastas and Chamberlain, 2021) but the level bottom mollusk community has not been studied. Therefore, the present study focuses on the functional ecology and body size changes of the shelf macrofauna of Malvern, AR and comparison of these results to other K/Pg boundary sites across the continental shelf of the U.S. Gulf Coast. The Malvern, AR site is unique in its placement far to the north within the Mississippi Embayment and its median location among previous studies from the eastern and western areas of the GCP (Fig. 1). The Malvern, AR site within the Mississippi Embayment may have experienced different oceanographic conditions including more terrestrially derived nutrients than sites facing the Gulf of Mexico (Pryor, 1960). Benthic macroinvertebrate richness, proportional abundance, and functional ecology of Danian mollusk assemblages in Alabama, Georgia, and Texas were compared to the Danian assemblage at the new Malvern, AR site using collections downloaded from the Paleobiological Database (PBDB). The differences between the ecology and body size of the benthic communities at the two sites contribute to understanding of broader patterns of recovery in the early Paleogene.
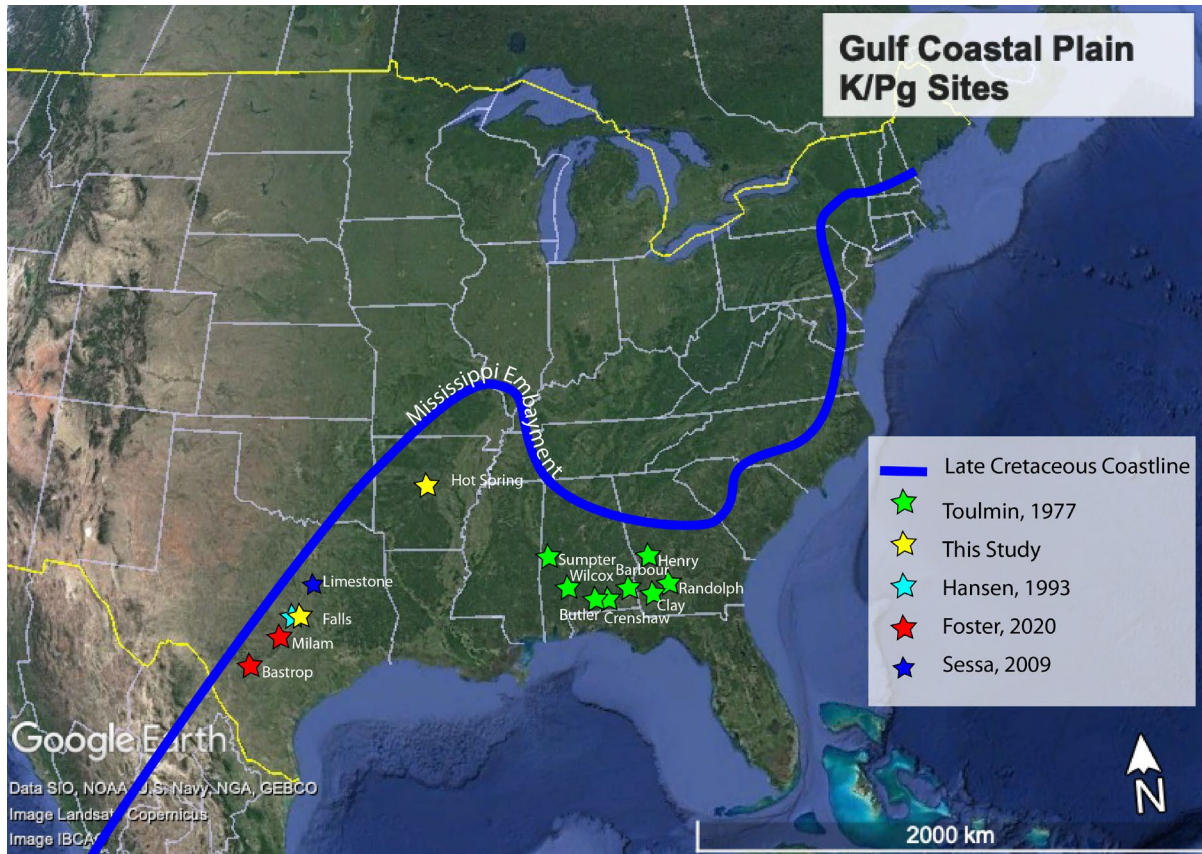
Figure 1: Map of the approximate late Cretaceous shoreline overlain on current US state boundaries. K/Pg boundary sites with benthic mollusk data available in the Paleobiological Database are marked with stars and labelled by county. Yellow: This study; Light Blue: Hansen 1993, and Foster 2020; Dark Blue: Sessa 2009; Red: Foster 2020; Green: Toulmin 1977.

SCIENTIFIC BACKGROUND

There have been five major mass extinction events documented in the history of life on Earth dubbed "the Big 5" (Raup and Sepkoski, 1982; McGhee et al., 2004). These events include the end-Ordovician (444 Ma), the end-Devonian (359 Ma), the end-Permian (252 Ma), the end-Triassic (201 Ma) and the end-Cretaceous (66 Ma), with impacts on the biosphere so devastating that they were used to recognize geologic period boundaries before the concept of extinction truly existed (Raup and Sepkoski, 1982). Most major biodiversity crises are correlated with changes to Earth's climate, though the cause for climate change varies. For example, global warming related to flood basalt volcanism from large igneous provinces is implicated as the main extinction mechanism of the end- Permian (252 Mya) and end-Triassic extinctions (201 Mya) (Thibodeau et al., 2016; Burgess et al., 2017). The K/Pg is similar to other major mass extinction events in that it shows not only broad taxonomic loss, but structural changes within ecosystems including the appearance or disappearance of entire modes of life, particularly amongst nektonic predators such as large marine reptiles and ammonoids (McGhee et al., 2004). The end-Cretaceous is ranked third in terms of taxonomic loss, but in terms of ecological severity, the K/Pg is ranked second only to the end-Permian (Bambach et al., 2004; McGhee et al., 2013). Like others of the Big 5 mass extinctions, the end-Cretaceous altered the biosphere in the benthic and pelagic marine realms, as well as in terrestrial and freshwater ecosystems. In contrast to other mass extinction events, the extinction and recovery from the end-Cretaceous took place over much shorter time scales (decades and 1.5 My respectively) compared to 100,000s of years of extinction and 2 to 5 My for recovery following other Mesozoic mass extinction events (Raup and Sepkoski, 1982; McGhee et al., 2004).

Extinction and Kill Mechanisms

One of the greatest remaining debates surrounding the K/Pg is the question of the extinction mechanism. One possibility is volcanic outgassing at the Deccan Traps, located in present-day India, from about 68 to 65 million years ago (Keller, 2016). These eruptive events may have triggered global warming, sluggish ocean circulation, and anoxia in a similar manner to flood basalts at the end-Permian (Song et al., 2014; Burgess et al., 2017) and end-Triassic extinctions (Thibodeau et al., 2016). The second possibility is a more sudden, catastrophic scenario caused by an extraterrestrial bolide impact 66 million years ago at the Chicxulub crater, near the Yucatan peninsula in modern-day Mexico (Hildebrand et al., 1991). Evidence for this event includes anomalously high levels of iridium detected in sediments spanning the K/Pg boundary in the Americas and in Europe (Alvarez et al., 1980; Schulte et al., 2010). Cores drilled from the peak ring of the Chicxulub crater indicate that the impact vaporized limestone and caused resurgent wave tsunamis in the hours to days after the event (Gulick et al., 2019).

The two extinction mechanisms are hypothesized to result in different kill mechanisms. Under the Deccan scenario, mercury and other contaminants from the volcanic eruptions may contribute to extinction via toxicity (Font et al., 2016). Global warming, ocean acidification, and anoxia due to increased atmospheric carbon dioxide are also frequently associated with long-term volcanism. At the end-Permian mass extinction, the result of large igneous province eruptions and additional volatile release from coal and carbonate rocks through contact metamorphism species with poorly buffered respiratory systems and calcareous shells were more vulnerable to extinction due to oceanic anoxia and acidification (Clapham and Payne, 2011; Burgess et al., 2017). In the Early Jurassic ocean, siliceous sponges showed

preferential recovery over calcareous taxa due to ocean acidification and weathering of silica-rich rocks into ocean shelf ecosystems (Corsetti et al., 2015). If flood basalts were the primary kill mechanism at the K/Pg, a preferential disappearance of calcareous taxa, and/or the resurgence of non-calcareous fauna in the immediate aftermath would be expected. Therefore, the lack of extinction selectivity bias against calcifying taxa at the K/Pg makes acidification an unlikely kill mechanism (Tyrrell et al., 2015; Hart et al., 2019). There is also no geologic record of a major Ocean Anoxic Event at the K/Pg (Leckie et al., 2002).

The bolide impact generated a dust and sulfur-aerosol filled upper atmosphere that blocked sunlight, leading to an "impact winter" and an average 26°C decrease in global mean temperatures for 10 years alongside a reduction in primary productivity and a weakened carbon pump, resulting in biotic collapse at all trophic levels (Alvarez et al., 1980; Schulte et al., 2006; Robertson et al., 2013; Vellekoop et al., 2014; Brugger et al., 2017; Birch et al., 2021; Junium et al., 2022). This theory has been criticized as there is no paleontological proxy for ancient light levels (Twitchett, 2006), however, more recent geochemical studies have found strong evidence for short-term global cooling and a slowdown of the marine carbon pump after the impact event (Vellekoop et al., 2014; Birch et al., 2016; Birch et al., 2021). Recent modeling has also shown that high concentrations of sulfates and hydrocarbons in the carbonate shelf at the impact site would have increased the degree of atmospheric perturbation, beyond the effects of the vaporization of the bolide at impact (Kaiho and Oshima, 2017).

In addition to the influence on extinction selectivity, there are different expectations for rates of extinction and recovery for each of these possible kill mechanisms (Table 1). Volcanism from the Deccan traps would be expected to cause a more gradual biotic decline

than a bolide impact, which is likely more abrupt. Reduced speciation rates in some dinosaur lineages have been observed for tens of millions of years throughout the late Cretaceous before the final extinction (Sakamoto et al., 2016; Condamine et al., 2021), but a downturn may not have been a prevailing trend through the entire clade (Bonsor et al., 2020). Additionally, different temperature proxies have revealed that peak outgassing at the Deccan occurred earlier than peak lava emplacement and warming from this outgassing is not well-correlated with the biotic crisis (Hull et al., 2020), with 2-3 °C of warming occurring as early as 69.5 Ma (Keller et al., 2016). Terrestrial plant fossil records do not show accelerated extinction rates at the end of the Cretaceous, nor do most marine communities (Schulte et al., 2010; Witts et al., 2016; Whittle et al., 2019). Other studies of benthic mollusks have shown an abrupt extinction event at the K/Pg, even in formations that are distal to the impact site (e.g. Patagonia and Antarctica) (Aberhan and Kiessling, 2014; 2015; Witts et al., 2016). However, stratigraphic and geochemical analyses still show some uncertainty in temporal correlation between the peak of Deccan volcanism, the Chicxulub impact, and the biological extinction boundary (Schulte et al., 2010; Keller et al., 2010; Burgess, 2019).

Table 1. Expected extinction and recovery time frames for each kill mechanism

	Volcanism	Impact
Extinction time frame	Tens of thousands to hundreds of thousands of years of global warming, slowed ocean circulation, surface water acidification, and mercury contamination. (Keller et al., 2016; Font et al., 2016)	Hours to days of ejecta fallout, widespread firestorms, tsunamis, and seiches. Decade of global cooling. Millennial havoc on the carbon cycle. (Alvarez et al., 1980; Schulte et al., 2006; Vellekoop et al., 2014; Birch et al., 2016)
Ecological impact	Selective extinction of hyper-calcifying taxa (e.g. corals) and loss of poorly buffered marine taxa (Knoll et al., 2007).	Selective extinction of species most dependent on primary productivity (Sheehan and Hansen, 1986)
Recovery rate/time frame	3-5 My to re-equilibrate global climate based on end-Permian and end-Triassic (Burgess et al., 2017; Song et al., 2014)	Years to decades for aerosols to settle and climate to recover. 1.7 My for carbon cycle to recover (Birch et al., 2016)

Ecology

One of the of simplest ways to assess biodiversity in an ecosystem is to study the richness (total number of species), and evenness (the relative abundance of each species) within the community (Fig. 2) While this provides a broad understanding of the taxonomic severity of an extinction event, it does little to assess the kill mechanisms, so other ecological methods must be applied. Several physiological and ecological factors may influence a taxa's extinction or survival during a global crisis.

In palaeoecological studies of marine organisms, taxa are commonly grouped into ecological guilds based on position relative to the sediment-water interface, feeding style, and motility; and the combination of these categories defines that taxa's mode of life (Bambach et al., 2007; Bush et al., 2007). Feeding is subdivided into predatory carnivores,
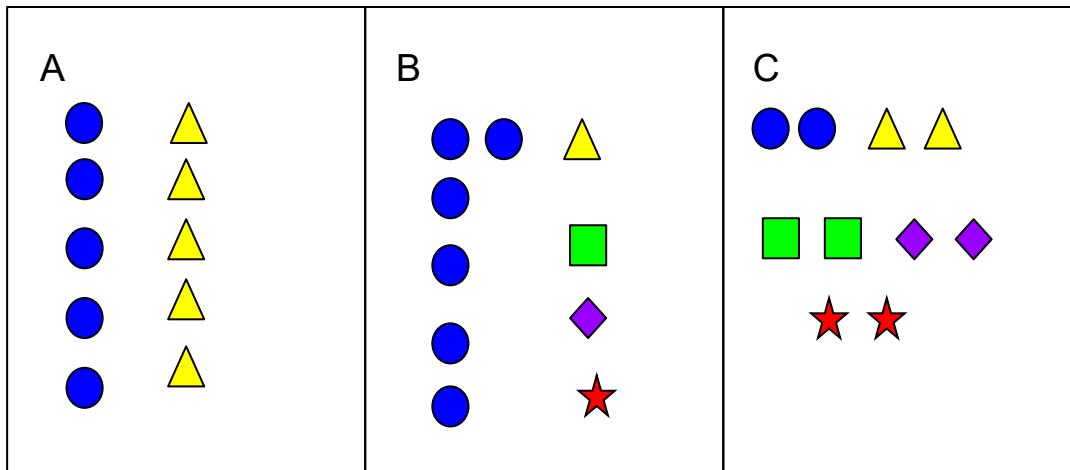
Figure 2: Conceptual illustration of richness and evenness in an ecosystem. Each shape type represents a species, and each community has ten individuals. **(A)** Sample community with low richness and high evenness, **(B)** Sample community with high richness and low evenness, **(C)** Sample community with high richness and high evenness.

herbivorous grazers, miners (digging into the sediment for organic matter), deposit feeders (consuming decaying organic matter from of the sediment), and suspension feeders (filtering food from the water column). Movement categories range from fully motile species to facultatively mobile species to immobile species and differentiate based on whether the species have adaptations to attach to the substrate. Tiering (sometimes referred to as life habit) describes the organism's position relative to the substrate, from infaunal (buried) to epifaunal (living on the sediment surface) to pelagic (living in the water column). The number of life modes utilized in ocean ecosystems has increased throughout the Phanerozoic (Bambach et al., 2007; Bush et al., 2007).

Changes in proportional abundance of different life modes over time may indicate large-scale ecological changes, particularly at mass extinctions (McGhee et al., 2013). The general restructuring of benthic marine ecosystems at the K/Pg includes a marked increase in bivalve speciation rates that has continued through the Cenozoic (Krug et al., 2009), as well as persistent shifts towards mobile, infaunal, deposit-feeding and carnivorous life modes,

particularly during the crisis interval (Sheehan and Hansen, 1986; Aberhan and Kiessling, 2015). Detritivore survival over suspension feeding is interpreted as a response to reduced primary productivity in the immediate aftermath of the bolide impact (Sheehan and Hansen, 1986). Feeding strategy was likewise the main selectivity factor in survival of deposit-feeding echinoid genera across the K/Pg boundary, with a higher extinction rate among surface sievers than selective detritivores. (Jefferey, 2001). Mobility has been shown to be a biasing factor in survivorship at other mass extinction events as well, as less motile species tend to have less robust respiration systems and poorer extracellular acid-base regulation and were therefore more vulnerable to hypercapnia and anoxia (Knoll et al., 2007; Clapham, 2017).

Calcification was another risk factor at the end-Permian (Knoll et al., 2007; Clapham and Payne, 2011) due to high atmospheric CO_2 that contributed to ocean acidification, making it more difficult for calcifying taxa to precipitate shells. Shell mineralogy (calcite vs aragonite) may also influence survival during ocean acidification events, but this also biases preservation in the fossil record, so a lack of aragonitic shells in a section may be an artefact of taphonomy (e.g. dissolution), not selection. selection (Flessa et al., 1993; Zuschin et al., 2003).

Marine invertebrates also have a variety of reproductive strategies which impact their broader evolutionary trajectories: benthic taxa with planktotrophic larvae (larvae which feed and develop in the water column) tend to have wider spatial range and therefore more genetic interconnectedness, leading to decreased speciation rates, while those species that have a shorter planktic stage, or brood their eggs, tend to recruit larva locally, resulting in genetic isolation of regional populations and increased rates of speciation (Hansen et al., 1988;

Jablonski, 1998). Benthic marine invertebrate reproductive strategies include r-selected, producing many offspring with little parental investment; or K-selected, producing fewer offspring with more parental investment. In the earliest Paleocene there was a "bloom" of speciation in families of opportunistic generalist mollusks with rapid reproduction and planktotrophic larval dispersal, which would allow for more rapid colonization of shelf space in the immediate aftermath of the extinction event (Hansen, 1988). A study of K/Pg foraminifera also found fewer large, specialized K-strategists and more small, generalist r-strategists in the earliest Paleocene biozones P0 and P1a (Keller and Abramovich, 2009). Rates of reproduction and speciation directly influence survival at mass extinctions, as well as new radiations of species during the recovery period (Harries et al., 1996; Kauffman and Harries, 1996).

Body Size

Reduction in body size of planktic and benthic invertebrate assemblages across mass extinction boundaries are known as the Lilliput effect, originally defined as a reduction of body size within a single species during the immediate aftermath of the event (Urbaneck, 1993; Twitchett 2006). The term has been deployed more generally in recent publications that have postulated various mechanisms for a smaller average size in a fossil assemblage in the aftermath of an extinction event including selective extinction of large species that do not necessitate dwarfing within any particular lineage (Payne, 2005; Twitchett 2006, Harries, 2009). The average body size of a fossil assemblage could also be reduced by the proliferation of small taxa (Twitchett, 2006), and body size biases have been found in several invertebrate classes for both origination and extinction (Monarrez et al., 2021). Additionally, the loss of large taxa can be an artefact of preservation; large taxa were rare in the living

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assemblage and therefore appear as "Lazarus taxa", when rare taxa are not preserved in a fossil assemblage after an extinction event but re-appear in later strata when abundance increases (Twitchett, 2007). Despite the common reduction in mean body size after mass extinctions, on a global scale, through the entire Phanerozoic, small taxa seem to have higher extinction rates than large-bodied organisms, even after accounting for preservational biases (Payne and Heim, 2020).

Generally, at the K/Pg, there seems to be little selective extinction of large taxa, and some within-species or within-genus dwarfing (Twitchett, 2006; Wiest et al., 2015). Body size studies of the boundary in the southeastern United States, close to the Chicxulub impact site, have shown signs of dwarfing in a diverse array of taxa. Wiest et al. (2015) found a 22% reduction in the diameter of *Thalassinoides* ichnofossils from the late Maastrichtian to early Danian, implying a reduced body size of the tracemaker. In planktic foraminifera, the post-extinction "disaster assemblage" consisted only of smaller, fast-reproducing species in the immediate aftermath of the mass extinction, as well as intraspecies size reduction in the surviving taxa (Keller and Abramovich, 2009). A study of echinoids in worldwide museum collections shows that 75% of genera that survived the K/Pg were smaller in the Danian than in the Maastrichtian (Jefferey, 2001). In one study, benthic mollusks at more distal latitudes (Antarctica) show no significant Lilliput effect at the K/Pg and only a reduction in diversity (Whittle et al., 2019).

GEOLOGIC SETTING

During the Mesozoic, high sea levels submerged much of North America in a shallow epicontinental sea called the Western Interior Seaway (WIS). By the latest Cretaceous, the seaway had retreated somewhat, but much of the Gulf Coastal Plain remained submerged into the early Cenozoic (Pryor, 1960; Ebersole, 2009; VanArsdale, 2009). A southwest-dipping troughlike basin, called the Mississippi Embayment, reached inland from the Cretaceous coast, with the shoreline reaching as far north as southern Missouri and Illinois (Mancini et al., 1996; Larina et al., 2016) and a possible river delta in the farthest northeast section (Pryor, 1960) (Fig. 1). While the Brazos, TX, and Malvern, AR sites are lithologically similar and were deposited on the continental shelf below storm wave base (~30m below sea level), it is possible that the Brazos site was at a deeper water depth (between 70 to 125 m below sea level) based on the preserved foraminifera (Hart et al., 2013). Study of the foraminifera at Malvern, AR has not yet been completed, but the lack of planktic taxa indicates a shallow environment of less than 100m below sea level (C. Lowery, personal comm.).

In Texas, the K/Pg boundary is represented by the Late Cretaceous, Maastrichtian Stage Corsicana Formation and the Paleocene, Danian Stage, Kincaid Formation (Fig. 3). The Kincaid is overlain by the late Danian Wills Point Formation. In Arkansas, Mississippi, and Alabama, the latest Cretaceous, Maastrichtian stage is recorded by the Arkadelphia Formation in Arkansas, the Owl Creek Formation from southern Missouri to northern Mississippi, and the Prairie Bluff Chalk eastern Mississippi and Alabama. In the eastern Gulf Coast, the earliest Paleocene, Danian stage is recorded in the Clayton Formation followed by the later Danian Porter's Creek Formation (Fig. 3) (Hansen et al., 1987; Mancini

et al., 1996; Larina et al., 2016; Foster et al., 2020). The different unit names for Late Cretaceous formations reflects the different sediment input (in-situ chalk deposition vs terrigenous sand) along the Cretaceous coastline. Foraminiferal data from the Gulf Coastal Plain has indicated that several Prairie Bluff Chalk sites in Alabama were deposited at shallower depths than what was preserved in the Texas Corsicana and Kincaid Formations (Hart et al., 2013). Further to the northeast, parts of the Owl Creek Formation contain more sand and silt, indicating fluvio-deltaic and marginal marine environments (Pryor, 1960; Larina et al., 2016). As part of an inland embayment, it is possible that the Arkansas site likewise received terrestrial input, but the chondrichthyes and ostracod fossils in the Maastrichtian Arkadelphia Formation do not indicate freshwater influence (Becker et al., 2006). The temporal correlation across K/Pg sites uses ammonite, foraminifera, and nannoplankton biostratigraphy for the Maastrichtian sediments (Larina et al., 2016). Danian biostratigraphic zones are defined by planktic foraminifera and nannoplankton biozones (Fig. 3) (Yancey and Liu, 2013; Hart et al., 2013). The duration of disconformities at the boundary varies between localities, with some sections recording up to a 350,000-year gap as a result of the erosion of Cretaceous sediment and sea level change (Larina et al., 2016).

The Gulf Coastal Plain preserves a taxonomically rich invertebrate fossil assemblage recorded in catalogs of the Cretaceous shallow marine invertebrate fauna (Stephenson, 1914; Stephenson, 1955; Taylor and Sohl, 1962; Sohl, 1964; Sohl and Koch, 1983) and a comprehensive survey of mollusks and other macroinvertebrate taxa in Paleocene and Eocene strata, particularly in Texas, Alabama, Mississippi, and Georgia (Palmer and Brann
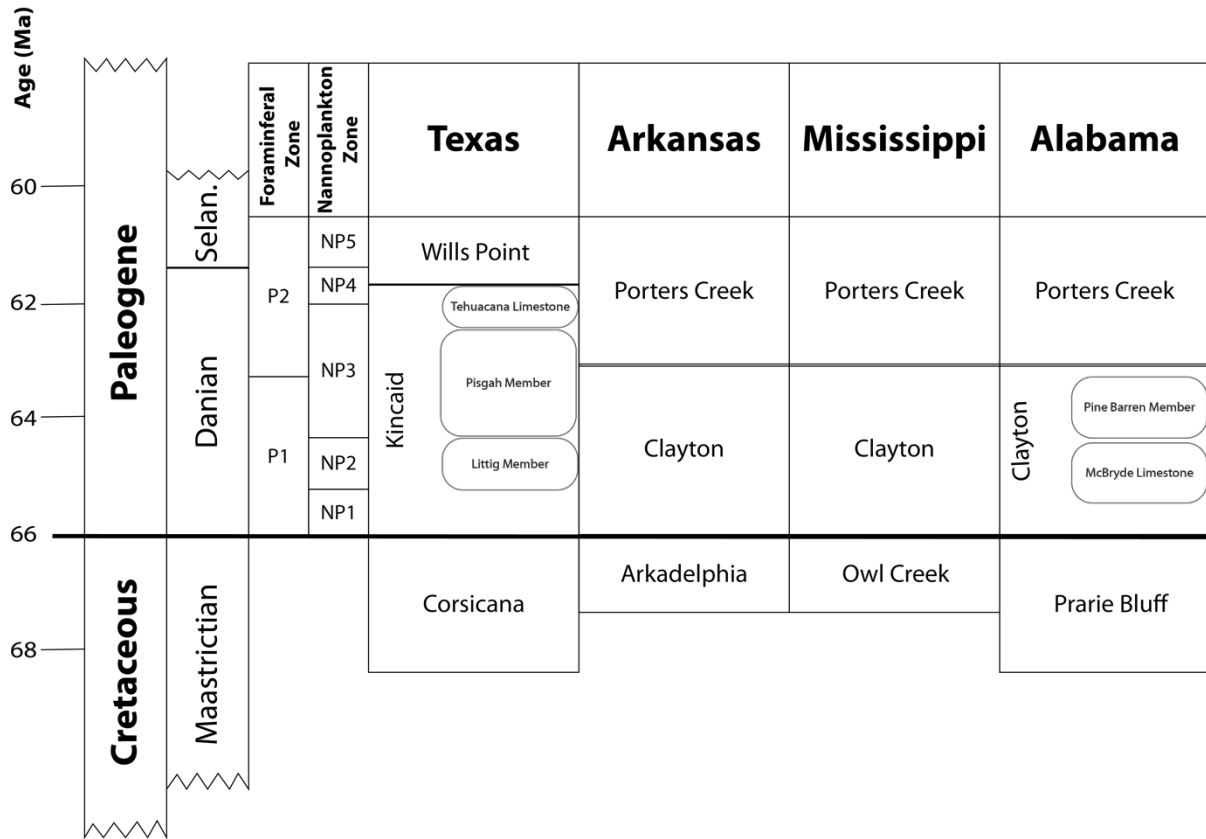
Figure 3: Stratigraphic correlation of major formations and members around the K/Pg boundary on the Gulf Coastal Plain. P= Foraminiferal zones; NP= Nannoplankton Biozones. Modified from Larina et al., 2016 and Foster et al., 2020.

1966; Toulmin, 1977; Bryan and Jones, 1989; Hansen et al., 1993). From these, a comprehensive list of expected genera of benthic macroinvertebrates in the region can be compiled. The inclusion of more recent species richness and paleoecological data sets collected by Sessa et al. (2009) and Foster et al. (2020) allows for comparison of trends across the US Gulf Coastal Plain (Fig. 1).

Brazos River, Texas

The Brazos River and its tributaries, Darting Minnow Creek and Cottonmouth Creek in Falls County, Texas, reveal outcrops where the late Maastrichtian Corsicana Formation is overlain by the Danian Kincaid Formation, making it one of the more well-studied Gulf Coastal Plain K/Pg boundary sites in the United States (Figs. 4 and 5) (Bourgeois et al, 1988;

Hansen, 1993; Yancey, 1996; Schulte et al., 2006; Hart et al., 2012; Yancey and Liu, 2013; Hart et al., 2019). The Brazos site is of particular interest because there is a contentious unit of hummocky cross-stratified sandstone that lies directly below the iridium anomaly (Fig. 5C). This has been interpreted by some as a deposit from a tsunami as a direct effect of the bolide impact at Chicxulub (Bourgeois et al., 1988; Hansen, 1993; Hart et al., 2012); although it has also been suggested that parts of the event deposit were not directly attributable to tsunami waves, but instead were mudflows triggered by impact-related seismic shaking of the seafloor (Yancey and Liu, 2013).

Figure 4: Map of the Brazos River region in eastern Texas. Fossils from this study were taken from Darting Minnow Creek, marked with a yellow box. Satellite image from Google Earth.

The outcrops through the upper Cretaceous and early Paleocene are primarily mudstone and siltstone, with shell lags, sandstone beds, and concretion horizons (Fig. 6). The sedimentology at Brazos indicates a shelf environment below storm wave base, and benthic

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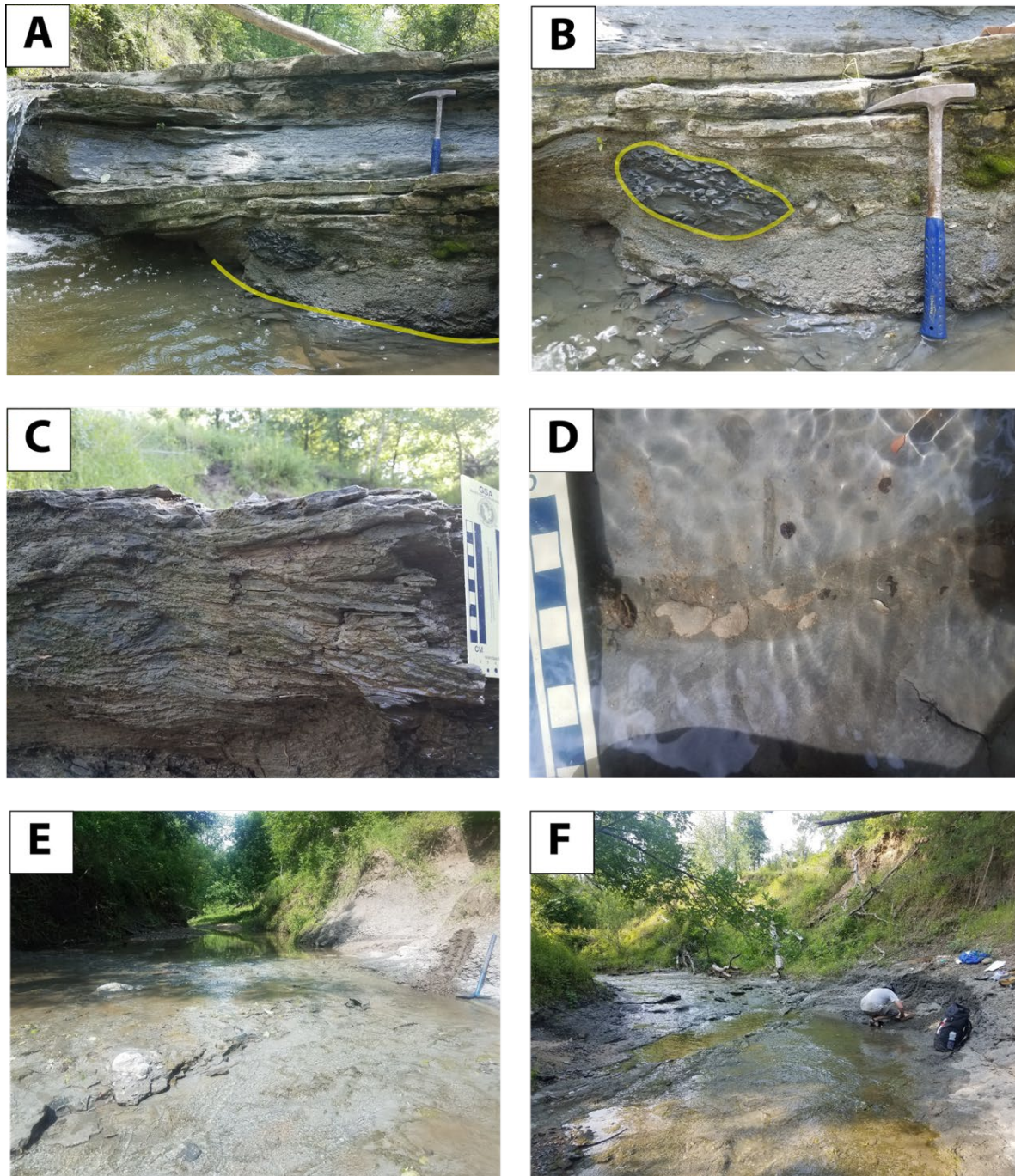
Figure 5: Outcrops at the Brazos River tributary Darting Minnow Creek in Falls County, TX. **(A)** Event horizon with K/Pg boundary highlighted. **(B)** Contact between the boundary sand and the underlying Corsicana mudstone, including large rip-up clast. **(C)** Hummocky cross-stratified sandstone tsunami deposit. **(D)** Early Paleogene section showing dark gray *Thalasinoides* burrows in light matrix exposed in the stream bed **(E)** Lower Concretion Horizon exposure in the Darting Minnow Creek streambed, with sampling location. **(F)** Sampling above and below the Middle Sandstone Bed at Darting Minnow Creek, looking down-section.

foraminifera provide an estimate of a water depth of 75 to 125m, with gradual deepening

through the early Paleogene (Yancey and Liu, 2013). Maastrichtian exposure of the

Corsicana Formation is limited, but it is constructed primarily of mudstones that contain

well-preserved foraminifera and macroinvertebrates (Hansen et al., 1993; Yancey, 1996; Hart

et al., 2012). There appears to be some erosion of the Cretaceous mudstones before the event

bed and Paleogene strata although the disturbance of these muds may have been due to

seismic instability in the immediate aftermath of the asteroid impact (Hart et al., 2012, Hart

et al., 2019). Recent studies at the Brazos River have confirmed Hansen's (1993)

interpretation of the boundary placement at the base of the hummocky cross stratified

sandstone (Fig. 6) (Schulte et al., 2006; Hart et al., 2012). The Paleocene succession

preserves a few million years of time, spanning foraminiferal zones P0 and Pα from the

boundary sand to the Lower Concretion Horizon. Foraminiferal zone P1a begins

approximately 80-100kyrs after the impact and spans the Lower Concretion Horizon to the

Middle Sandstone Bed, with P2a beginning above the Middle Sandstone Bed (Fig. 6) (Hart et

al., 2019). In addition to foraminifera biozones, several lithostratigraphic marker beds

(Lower Calcareous Concretion Horizon [LCH], Middle Sandstone Bed [MSB], Dirty

Sandstone Bed [DSB], Upper Calcareous Concretion Horizon [UCH], Rusty Pyrite

Concretion Horizon [RPH]) were described by Yancey (1996) and allow for correlation of

the Danian Kincaid Formation stratigraphy among the main river and tributary sites (Fig. 6)

(Hart et al., 2012). The samples collected for this study come from foraminiferal zones P1a

and P1b (Yancey et al., 1996).

Figure 6: Stratigraphic column of the Brazos, TX site, modified from Hart et al. (2012), with foraminferal zones from Yancey et al. (1996). Lithological marker beds are labelled, and sampling horizons for this study are marked with triangles.

Malvern, Arkansas

The Ouachita River in Malvern, Arkansas contains outcrops of the Late Cretaceous

Arkadelphia Formation overlain by the lower Danian Clayton Formation, and preserves a

diverse fauna of mollusks, chondrichthyes and osteichthyes (Becker et al., 2006; Becker et

al., 2010). There are two exposures at the site: one in the main riverbank channel (AMNH

3596), and another on a small island roughly 500 meters upstream (Fig. 7). The K/Pg

boundary is represented by a convolute poorly sorted sandstone bed which includes impact

spherules (Fig. 8).

Figure 7: Map of the Ouachita River region near Malvern, AR. Main channel (AMNH
3596) and island outcrop are highlighted.
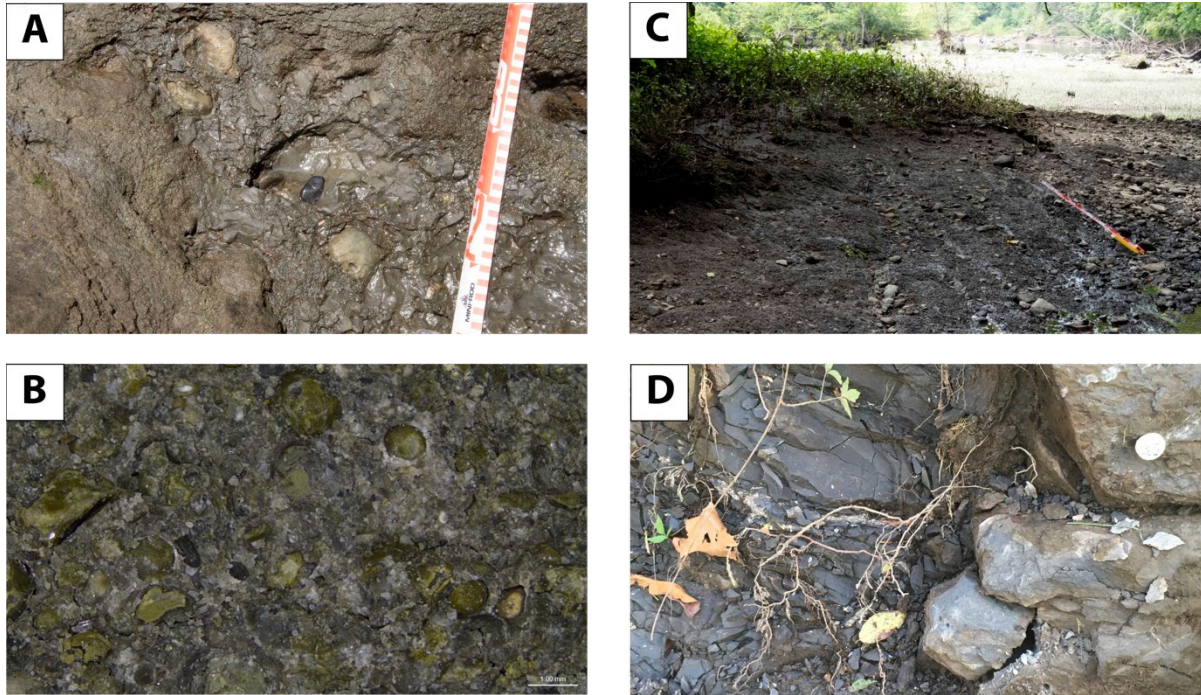
Figure 8: Outcrops at the Malvern Ouachita River site (AMNH 3596). **(A)** Event bed in the main riverbank (channel) section. **(B)** Sand and impact spherules from the event bed in the channel section (scale bar is 1mm). **(C)** Danian main channel outcrop, looking up-section from the K/Pg boundary. Meter stick is perpendicular to strike. **(D)** Contact between marl and limestone beds 3.5m above the boundary in the channel section (white pin is 2.5cm wide).

There appears to be no difference in depositional environments between the Maastrichtian and Danian sediments, as the section on both sides of the boundary sandstone is lithologically similar marl and mudstone (Fig. 8). Roughly 9 meters of Maastrichtian marl are exposed on the riverbank. The K/Pg boundary at the Ouachita riverbank outcrop has been identified using ammonite biostratigraphy and dinoflagellate micropaleontology (Larina et al., 2016; Dastas and Chamberlain, 2021), while foraminifera from the site have not been age-diagnostic (C. Lowrey pers. comm). The Maastrichtian section is assigned to the *Discoscaphites iris* ammonite zone, and both *D. iris* and *D. minardi* have been collected from the marl 4.5m below the K/Pg boundary (Larina et al., 2016). Although the boundary

sandstone is lithologically distinct from the marl above and below it, dinoflagellate micropaleontology suggests the section is relatively complete, with Maastrichtian, boundary-crossing, and Danian taxa appearing in the sequence (Dastas et al., 2021). Danian indicator species appear 2 meters above the base of the boundary sand alongside some Cretaceous species, which may have been reworked (Dastas et al., 2021).

METHODS

The present study had five major objectives: 1) Identify the fossils in the samples collected from the Danian recovery interval at both sites; 2) Characterize the ecological life modes of specimens in these fossil assemblage; 3) Measure shell volume as a proxy for body size of complete specimens; 4) Analyze changes in niche occupation and body size between the pre-extinction and recovery communities; and 5) compare the assemblage at Brazos and Malvern to those found at other K/Pg sites on the Gulf Coastal Plain.

Fossil Collection and Identification

Samples were collected from the Darting Minnow Creek outcrop near the Brazos River in Texas in April 2017, and from the Ouachita River outcrop near Malvern, AR in October 2019. At both sites, bulk samples were collected directly from the exposed outcrop. Volumetric samples were collected in gallon-sized bags to control the total volume of material from each stratigraphic horizon, to allow for meaningful comparisons of fossil abundance. At Darting Minnow, a total of 3 Paleogene-aged samples were collected from three fossiliferous horizons: above the Lower Concretion Horizon at 120 cm above the K/Pg, just below and above the Middle Sandstone Bed, and at 180cm and 210cm above the K/Pg (Fig. 6). At the Ouachita Riverbank, a total of 9 Paleogene-aged samples were collected at an interval of 50 cm, starting at the disturbed K/Pg boundary sediments and continuing into the recovery interval for 4 meters. One sample, at 2 meters above the boundary, was excluded due to standing water and extensive vegetation which made this part of the riverbank difficult to access.

Samples were then returned to the lab for processing. Specimens were extracted from the matrix primarily by hand using dental picks, though an airscribe or a manual chisel were used

on some of the more lithified samples. Whole or partial bivalve specimens that contain the external hinge morphology, at least 50% of the shell outline, and were taller and/or longer than 2mm and gastropod specimens that include at least 2 to 3 body whorls and were longer than 2mm were considered well preserved for identification to at least the family level. Shark and fish teeth, solitary corals, and echinoid spines were also counted.

The sampled specimens were identified using type-specimen photographs and species descriptions sourced from online databases such as the World Register of Marine Species (WoRMS marinespecies.org), the Digital Atlas of Ancient Life (Hendricks et al., 2015) Wikimedia Commons and in species lists and plates from print publications of the macrofossils from the Gulf Coastal Plain (Cannon, 1922; Stephenson, 1914; Toulmin, 1977; Bryan and Jones, 1989; Hansen et al., 1993).

Ecology

Every taxonomic family of fossil mollusks is assigned an ecological classification which includes feeding strategy, motility, and position relative to seafloor (Bambach, 2007). For ecological analysis, family-level is sufficient, because genera and species within a taxonomic family generally share the same ecospace occupation (Bambach, 2007). These classifications are based on comparisons of fossil species to modern congeners or confamilials, where ecological uniformitarianism is assumed (Gould, 1980). For families with no modern representatives, gross shell morphology is used to assign ecological guilds based on convergence of shell shape for ecological functions. Ecological guild designation in this work was based on determinations reported in the Paleobiological Database (PBDB). Many of the sampled fossil specimens from Brazos, TX are steinkerns (internal molds), which can be assigned to families based on shape, but cannot be identified to finer taxonomic levels

when external shell ornamentation is not preserved. At Malvern, AR original shell mineralogy is present in some strata, but most shells have been fragmented, compacted, and undergone calcite recrystallization preventing precise genus- or species-level identification. For each sample in this study, the number of specimens in each family was tallied, then assigned the corresponding ecological life mode information. This allows for analysis of changing proportional abundances of different life modes throughout the recovery interval (Aberhan and Kiessling 2015).

Body Size

Shell volume as a proxy for body size for complete fossils was measured using a modified ATD model, in which volume is calculated as the product of the three major body axes (anteroposterior, transverse, and dorsoventral) as in Novack-Gottshall (2008). Specimens with at least 70% of the shell intact were photographed at two angles against a contrasting background and ImageJ digital calipers used to measure the three axes. Entire shell volume was approximated by modelling each specimen as an ellipsoid, with volume calculated by multiplying the product of the radius of all three axes by $4/3\pi$ (Fig. 9). Steinkerns made up most of the fossil assemblage at Brazos, TX and were readily measured along all three axes. At Malvern, AR, only a single valve was preserved for most specimens and the shell width could not be measured, so it was approximated as the shorter of the length or height measurements. All aragonitic gastropods and bivalves were included in the body size analysis at Brazos, TX but calcitic oysters were too fragmented to be included. At Malvern, AR only aragonitic bivalves were included in body size analysis, as gastropods were too scarce and oysters were too fragmented.
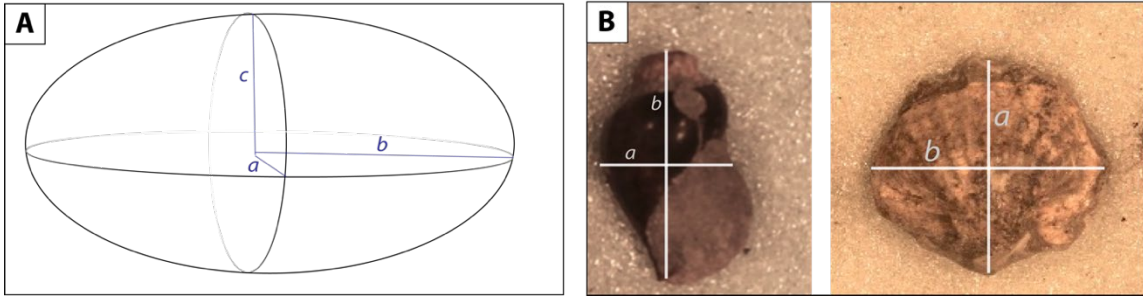
Figure 9: **(A)** Mollusk shells were modelled as ellipsoids to calculate volume as a proxy for body size after Novack-Gotshell (2008) Volume of an ellipsoid is calculated by the radius of all three axes. **(B)** Gastropods and bivalves were measured along all 3 body axes. In cases where only one valve was present and the dorsoventral depth could not be measured directly, it was approximated as equal to the shorter axis.

Analysis

Rarefaction curves are commonly used in ecological sampling to assess sample completeness, displaying the number of taxa found per unit of sampling effort, here measured as the total number of individual specimens sampled (Fig. 10) (Sanders, 1968; Heck et al., 1975; Hsieh et al.,2016). For all study samples, the rarefaction plots plateau, demonstrating that additional sampling effort (more specimens) would not increase the overall diversity of the sample. Therefore, both common and rare taxa are sufficiently sampled.

Diversity metrics were calculated for each sample. Family-level richness was tallied based on the presence of each family within a sample. Taxonomic richness (number of families) and specimen abundance (within families) between sequential samples were then used to compute Simpson, Shannon, and Fisher-alpha Diversity. These are commonly used as diversity metrics in ecological studies because they account for both richness and relative abundance of each family (Hammer and Harper, 2005). Simpson's index is a measure of evenness, calculating the probability that two specimens selected at random from a sample dataset will belong to the same group, and ranges from 0 (a single taxon dominates the entire

Rarefaction Curves
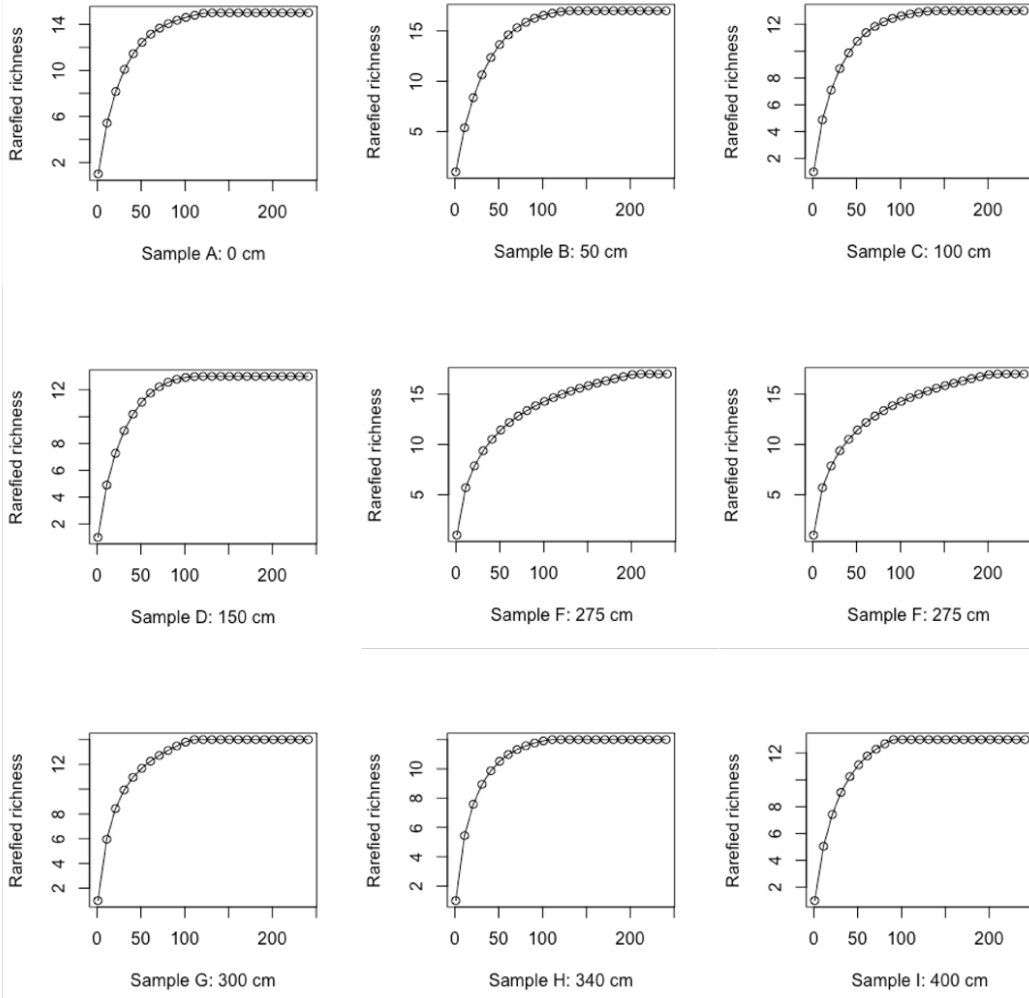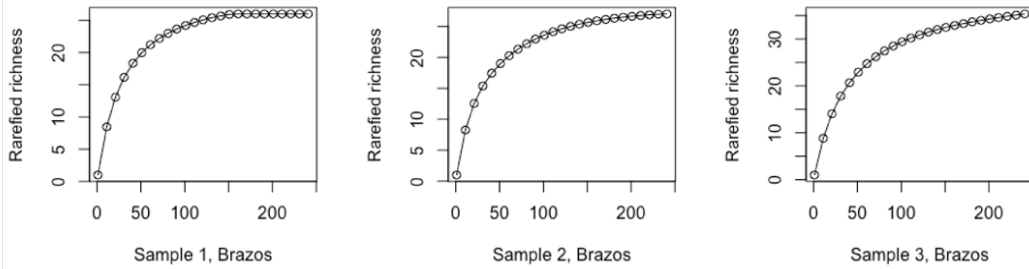
Figure 10: Rarefaction curves for all nine Malvern, AR samples **(A);** and three at Brazos, TX **(B)** show adequate sample at both sites.

community) to 1 (all taxa are equally present) (Simpson, 1949). Shannon's diversity index accounts for both richness and evenness and is calculated as the sum of the proportional abundance of each species, multiplied by its natural log (Shannon, 1948). Fisher's alpha is popularly used in paleoecological studies, where taphonomy and sampling bias is common, as this index is agnostic to sample size, and produces relatively stable values even at low sample completeness (Fisher et al., 1943; Beck and Schwanghart, 2010). Rarefaction and all diversity indices were calculated using the R package *vegan* (Oksanen et al., 2019).

Changes in assemblage ecology over time can be compared between the samples by tracking the changes in proportional abundance of each motility strategy, feeding strategy, and position relative to the sediment-water interface (Bambach, 2007). Ecological life mode distributions for each sample were compared with a Morisita-Horn similarity test, which compares proportional abundances between pairs of samples and returns a value between 0 (no similarity) and 1 (identical samples) (Morisita, 1962; Horn, 1966). Body size changes were tracked throughout the sampling interval by comparing the distribution of body sizes (measured as the log of modelled shell volume) at each sampling horizon. A Wilcox test with a Bonferroni-corrected alpha value of 0.05/36= 0.00138 was used to compare the significance of differences in body volume distributions between each stratigraphically consecutive set of the nine Malvern, AR samples. For the comparison between the three Brazos, TX samples, the Bonferroni-corrected alpha value was 0.05/3=0.0167.

Literature comparisons

To compare the present study to the richness and ecological occupation of other Gulf Coastal Plain sites, Danian mollusk abundance data were downloaded from the Paleobiological Database (PBDB) [Nov 12, 2021] (Toulmin, 1977; Hansen et al., 1993;

Sessa et al., 2009; and Foster et al., 2020). Cephalopods and scaphopods were removed from the PBDB dataset, so only gastropods and bivalves were included in the comparison. Ecospace occupation for each family was included in the PBDB data. The PBDB data was then sorted by both spatial location across the shelf and stratigraphic formation and member.

RESULTS

Stratigraphy at Malvern, AR

The riverbank outcrop at Malvern, AR consists of blocky marl, interspersed with ~10 cm beds of well-lithifiedlight grey beds of calcareous siltstone. The KPg boundary itself is represented by a disturbed bed of poorly-sorted coarse grained quartz sandstone which contains impact spherules, fragmented shells, and phosphate nodules (Fig. 8A,B). In the boundary sandstone, few unaltered shells are present, but oyster fragments are abundant, and some moldic bivalves are present. Shell lags are interspersed throughout the marl on both sides of the boundary and contain bivalve and chondrichthyan material (Fig. 11).

Ecology

The Brazos, TX benthic mollusk fauna shows a significant increase in body size from 80,000 to100,000 years after the impact event an increase in total specimen abundance in the uppermost sample, but no significant differences in proportional abundance of life modes in this interval of the recovery. At Malvern, body size and total fossil abundance peak 2.5 meters into the Danian, and there was a significant shift at this time from an oyster-dominated disaster assemblage to an infaunal clam-dominated recovery assemblage.

Brazos, TX

The benthic mollusk invertebrate assemblage at Brazos, TX is composed of bivalves (61% by total abundance) and gastropods (39% by total abundance). Gastropod and aragonitic bivalve fossils at Brazos are fossilized as steinkerns and external molds, with very little original shell preserved (Figs. 12 and 13). The gastropod assemblage was dominated by
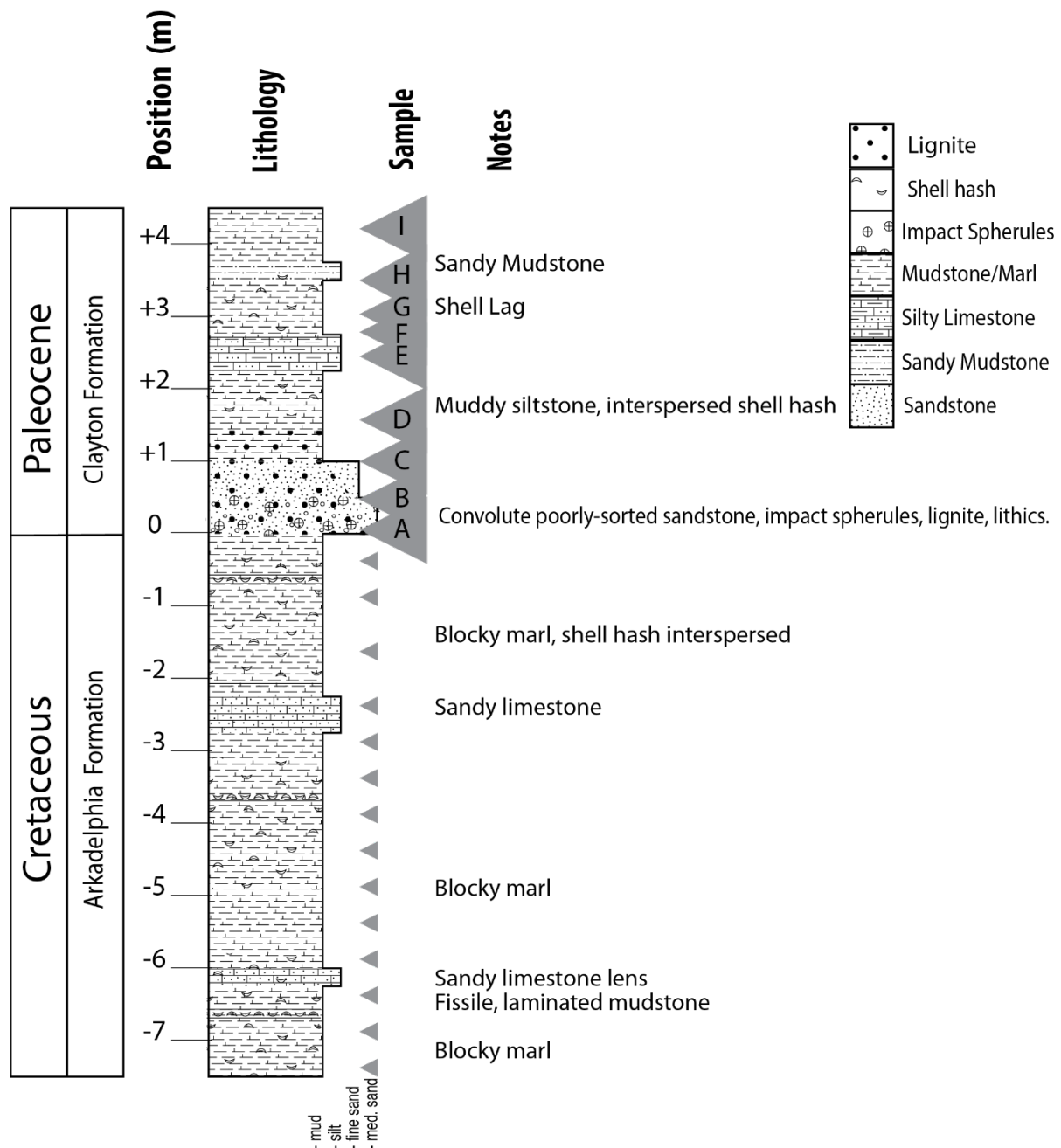
Figure 11: Stratigraphic column of the K/Pg boundary section at Malvern, AR. Samples A-I were taken from the Danian-aged Clayton Formation.

epifaunal, mobile carnivores in the families Buccinopsidae (true whelks), Cancellariide (nutmeg snails), and Fasciolaridae (tulip snails); as well as infaunal carnivores Naticidae (moon snails) and epifaunal suspension feeding Turritellidae (turret shells). The proportional

Figure 12: Most abundant families of bivalves at Brazos, TX site (>20 specimens through section). Scale bar is 1 cm in each photo.
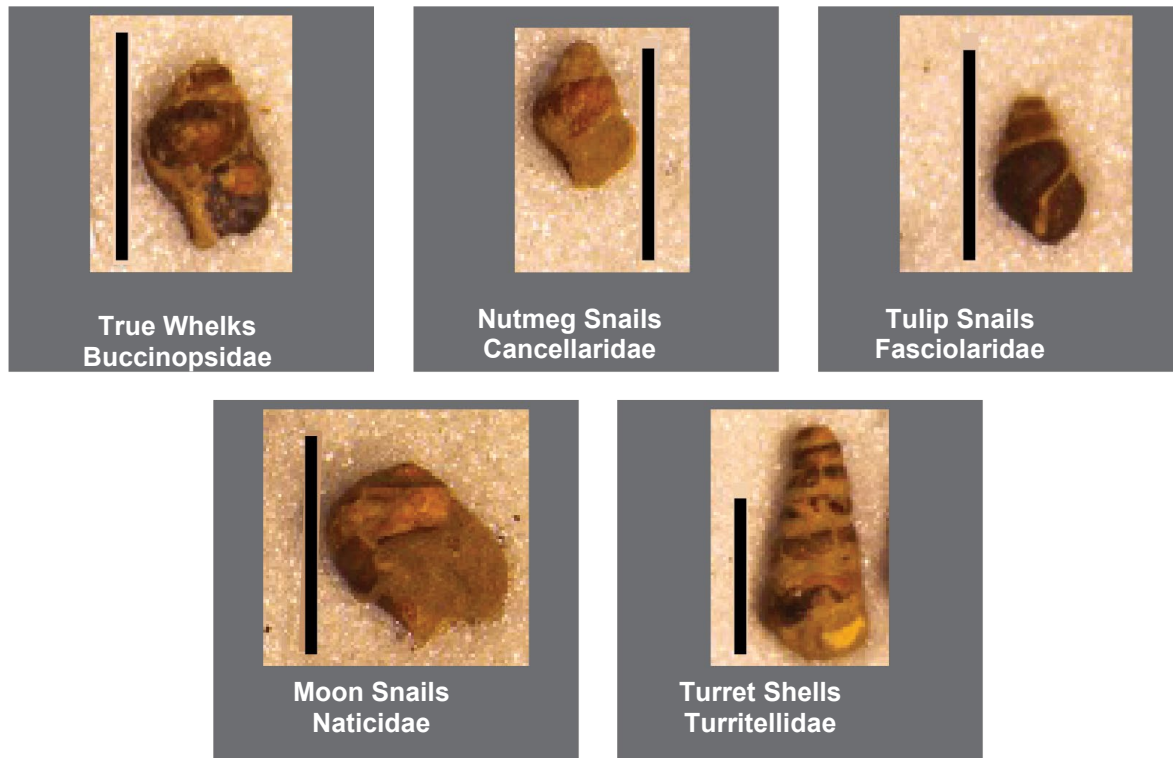
Figure 13: Most abundant families of gastropods at Brazos, TX site (>20 specimens through section). Scale bar is 1 cm in each photo.

abundance of these five families changed little throughout the section (Fig. 14). Fragments of

calcitic oysters were present throughout the section and are preserved as their original shell.
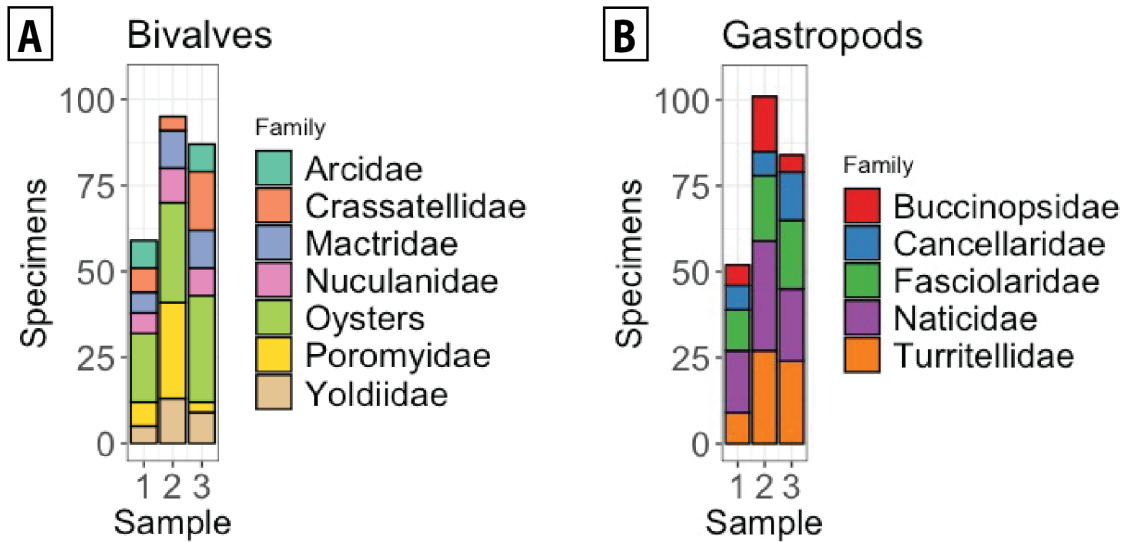
Figure 14: Abundance of the most common (>20 specimens) bivalve **(A)** and gastropod **(B)** taxonomic families at Brazos, TX. While there is an increase in total abundance from Samples 1 to 2, there is little change in proportional abundance of each family.

In addition to the mollusks, echinoid spines and solitary corals were present throughout

the section. Vertebrate material was scarce, with only a few scattered chondrichthyan teeth

(Table 2). Sample 2 (below the Middle Sandstone Bed) also included several millimeter-

scale preserved burrows. Calcareous foraminifera were abundant in Sample 1 and 2 and

uncommon in Sample 3.

Table 2. Abundance of each of the reported macrofossils at the Brazos, TX site, Darting Minnow Creek section. Sample height is distance from the K/Pg boundary as in Hart (2012)

Horizon	Bivalves	Oysters	Gastropods	Foraminifera	Echinoid spines	Corals	Fish teeth	Shark teeth	Trace Fossils
Sample 1 (120 cm)	64	20	71	common	2	9	0	2	3
Sample 2 (180 cm)	148	53	104	common	13	76	0	4	40
Sample 3 (210 cm)	117	57	124	uncommon	4	21	1	2	1

The gastropod assemblage in all three samples was dominated by mobile carnivores and some suspension feeders (Fig. 15). In the lowest sample, no detritivores were present, and in the middle sample, neither grazers nor detritivores appeared, whereas the final sample contained all four gastropod feeding styles (carnivores, suspension feeders, grazers, and detritivores). Bivalves were primarily suspension feeders, but deposit feeders were present in all three samples, with one family of carnivores (Poromyidae) occurring throughout the entire section, and one family of chemosymbionts (Lucindae) appearing in the upper two samples. The stratigraphically lowest sample also has the highest abundance of actively mobile gastropods, with slow-moving and facultatively mobile species increasing in abundance through time. All bivalves were either facultatively mobile or stationary, and the proportional abundance of each motility class changed little between the samples. Roughly 30-40% of the bivalves in all three samples were epifaunal, while 70-75% of the gastropods lived above the sediment-water interface (Fig. 15). Morisita-Horn tests, which return a value of 0 for identical samples and 1 for completely different samples, gave low values for each pair of Brazos samples. (Table 3). This result was surprising given the similar appearance of the ecological composition of each sample. Morisita-Horn is sensitive to abundance so the differences in specimen counts might drive this result.

Bivalve and gastropod molds from all three samples ranged from 3-20 mm in the longest body axis, although the maximum size in Sample 3 was substantially larger. A Wilcoxon rank-sum test with a Bonferroni-corrected alpha of 0.05/3=0.0167 yielded a significant difference in size distribution between samples 2 and 3 (Fig. 16; Table 4). The recovery interval's size increase was primarily driven by size increase in the gastropod assemblage,
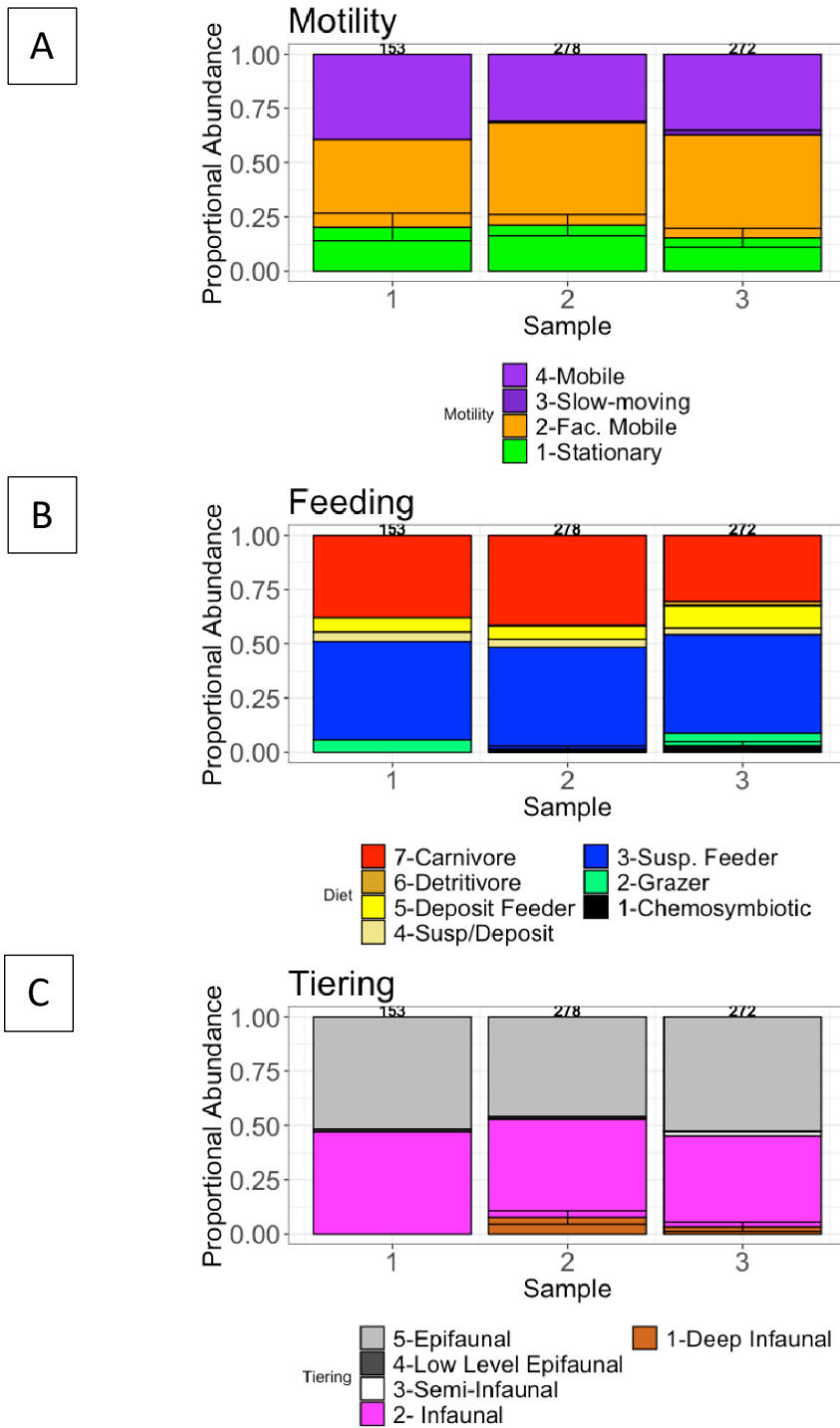
Figure 15: Ecospace occupation at Brazos, TX includes benthic invertebrate motility (A), feeding strategy (B), and tiering (C) in relation to the sediment-water interface. Total number of specimens in each sample displayed above the column. Error bars are calculated from the selected base level. Sampling horizons as in Table 2.

Table 3. Morisita-Horn similarity values of ecospace occupation based on proportional abundance of ecological life-modes at Brazos, TX. Sampling horizons as in Table 2. Morisita-Horn values of 1= complete similarity; 0= no similarity)

	Sample 2	Sample 3
Sample 1	0.0390	0.0746
Sample 2	x	0.103
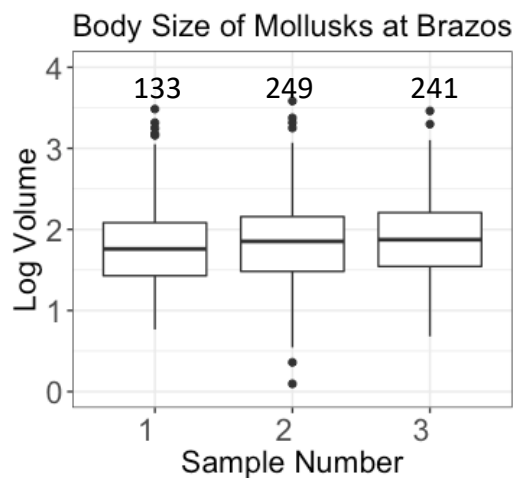
Figure 16: Box plots of overall distribution of the log of shell volume for as a proxy for body size in both bivalve (excluding oysters) and gastropod taxa in three samples from Brazos, TX. Total number of specimens is displayed above each box. Two-sided Wilcoxon tests using a Bonferroni-corrected alpha of 0.5/3=0.016 found no significant differences between the three assemblages.

Table 4: Wilcoxon comparisons of estimated bivalve body volume from three Danian-aged samples collected in Brazos, TX. (Bonferroni adjusted alpha α=0.0167). Comparisons in bold indicate a statistically significant body size difference between pairs. Sampling horizons as in Table 2.

	Sample 2	Sample 3
Sample 1	W=15242, p= 0.2005	W= 13687, p=0.0194
Sample 2	x	W=28091, p =0.221

though a few families of bivalves (Nuculanidae and Mactridae) showed a significant increase in mean body size between samples 2 and 3 (Fig. 17).
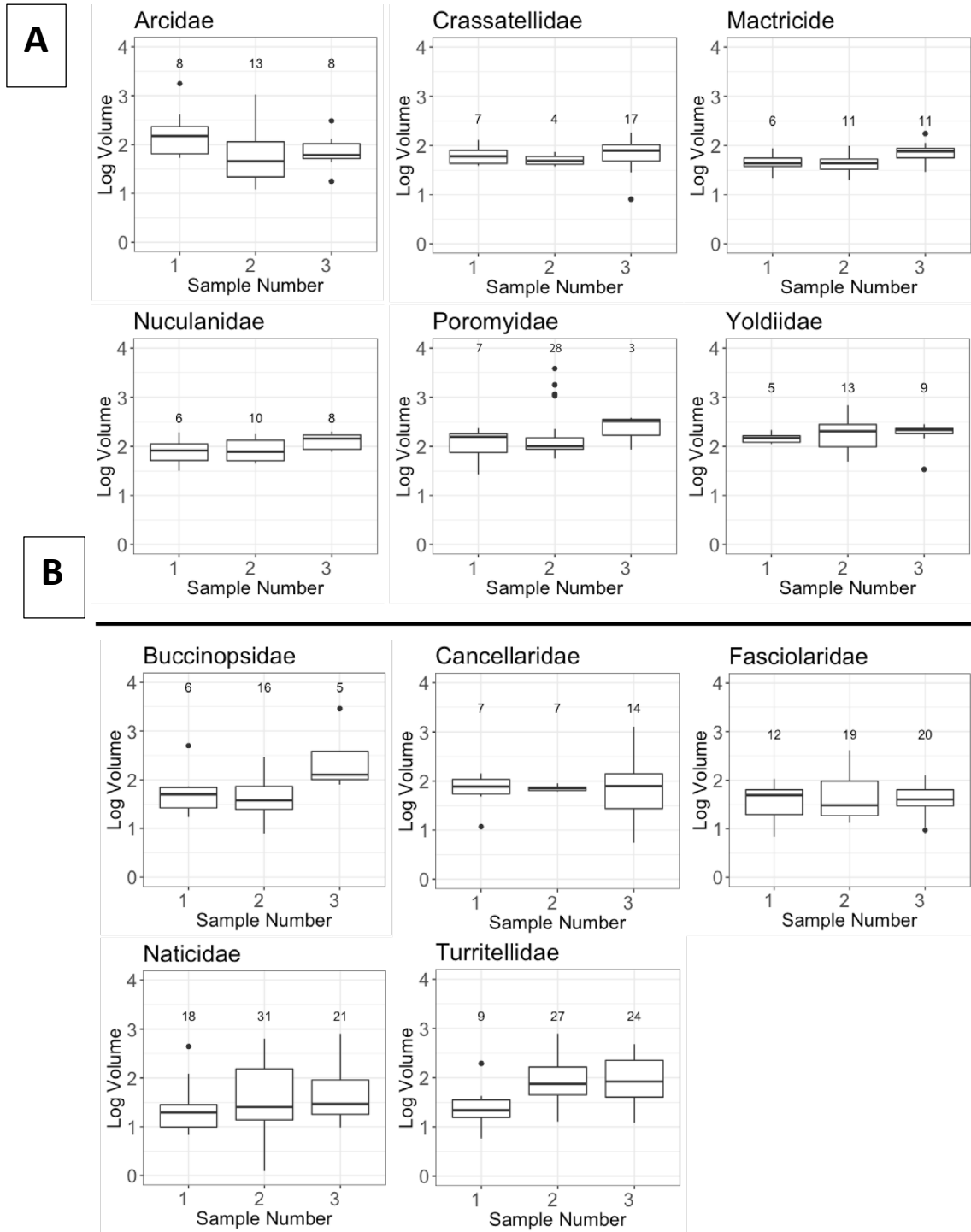
Figure 17: Size distributions of most common bivalve (A) and gastropod (B) families at Brazos, TX. (>20 individuals through the section). Number of specimens per sample is displayed above each box plot. Sampling horizons as in Table 2.

Malvern, AR

Fossil preservation at the Ouachita River site varied throughout the section. The
boundary sand contains primarily abraded molds and highly fragmented shell (Fig. 18A).
Starting 50 cm above the boundary (sample B), most benthic macroinvertebrates are
preserved as thin, chalky shell material (Figs. 18B,C), while fragmented but chemically
unaltered shells became common 2.5m above the KPg boundary (sample E) and continued
through the sampled section (Fig. 18D). Gastropods were scarce, accounting for only 5.3% of
the aragonitic mollusks found in the section. Fragments of calcitic oysters were abundant in
the lower part of the section but became less common 300-400cm above the boundary in
samples G, H, and I (Fig. 18E). The rest of the mollusk assemblage was composed of
aragonitic bivalves, with the most abundant families being *Nuculanidae* and *Veneridae.* (Fig.
19).
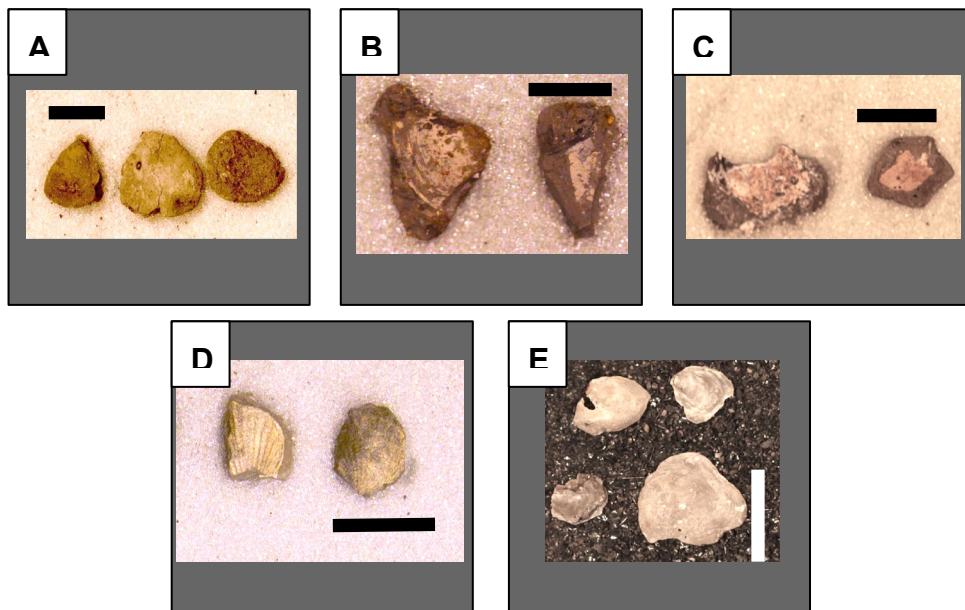
Figure 18: Preservation styles in the Malvern, AR section. Scale bar in each photo is 1 cm.
(A) Moldic fossils from the boundary layer, Sample A; **(B)** Chalky outlines of aragonitic
shells from Sample B, 0.5 meters above the K/Pg; **(C)** Chalky aragonite from Sample D, 1.5
m above the K/Pg; **(D)** Well-preserved aragonitic shell material, common in the top 2
meters of the sampled section. These specimens are from Sample E, 2.5 meters above the
K/Pg; **E)** Fragmented but chemically unaltered calcitic oysters from the boundary layer
Sample A. Oysters were common in the first 1.5 meters of the sampled section.
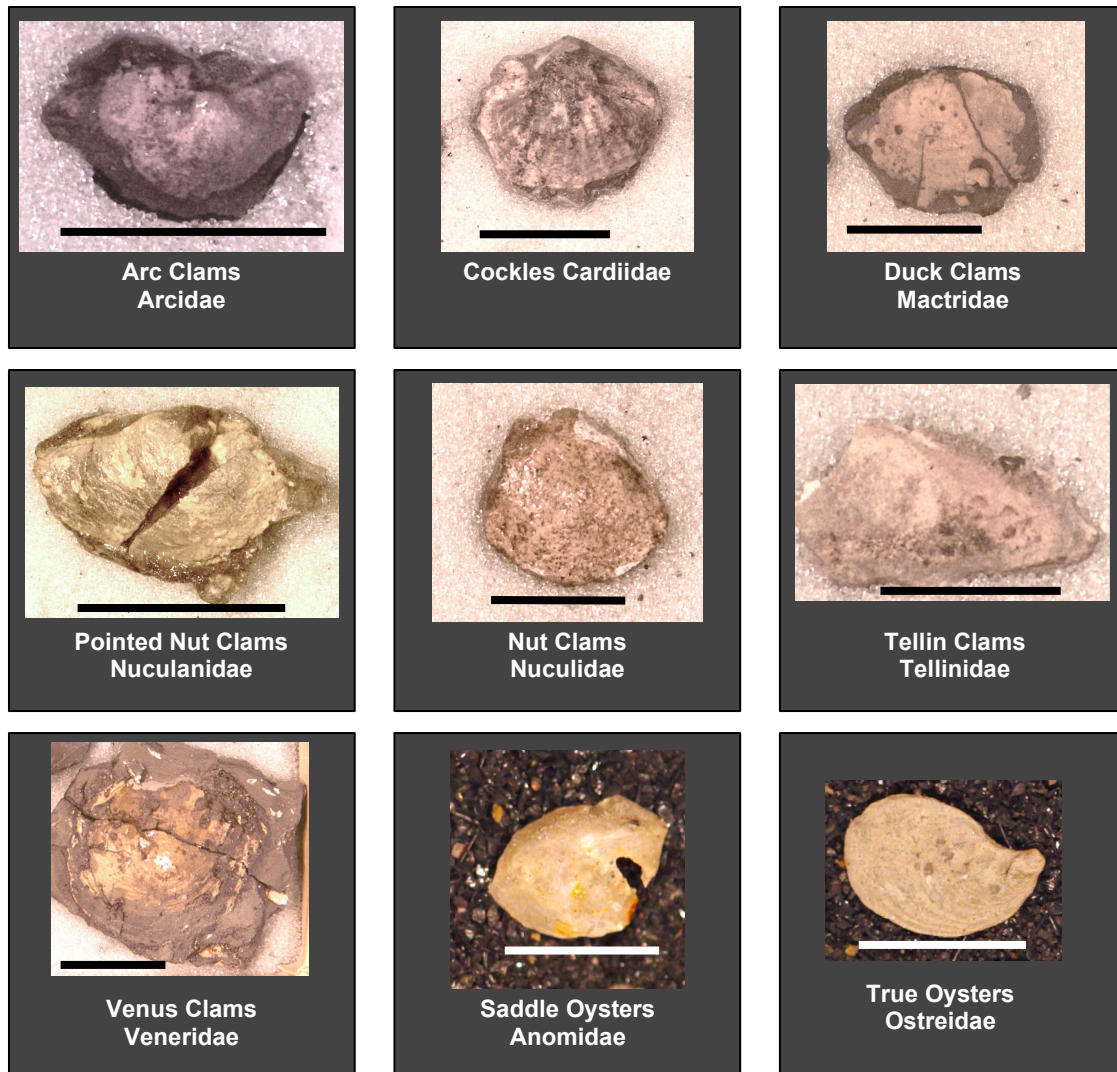
Figure 19: Most abundant (>30 specimens through section) families of bivalves at Malvern site. Scale bar is 1 cm in each photo.

Shark teeth, fish teeth, phosphatic nodules, and other fragmented vertebrate material are present throughout the section (Table 5). The K/Pg boundary was represented by a sand unit that was unique because it contained bryozoans, which were absent in the other samples. Echinoid spines and lignite were both common in the first 1.5 meters (Samples A, B, C, and D), but absent in the upper samples.

Table 5. Abundance of each of the reported macrofossils at the Malvern, AR site. Sample heights measured from the top of the KPg boundary spherule bed.

Sample	Bivalves	Oysters	Gastro-pods	Forami-nifera	Echinoid spines	Corals	Fish teeth	Shark teeth	Other vertebrate	Burrow Fill	Bryozoan
A (0cm)	48	64	13	sparse	77	1	23	14	171	4	23
B (50 cm)	52	72	8	abundant	21	0	13	6	12	5	2
C (100 cm)	56	74	9	abundant	21	0	24	6	31	5	0
D (150 cm)	42	68	8	abundant	15	0	32	2	16	0	0
E (250 cm)	253	20	3	sparse	0	0	6	8	18	0	0
F (275 cm)	158	109	0	sparse	0	0	4	20	12	0	1
G (300 cm)	105	0	2	sparse	0	0	8	2	14	0	0
H (340 cm)	93	19	0	sparse	0	0	6	4	19	0	0
I (400 cm)	89	0	1	sparse	0	0	2	0	14	0	0

Oysters of the families Anomidae (saddle oysters) (2.5% of the total assemblage) and Ostreidae (true oysters) (27.3% of the total assemblage) are the most abundant in the first 2.5 meters of the Danian section (samples A-F), and then decreased in abundance (Fig. 20). Oysters are immobile epifaunal suspension-feeders (Fig. 21). The most abundant families of clams at the Malvern site include Nuculanidae (pointed nut clams) which accounted for an average of 38.3% of aragonitic bivalves across all 9 samples; and Veneridae (Venus clams) made up 10.6 %. Nuculanids are facultatively mobile infaunal bivalves that are primarily deposit-feeders but occasionally supplement their diets with suspension-feeding. Venerids are also facultatively mobile, infaunal, but primarily suspension feed (Fig. 21, Table 6).

Other common families of bivalves included Arcidae, Tellinididae, Nuculididae (nut clams), Cardiidae (cockles), and Mactridae (duck clams) (Fig. 20). Gastropods were
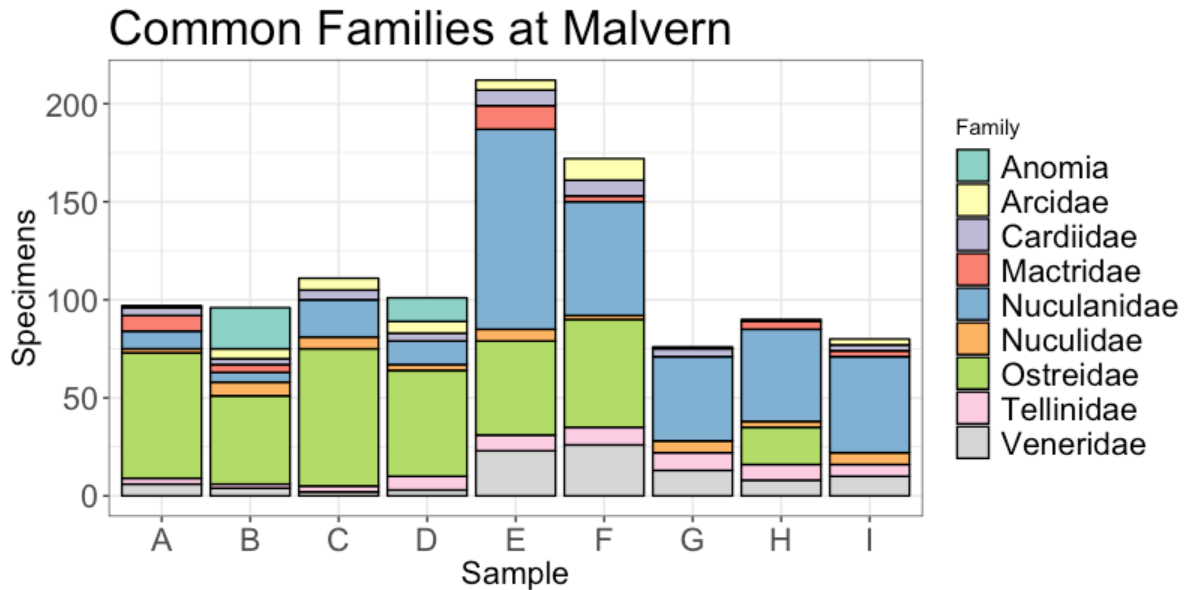
Figure 20: Abundance of most common taxonomic families (>30 specimens) at Malvern shows a dominance of Ostreidae in the first 2.5 meters of the section (sample A to E) and a dominance of Nuculanidae for the last 1.5m from sample E onward. Sample horizons as in Table 5.

uncommon in the Malvern section, but those that were present are primarily epifaunal, mobile carnivores or suspension feeders.

The most ecologically similar samples are those at the top of the section (2.5 to 4 m, samples F to I). Samples A to D appear similar (Fig. 21) but differences in the proportional abundance of ecological guild occupation yield low similarity values (Table 6).

Specimens from sample A are reworked Cretaceous material within a Danian-age deposit so their body volume estimates reflect a Late-Maastrichtian assemblage (Fig. 22). In the first three Danian samples, estimated bivalve body volume was significantly smaller than the Cretaceous fauna (Fig. 22). Two meters after the KPg boundary mean and maximum estimated bivalve volume saw a sudden, significant increase in the siltstone bed and shell lag (Samples E and F, at 2.5m and 2.75m above the boundary, respectively) followed by a significant decrease at sample in G (3m above the KPg boundary) (Fig. 22). Wilcoxon tests between sample pairs showed a high degree of similarity in clusters of adjacent samples: B,
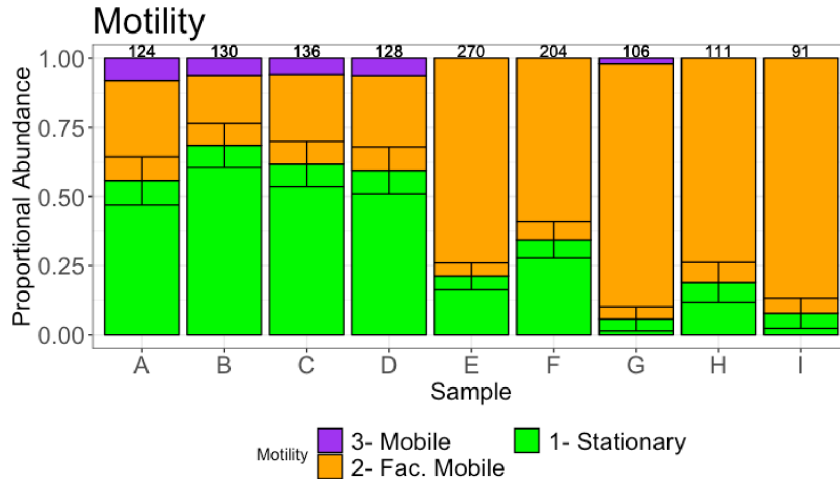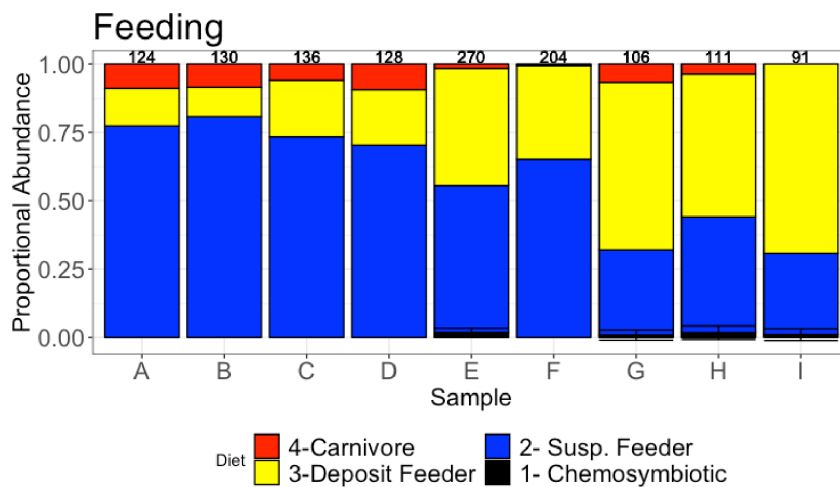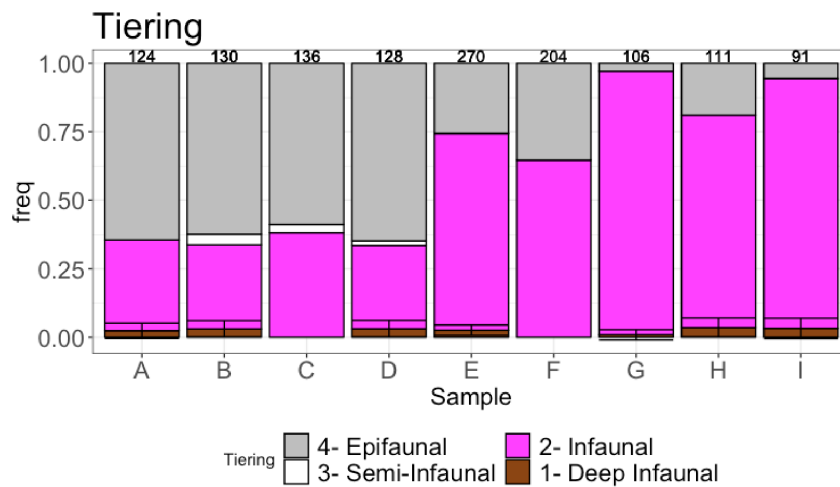
Figure 21: Ecospace occupation at Malvern, AR includes benthic inverebrate motility **(A),** feeding strategy **(B)**, and tiering **(C)** in relation to the sediment-water interface. Sampling horizons as in Table 5. Error bars are calculated from selected base level. In 4 meters of Danian section, a shift takes place from an assemblage dominated by epifaunal stationary suspension-feeders inlcuding Ostreidae (samples A to E) to infaunal facultatively mobile deposit-feeders like Nuculanidae (samples F to I).

Table 6. Morisita-Horn similarity values of ecospace occupation based on proportional abundance of ecological life-modes at Malvern, AR. Letters represent sample horizon (see Table 5) Morisita-Horn values of 1= complete similarity; 0= no similarity)

	A	B	C	D	E	F	G	H
B	0.0168	x						
C	0.0291	0.0111	x					
D	0.432	0.404	0.469	x				
E	0.186	0.187	0.236	0.0779	x			
F	0.702	0.681	0.744	0.104	0.258	x		
G	0.452	0.416	0.478	0.0108	0.0928	0.0776	x	
H	0.696	0.639	0.709	0.0718	0.254	0.0539	0.0559	x
I	0.0204	0.0164	0.0113	0.528	0.265	0.799	0.538	0.785
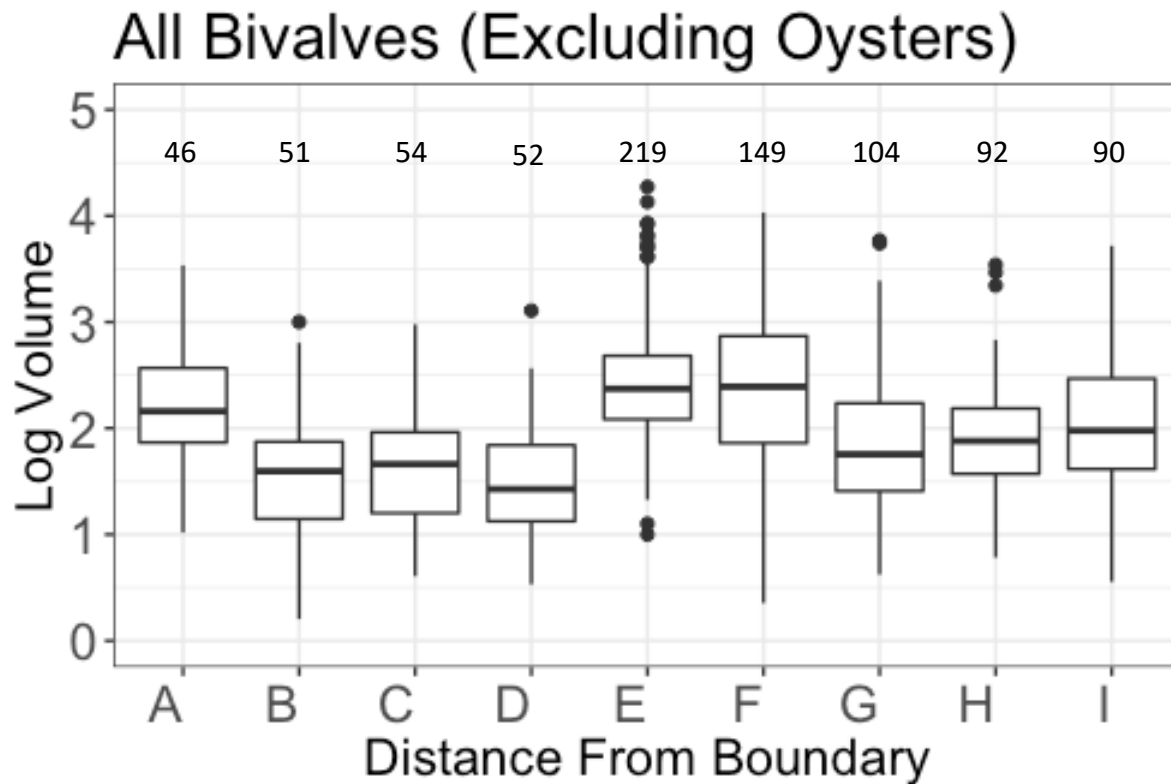
Figure 22: Box plots of body volume estimates of all aragonitic bivalves in the Early Danian of Malvern, AR. Number of specimens is displayed over each plot. Sample horizons as in Table 5.

C, D; E and F; and G, H, I (Table 7). Sample A was most similar in body size distribution to E, F, H, and I. The six most common aragonitic bivalve families (>30 specimens through 4m of section) with sufficient sampling throughout the study interval include Nuculidae, Nuculanidae, Cardiidae, Corbulidae, Tellinidae, and Veneridae. When analyzed separately, these six clades show that the size increase in samples D and E is shared among these ecologically disparate clades while size history is more variable in the final three samples G, H, and I) (Fig. 23).

Table 7. Wilcoxon comparisons of estimated bivalve body volume from nine Danian-aged samples collected in Malvern, AR. (Bonferroni adjusted alpha α=0.00138). Comparisons in bold indicate a statistically significant body size difference between pairs.

	A	B	C	D	E	F	G	H
B	**W= 1864, p= 6.082e-07**	x						
C	**W = 1901, p= 5.259e-06**	W = 1226, p= 0.3346	x					
D	**W = 2012, p= 6.429e-09**	W = 1452, p= 0.4078	W = 1693, p= 0.06827	x				
E	W = 4355, p= 0.1492	**W = 2094, p= 3.665e-12**	**W = 2439, p= 2.311e-11**	**W = 1805, p= 1.947e-14**	x			
F	W = 2919, p= 0.1293	**W = 1374, p= 1.067e-11**	**W = 1682, p= 2.477e-10**	**W = 1179, p= 8.585e-14**	W = 15741, p= 0.5666	x		
G	**W = 3193, p= 0.001104**	W = 1939, p= 0.00666	W = 2281, p= 0.0536	**W = 1699, p= 0.0001591**	**W = 16059, p= 2.584e-09**	**W = 12967, p= 1.296e-05**	x	
H	W= 2785, p=0.002533	W = 1473, p= 0.000236	W = 1836, p= 0.008672	**W = 1252, p= 2.143e-06**	**W = 14344, p= 3.652e-09**	**W = 9682, p-value = 7.543e-08**	W = 4419, p= 0.3577	x
I	W = 2517, p= 0.04	**W = 1383, p= 9.188e-05**	W = 1660, p-value = 0.001496	**W = 1192, p= 1.179e-06**	**W = 12967, p= 1.296e-05**	**W = 8944, p= 1.543e-05**	W = 4061, p= 0.1128	W = 3812, p= 0.3567
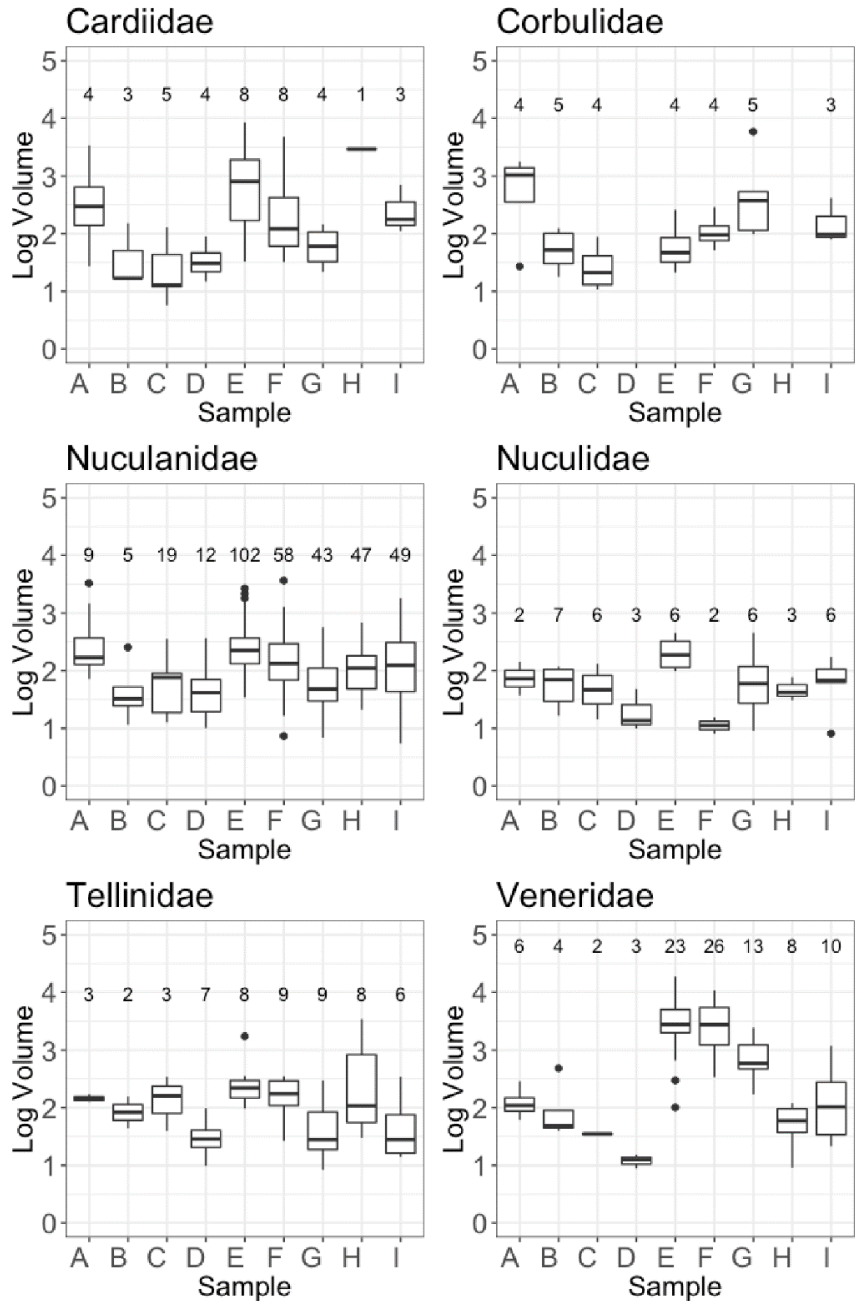
Figure 23: Box plots of body volume estimates for six bivalve families that were the most abundant (>30 specimens) throughout the Danian section at Malvern, AR. Numbers at the top of the plot represent total shell valves measured. Sample horizons as in Table 5.

Gulf Coastal Plain Comparison

We find substantial spatial variability in mollusk fossil assemblages in the recovery from

the KPg mass extinction sampled at Brazos, TX and Malvern, AR. The fossil assemblage

represented by sparse calcitic oysters and an even abundance of aragonitic gastropods and bivalves at Brazos, TX displays a substantial increase in total abundance ~2m (80,000 yrs) above the KPg boundary (Fig. 24). At Malvern, AR mollusk total abundance is more variable and oysters and other bivalves dominated the fauna with few gastropods recovered from the section (Fig. 24).
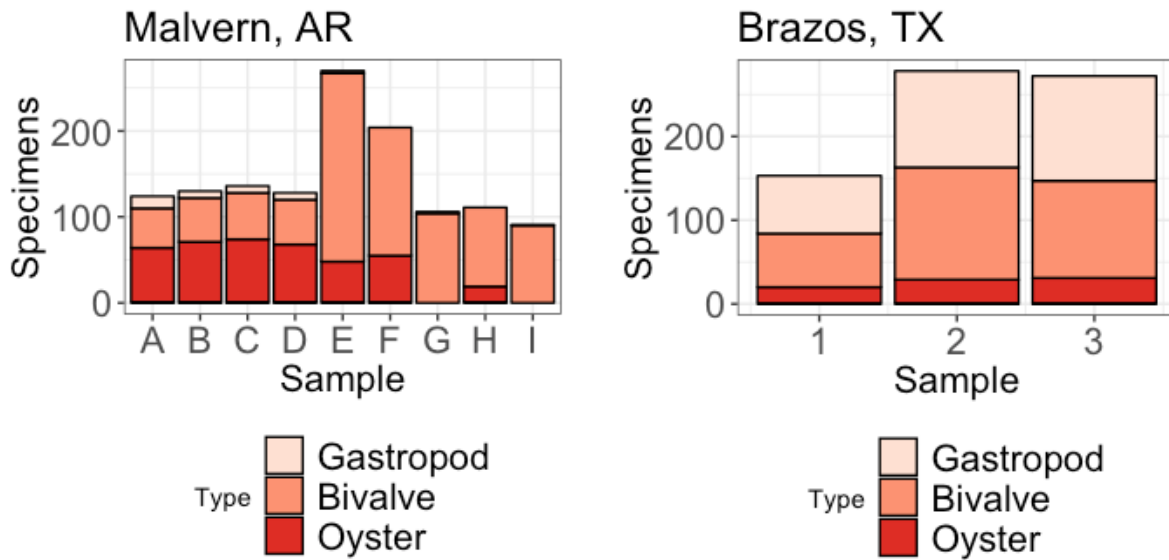
Figure 24: Comparison of abundance of oysters, other bivalves, and gastropods from Malvern, AR and Brazos, TX.

Family-level richness and diversity metrics were higher at Brazos, TX than at Malvern, AR and increased from sample 2 to 3 (Fig. 25). At Malvern, AR family-level richness and diversity metrics were more variable, somewhat tracking the abundance structure (Fig. 25).

The Brazos, TX benthic mollusk fossil assemblage shows similar ecospace occupation to other Danian sites in East Texas based on the proportional abundance of level-bottom Danian mollusks that were active or facultatively mobile, carnivores or suspension feeders, and semi-infaunal or infaunal (Fig. 26) (Hansen et al., 1993; Sessa et al., 2009; Foster et al., 2020).
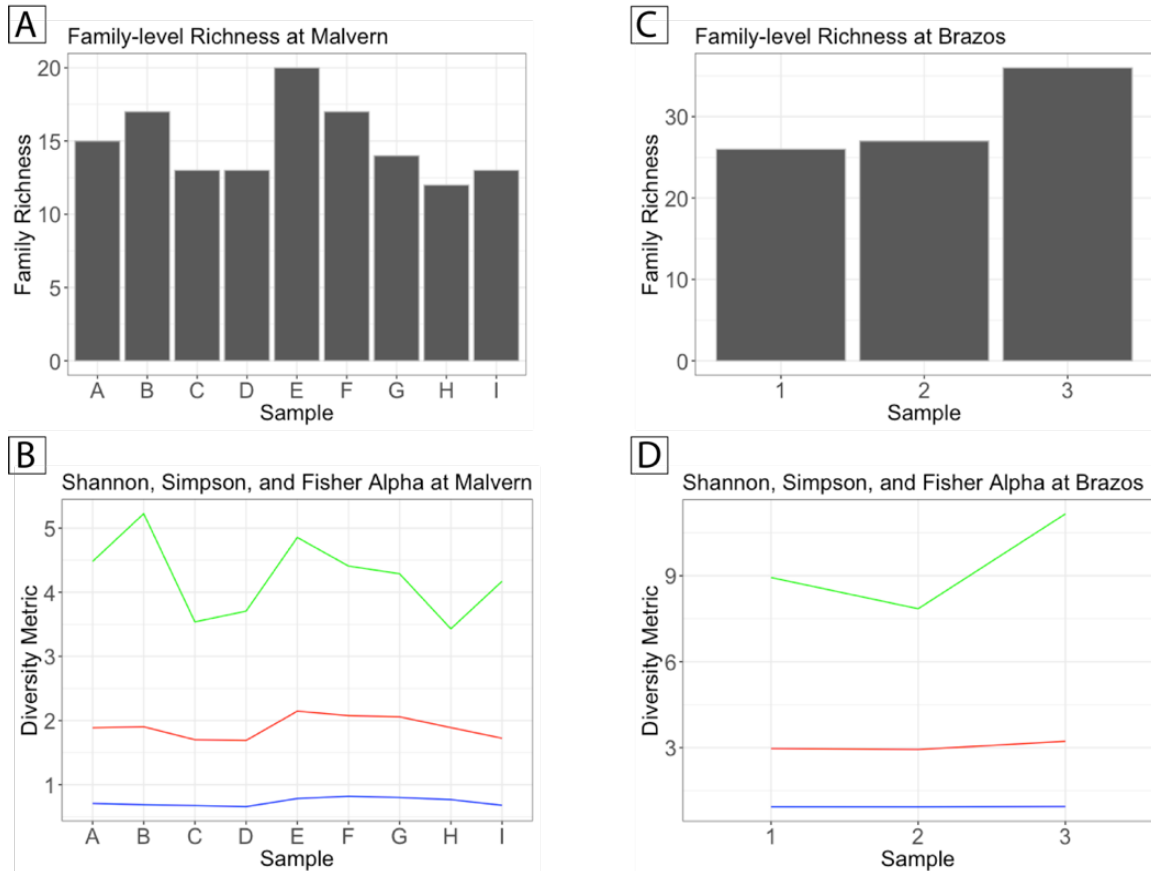
Figure 25: Richness and diversity plots from both sites. **(A)** Family-level taxonomic richness at Malvern, AR reaches a peak at Sample E, 2.5m above the K/Pg boundary. **(B)** Fisher Alpha (green), Shannon (red), and Simpson (blue) diversity metrics at Malvern, AR. **(C)** Family-level taxonomic richness at Brazos, TX increases throughout the section, **(D)** Fisher Alpha (green), Shannon (red), and Simpson (blue) diversity metrics at Brazos, TX.

The Malvern, AR oyster-dominated (epifaunal, attached, suspension-feeding) fauna bears the most resemblance to collections from the Clayton Formation in eastern Alabama and Georgia (Fig. 26) (Toulmin 1977**).** The deposit-feeding bivalve-dominated fauna in the upper part of

the Malvern, AR section (starting at Sample E) (Fig. 21) is not documented in PBDB

collections from the Clayton Formation in Alabama and Georgia (Fig. 26). Instead, the

Malvern infaunal assemblage is most similar to the proportional abundance distribution of

infaunal deposit-feeding and carnivore dominated benthic mollusk faunas documented for the

McBryde Limestone of the upper Clayton Formation and the Porter's Creek Formation of

western Alabama (Fig. 26).
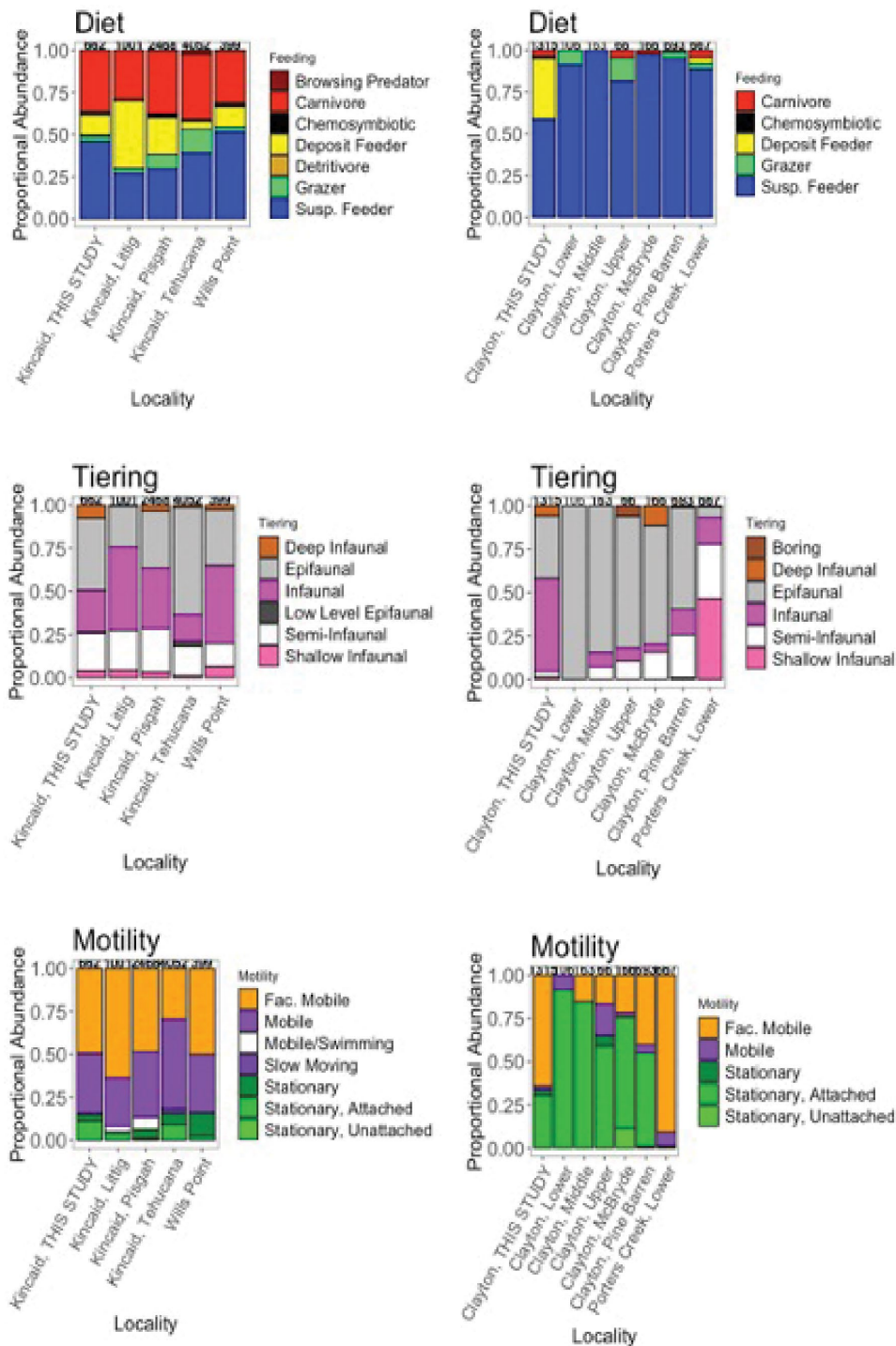
Figure 26: Proportional abundance of functional ecological life modes of bivalves and gastropods from Danian horizons grouped by stratigraphic members and formations from East Texas, Alabama, and Georgia (See Fig. 3). Data from outside of this study is taken from the PBDB (see Fig. 1). Total number of specimens is displayed over each bar. The Littig, Pisgah, Tehuacana are consecutive members of the Kincaid Formation in East Texas. The Pine Barren and McBryde members subdivide the Clayton Formation in Alabama.

DISCUSSION

The community structure at Brazos, TX was largely consistent with the proportional abundance of ecological guilds observed at other localities from the lower Kincaid Formation in Texas. Our results are similar to previous analyses of shallow marine invertebrates in the region: we found the same ecological guilds, with epifaunal carnivorous gastropods and infaunal suspension-feeding bivalves dominating the fossil assemblage (Sheehan and Hansen, 1986; ic et al., 1993; Sessa et al., 2009; Foster et al., 2020). When we examine taxonomic diversity of our samples from Brazos, TX we found similar taxonomic patterns. Abundant Ostreidae (oysters), Carditidae (heart clams), Turritellidae (tower snails), and Cuculaeidae (false ark shells) have previously been observed in the earliest Danian Kincaid Formation, (foraminiferal zones P0 through P1b) [66 to 64.9Mya] (Hansen, 1988; Hansen et al., 1993; Keller et al., 2016). These families then decreased in abundance later in the Danian as represented by the Porter's Creek Formation (Fig. 26). Bryan (1989) also notes an abundance of Cucullaeidae, Carditidae, and Crassatellidae in the earliest Paleocene Clayton Formation near Braggs, AL. Hansen (1988) suggested these fossils represented a disaster bloom of families that were capable of thriving following the environmental perturbations of a mass extinction event due to their ecological and reproductive strategies. Each of the "disaster bloom" families that have previously been identified are suspension feeders, but many other epifaunal and shallow infaunal suspension feeders such as Arcidae, Cardiidae, and Glycymeridae show a dramatic decline in abundance immediately after the K/Pg and do not rebound until foraminiferal zone P1b [64.9 Mya] (Keller et al., 2016). This suggests some aspect of the abundant oysters, turritellids, cardiid clams, and cuclaeids' life-history strategy other than feeding mechanism and life-mode supported their preferential survival in the mass

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extinction aftermath. Modern and presumably fossil species of Turritellidae, Carditidae, and Ostreaidae use a mixture of reproductive strategies including both broadly dispersed planktic larvae and brooded eggs with local recruitment of larvae, which would have allowed them to re-populate rapidly following the environmental stress (Hansen, 1988).

Food shortages due to reduced primary productivity are implicated as one of the main causes for dwarfing of communities in the aftermath of the K/Pg (Twitchett, 2007). Although body size did not change significantly within the first 100,000 years of the Danian at Brazos, TX (Fig. 16), fossil abundance and family-level richness increased. However, there is no corresponding change in ecospace occupation in the Kincaid Formation at Brazos, TX (Fig. 15) or in the upper members of the Kincaid and the overlying Wills Point Formation (62 to 58Mya) of East Texas (Fig. 26). While limited by sampling resolution, this pattern suggests a rapid repopulation of major ecological guilds followed by secondary infilling of diversity. The return of ecological function before diversity is observed for the benthic marine invertebrate recovery from the end-Permian mass extinction (Foster and Twitchett 2014) and for the nannoplankton recovery of the end-Cretaceous (Alvarez et al., 2019). These results suggest that functional ecology experienced limited selective pressure at the K/Pg extinction boundary in this locality.

The most significant change in richness, and Shannon diversity at Brazos, TX occurred between Samples 2 and 3: above and below the Middle Sandstone Bed (MSB), respectively. Hansen (1988) places the "recovery" interval for most invertebrate families at foraminiferal zone P1b, which Yancey (1996) places at the base of the MSB. The increase in size, taxonomic richness, and abundance of macroinvertebrates from sample 1 to sample 3 could represent steps of recovery in the early stages of the Danian level-bottom recovery. The

observed corresponding increase in abundance of benthic mollusks is interpreted as an increase in the total amount of trophic energy available on the shelf to support larger, abundant, and active mollusks. The explanation of increased availability of trophic energy driving the benthic mollusk recovery is supported by observations indicating the first stage of carbon cycle recovery took place within 300,000 years of the K/Pg extinction boundary (Birch et al., 2016).

The high-resolution sampling at fossil Malvern, AR revealed trends that were not documented in other studied sections of the eastern Clayton Formation. One of the most unique aspects of the Malvern., AR section was the dominance of Nuculanidae (pointed nut clams), which is not apparent at other Gulf Coastal Plain sites (Toulmin, 1977, Hansen et al., 1993, Sessa et al., 2009, Foster et al., 2020). Nuculanidae is a family of facultatively mobile, infaunal deposit-feeders which are listed along with Arcidae (ark clam), Carditidae (heart clam), and Lucinidae (lucine clam) as crisis progenitors on the Gulf Coastal Plain at the K/Pg by Kauffman and Harries (1996). These so-called crisis progenitors follow a pattern of intense radiation during the early recovery period, while being relatively rare in pre-extinction communities.

The shift from an oyster-dominated to Nuculanidae-dominated community at Malvern, may reflect depositional or environmental changes to the shelf environment. At Malvern, AR the presence of shell lags in the top half of the section could indicate a decrease in sedimentation rate following a marine transgressive event and/or increased sediment winnowing and shell concentration due to shelf currents (Patzkowsky and Holland, 2012). However, there were no substantial facies changes to support a change in depositional setting. Therefore, the shift from a suspension-feeding fauna to a deosit feeding fauna might

have been driven by other environmental (abiotic) changes or biological interactions during the recovery interval and not simply local sedimentation rate shifts. Modern oysters suffer local extinctions due to eutrophication (excessive nutrients leading to deoxygenation of the water column) and dredging (disruption of the seafloor)(Jackson, 2008). Oyster populations in the aftermath of the end-Cretaceous may have been vulnerable to changes in sediment and nutrient runoff, possibly due to an increase in erosion as plant communities changed in the disaster interval (Sheehan and Hansen, 1986). Nuculanidae grow larger in regions with higher chlorophyll levels in the modern Gulf of Mexico, and tolerate lower oxygen levels (Calderaro et al., 2021). Modern species of the Nuculanid bivalve genus *Yoldia* have been shown to emerge from the sediment to feed during influxes of sinking phytoplankton (Stead and Thompson, 2006); and produce more and larger oocytes when supplied with high concentrations of phytodetritus (Jaramillo and Thompson, 2008). An increase in terrestrially derived nutrients in the Danian could have supported the increase in abundance of nuculanids.

Carnivorous gastropods were considerably less common at Malvern, AR than at Brazos, TX consistent with other studies on the lower Clayton Formation (Toulmin, 1977). Gastropods become much more abundant in the Porter's Creek Formation (Danian Age range) on the eastern part of the shelf (Toulmin, 1977). Reasons for the relative rarity of gastropods in the Clayton Formation has not been addressed in the literature. There may be a preservational or taphonomic difference between bivalves and gastropods resulting in a difference in the assemblages. For example, gastropods were rarer in the recovery from the end-Permian mass extinction, re-appearing as Lazarus taxa millions of years after the mass extinction event (Nutzel, 2005). A similar explanation for the gastropod recovery following

the K/Pg mass extinction requires further study. If there is a true ecological reason, it is important to note that gastropods tend to occupy a greater diversity of life modes compared with bivalve mollusks, so there may be more unexplained variance in abundance across the class as a whole (Egilsdottir et al., 2019).

Bivalve specimens in samples B, C, and D at Malvern, AR are significantly smaller than the reworked Cretaceous material found in the coarse sand and spherule layer of sample A, consistent with an interpretation of a small-bodied disaster fauna (Fig. 22). Sample preservation and coarse identification to the family level prevents an interpretation of a mechanism for this size decrease whether through selective extinction of large individuals or species, survival or smaller taxa, or evolution at small body size (Twitchett 2007). The presence of boundary-crossing dinoflagellates in these horizons establishes this section as belonging to the Early Danian until further biostratigraphic constraints can be developed (Dastas et al., 2021). Body volume significantly increases from sample D (1.5m above the KPg), to sample E (2.5m above the KPg). Three of the most abundant bivalve families (Nuculanidae, Veneridae, and Cardiidae) exhibit this pronounced body volume increase from samples D to E suggesting this a community-wide trend, not driven by one family or ecological guild (Fig. 23). The increase in body size observed in the recovery at Malvern, AR indicates that both predators and prey were able to dedicate nutritional resources to growth rather than simply survival and reproduction. Larger size is an advantage as it allows more access to resources, improved reproductive success, and reduced vulnerability to predation (Blackenhorn, 2000).

The largest mean and maximum body volume corresponds to the maximum richness and highest Shannon diversity in the Danian (Fig. 25). Danian dinoflagellates appear 2m above

the KPg boundary sand, near Sample E indicating fully Danian strata (Dastas, 2021). Body volume was reduced in samples G, H, and I compared to samples D and E, and were more similar to that of the reworked Cretaceous samples in Sample A (Fig. 22). Family-level richness and Shannon diversity also decreased in these three final Danian samples. Body size data is not commonly collected or reported due to the time-consuming nature of data collection, so no shelf-wide comparisons with literature results are possible at this time.

It is important to note that Sample E was lithologically distinct from the other sampled horizons, this bed is a more well-cemented limestone, rather than the poorly lithified mudstone and marl of all other samples (except for the coarse-grained boundary sandstone and spherule layer). The high family-level richness, diversity, and larger estimated body volume may be an artefact of preservation and not ecology. The high concentration of shell material in Sample F indicates that it may be a lag deposit, where low sedimentation rates and/or current winnowing removed sediment matrix, concentrating shell material in a time-averaged deposit.

However, the significant size changes occurring alongside shifts in ecological assemblages, with smaller bivalves common in the Ostreidae-dominated lower section and larger sizes in the later Nuculanidae-dominated assemblage, implies a genuine increase in nutrient availability throughout the section. This is consistent with the expectation of increased input from runoff as terrestrial ecosystems degraded in the aftermath of the bolide impact (Sheehan and Hansen, 1986).

The differences between the two sites indicate a significant spatial variability across the Gulf Coastal Plain in the Early Paleocene. The increase in body size and biodiversity at both sites implies an increase in nutrient availability throughout the section, which may be

correlated with a restoration of primary productivity and recovery of the global carbon cycle in the aftermath of the K/Pg. However, the ecologically dominant taxa at each site are dissimilar, and imply varied local conditions, and different levels of terrigenous sedimentary input.

CONCLUSION

The community ecology of benthic mollusks at Darting Minnow Creek is consistent with other studies from the Brazos River region. The Ouachita Riverbank section in Malvern, Arkansas, appears to be somewhat similar to other lower Clayton Formation outcrops to the southeast, but is unique in the dominance of nuculanid bivalves. The shift from an Ostreidae-dominated assemblage to a Nuculanidae-dominated assemblage in the earliest part of the Danian at Malvern may be the result of a change in local environmental conditions. Difference between the two sites in this study, and other early Danian communities on the Gulf Coastal Plain, reveal spatial variation in communities across the shelf. The changes in proportional abundance of ecospace occupations, as well as increase in body size at the Malvern, AR site implies an increase in nutrient availability throughout the section, which is possibly the result of increased in terrigenous runoff. At the site in Brazos, TX, body size of some families increased, implying a similar change in nutrient availability, but ecological changes were not significant through the section. Most other benthic macroinvertebrate studies throughout the Gulf Coastal Plain do not document body size trends, but the increase in organism size found at the two study sites is consistent with recovery from a mass extinction crisis, as increasing body size after the boundary may be indicative of a return to pre-extinction levels of nutrient availability and primary productivity. The high-resolution sampling at the Malvern site particularly shows a rapidly changing community in the aftermath of the K/Pg and implies spatial variation across the shelf.

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