EXTINCTION AND SURVIVAL OF FROG CRABS (CRUSTACEA: BRACHYURA: RANINOIDA)

FROM THE EARLY CRETACEOUS TO THE PRESENT

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SUMMARY

Faunal turnover is a pattern of diversification and extinction that occurs in taxa throughout the geologic record. Patterns of repeated faunal turnovers are referred to as faunal progression. Understanding the driving factors behind faunal progression, which may be niche partitioning, competition between groups, movement to new environments, or extinction and radiation due to environmental factors, may be key to understanding the pasts and futures of our modern fauna. Within Decapoda, clawed lobsters, podotrematous crabs, and heterotrematous crabs experienced faunal progression. These groups diversified and faced high rates of extinction in succession. The transition between podotrematous crabs and heterotrematous crabs is the most recent such turnover and is therefore of particular interest when trying to understand the potential causes of decapod faunal progression as a whole. Section Raninoida, commonly called ‘frog crabs’, constitutes a major monophyletic group of crabs with podotrematous body forms, and closely follows broader trends of diversification and decline within the podotremes from the Cretaceous to the present day. Additionally, modern raninoids are highly specialized back burrowers, despite several extinct families displaying traits indicative of generalist lifestyles which would seem more likely to survive.

Data on rock type, age, location, and carapace morphology for each species within section Raninoida were analyzed for trends in diversity, taxon longevity, paleoenvironment type, and paleogeographic occurrences using Microsoft Excel, Python, PAST, and ArcGIS. Paleomaps were generated to visualize type specimen occurrences and overall diversity through time.

Declines in raninoid diversity aligned with mass extinction events and major climate shifts, especially those of cooling climate. Likewise, diversification within the section occurred in warm, greenhouse climates. Thus, a major factor in patterns of faunal turnover is likely to be environmental conditions. Raninoid families specializing in back-burrowing appeared to have survived the end-Cretaceous mass extinction event better than other families. However, generalist raninoid families did not go completely extinct at the end-Cretaceous yet failed to recover diversity in optimal climactic conditions as did specialist families. Given the diversification of heterotrematous crabs into a wide variety of niches throughout the Cenozoic, competition may be a secondary, but still crucial, factor in this faunal turnover. These findings help to illustrate the history of our modern decapod fauna and may aid in understanding similar patterns across other taxa.

INTRODUCTION

Decapods are important components of marine ecosystems, and they are present in the geologic record dating back to the Devonian (Schweitzer and Feldmann, 2015). They may have been some of the main drivers behind the Mesozoic Marine Revolution and otherwise have great influences on modern marine ecosystems (Schweitzer and Feldmann, 2010; Schweitzer and Feldmann, 2015). Decapods are particularly relevant to the study of faunal progression, strong patterns of which are present among the different taxa within Decapoda through time. Groups such as the clawed lobsters, podotrematous crabs, and heterotrematous crabs diversified then lost diversity in succession, declining shortly before the diversification of the next group (Schweitzer and Feldmann, 2015). It is unknown if this pattern is due to direct competition between these decapod groups, or if other environmental factors were at play and simply allowed each new group to establish dominance within the fauna by removing the previous competition (Schweitzer and Feldmann, 2015). This progression is also notable in that the groups that are part of it occupy similar, broad ranges of environments (Schweitzer and Feldmann, 2015). At their peaks, decapod groups within this progression make up large proportions of global decapod faunas (Schweitzer and Feldmann, 2015). Understanding the driving factors behind decapod faunal progression could allow understanding of a significant component of many marine ecosystems, as well as lead to new hypotheses about similar evolutionary patterns in other taxa.

Faunal turnover is characterized by one group of organisms losing diversity or abundance in the fossil record, while another group of organisms gains diversity or abundance simultaneously or shortly afterward (Brett et al., 2007; Schweitzer and Feldmann, 2015). Faunal progression is a repeated sequence of faunal turnovers. Proposed causes of faunal progression are niche partitioning, competition between groups, movement to new environments, or extinction and radiation due to environmental factors (Brett et al., 2007; Schweitzer and Feldmann, 2015). Niche partitioning is especially relevant to an evolutionary perspective on decapods, as it has affected the morphology and evolutionary history of these organisms (Jagt et al., 2015). Since only one species can successfully occupy a specific niche, it follows that taxa adapted to separate niches, rather than competing amongst each other, may be able to survive for longer periods of geologic time. In the case of two competing taxa, the one that is able to utilize the niche most efficiently is likely to be the one that persists (Schweitzer and Feldmann, 2015). Other cases may exist in which a niche is cleared by factors other than competition. These factors may include changes in environmental conditions, which make the niche unfavorable to the previous taxon and allow a new taxon to inhabit it with little to no competition (Brett et al., 2007; Schweitzer and Feldmann, 2015).

Paleoclimate:

To consider faunal progression in any period on the geologic timeline, it is important to understand the environmental factors those organisms may have been experiencing. Even when narrowing the time frame to between the Cretaceous and the modern day, a broad range of climates spanning both icehouse and greenhouse conditions occurred.

The Cretaceous was characterized by greenhouse climate conditions and warm, sluggishly circulating oceans (Bralower et al., 2002; Witkowski et al., 2018; Batenburg et al., 2016). Temperature gradients between the equator and the poles were low (Haq, 1980). These conditions allowed for high biological productivity throughout most of the epoch (Batenburg et al., 2016). Temperatures cooled slightly in the Maastrichtian, though greenhouse conditions continued into the Paleocene (Bralower et al., 2002).

The Paleocene and early Eocene were characterized by warm climates that were slightly cooler than the Cretaceous, but still characteristic of greenhouse climates (Witkowski et al., 2018; Baatsen et al., 2020). The Paleocene and Eocene were also punctuated by shorter-term but occasionally extreme warming events (Zachos et al., 1993; Bralower et al., 2002). The Paleocene-Eocene Thermal Maximum, or PETM, is one of the most well-known of such events, and occurred, as the name suggests, at the boundary between epochs (Zachos et al., 1993). Temperatures increased abruptly by 5-6°C, and temperature gradients between the equator and poles lowered once more (Zachos et al., 1993). Warming ceased after 20 kya and temperatures stabilized after just 150-200 kya (Zachos et al., 1993; Zachos et al., 2001; Bice & Marotzke, 2002). However, smaller magnitude warming events continued into the middle Eocene (Foster et al., 2013; Bowen, 2013; Henehan et al., 2020).

Near the end of the Eocene and into the beginning of the Oligocene, global climate began to cool (Baatsen et al., 2020). An abrupt cooling event, the Early Oligocene Oxygen Isotope Increase, occurred near the beginning of the Oligocene, lowering the temperature of oceanic bottom waters by 4-5°C for around 200 kya (Zachos et al., 1993; Sotak, 2010). This may have been associated with changes in ocean circulation and the initial formation of the Antarctic ice sheet (Lear et al., 2008). Temperatures warmed slightly after the early Oligocene, but continued to operate within icehouse conditions, fluctuating between glacial and interglacial periods (Zachos et al., 1993). Global temperatures warmed slightly at the end of the Oligocene and into the Miocene, peaking again at the Middle Miocene Climactic Optimum but not reaching temperatures as high as those in the early Eocene or Paleocene, as evidenced by the retention of ice sheets at the poles (Zachos et al., 2001). Subsequently, temperatures cooled gradually into the Pliocene and beyond (Zachos et al., 2001).

Mass Extinction Events:

Another relevant environmental factor for faunal progression is the occurrence of mass extinction events. Since these events lead to large losses in fauna, they are generally followed by radiations of new organisms evolving to fill empty niches. Mass extinctions do not amplify background extinction rates or cause extinction at random, instead creating new sets of pressures that select for traits that may be different than those that had previously conferred survival (Jablonski, 1986). Traits that previously resulted in a taxon being successful or prolific may not aid in survival during the rapidly changing conditions of the mass extinction, overturning previously successful and speciose taxa in favor of those with coincidental tolerances for the conditions created by mass extinction event. Selective conditions may return to normal after such an event, but species with previously successful strategies may have already gone extinct. While the specific traits mass extinction events select for can vary greatly based on taxon and circumstance, geographic range and less-specialized lifestyles are traits often displayed by species that survive (Jablonski, 1986).

The end-Cretaceous Mass Extinction event is the most recent major extinction event in the geologic record. While the end-Cretaceous mass extinction is usually construed as a short-term event, mounting evidence is beginning to suggest that extinctions began before the

Chicxulub impact itself. Climate change caused directly by the impact, while severe, likely occurred on an extremely brief timescale of 4-5 years (Bardeena et al., 2017). Additionally, global climate was already changing in the Maastrichtian (Bralower et al., 2002). These lines of evidence taken together may suggest a longer-term, more global extinction event leading up to the end-Cretaceous. This was potentially due to yet undiscovered asteroid impacts, or more likely, volcanism and a changing climate (Keller et al., 2004). Regardless of the exact cause and timeline of the end-Cretaceous mass extinction event, its effects on fauna are apparent. This is especially true in decapods, which showed high extinction rates across the globe (Schweitzer and Feldmann, 2022).

Evolutionary and Taxonomic Factors:

The most recent faunal turnover in decapods occurred between the Cretaceous and Paleocene and involved a transition between podotrematous crabs and heterotrematous crabs (Schweitzer and Feldmann, 2015). Podotremes are a group of primitive, less-derived crabs with female gonopores on the third pereiopod coxae (Karasawa et al., 2011; Davie et al., 2015; Karasawa et al., 2014). This is considered to be the basal state for brachyurans (Davie et al., 2015). Heterotremes are crabs with female gonopores on the sixth thoracic sternite and are considered to be the derived state (Davie et al., 2015). Crabs exhibiting a podotrematous reproductive condition made up a significant proportion of the decapod fauna from the Late Jurassic to Late Cretaceous, surpassing clawed lobsters (Schweitzer and Feldmann, 2015). Podotrematous diversity declined sharply after the Cretaceous, followed by a radiation of heterotrematous crabs during the Cenozoic (Schweitzer and Feldmann, 2015). Heterotremes appeared in the Early Cretaceous and began diversifying in the Late Cretaceous. However, the Cenozoic is when they began to make up significant proportions of the decapod fauna (Schweitzer and Feldmann, 2015). Most modern crabs are heterotrematous. In fact, heterotrematous crabs make up over half of the extant decapod fauna (Schweitzer and Feldmann, 2015).

The fall of the podotremes and rise of the heterotremes is the most recent transition in the pattern of decapod faunal progression. Understanding what caused podotrematous diversity to decline may have implications for the future of our modern decapod fauna, while understanding what caused heterotrematous diversity to rise has implications for its past. However, because the podotremes are a basal, polyphyletic group, diversity between podotremes and heterotremes is difficult to compare directly. It is necessary to look for a monophyletic group with which to compare heterotrematous crabs.

First described by De Haan in 1839, section Raninoida is a major monophyletic group with a podotrematous reproductive condition, ranging in the fossil record from the Early Cretaceous to the present day (Karasawa et al., 2011; van Bakel et al., 2012; Karasawa et al., 2014). The earliest raninoids likely originated in reef environments in the Berriasian (Karasawa et al., 2014; van Bakel et al., 2021). Raninoids diversified into several body forms throughout the Early Cretaceous (Karasawa et al., 2014). A gradient of specialization exists among the families of section Raninoida, with some families displaying traits such as elongate bodies streamlined for burying and others displaying traits such as round carapaces with strong ornamentation. The elongate carapaces of Palaeocorystidae, Lyreididae, and Raninidae likely lent themselves to fast and efficient burying and indicate a lifestyle specialized for back-burrowing behavior (van Bakel et al., 2012; Karasawa et al., 2014; van Bakel et al., 2021). Burying is a common behavior in brachyurans, where the body is buried in sediment for concealment from predators and protection from unfavorable environmental conditions (Lee, 2015). Note that burying is distinct from burrowing, as a permanent burrow structure is not maintained (Lee, 2015). Back-burrowing is a more specialized type of burying behavior where the crab uses its pereiopods to dig into the substrate with its posterior end first (van Bakel et al., 2012).

Peak raninoid diversity occurred in the Late Cretaceous when all families were present, with diversity diminishing through the Cenozoic (van Bakel et al., 2012; Karasawa et al., 2014). This aligns with trends in other crabs with podotrematous body forms (Schweitzer and Feldmann, 2015). In contrast to the Late Cretaceous, only a few genera of raninoids (often called "frog crabs") remain alive today (van Bakel et al., 2012; Karasawa et al., 2014). Extant raninoids are from the families Raninidae and Lyreididae exclusively. All extant species display family-characteristic traits that indicate specialization for back-burrowing, with elongated carapaces, modified pleurites, and sediment-gripping textures on otherwise unornamented carapaces (Haj et al., 2002; van Bakel et al., 2012).

Studying trends within section Raninoida offers an opportunity to examine differences between taxa that survive and those that become extinct. The fossil record contains information about a taxon's physical traits as well as its geographic range, habitat type, and the length of time over which a taxon existed. This offers an opportunity to compare these traits against each other and to examine if specific traits lead to longevity as compared to others. Specifically, broad geographic range and tolerance for a variety of habitat types are frequently discussed as factors that buffer a taxon against extinction (Jablonski, 1986; Finnegan et al., 2015; Knope et al., 2020). In general, it has been found that taxa which inhabit both a wide geographic range as well as many types of habitats may be less likely to go extinct (Jablonski, 1986; Finnegan et al., 2015; Knope et al., 2020). This may be because animals with more generalist lifestyles would be less dependent on specific strategies and resources for survival and stand better chances of overcoming catastrophic events that may impact them. However, modern raninoids appear to be scarce, highly specialized burrowers rather than ubiquitous, generalist survivors (van Bakel et al., 2012). This study investigates this apparent exception to the trend.

Hypotheses:

Herein, morphological and paleogeographical traits were examined across section Raninoida to determine what factors may have contributed to the survival of certain taxa. It is hypothesized that taxa with more generalist traits such as rounder bodies and unornamented carapaces, as well as broad environmental tolerances, exhibited greater longevity before and immediately after the end-Cretaceous. However, a transition to burrowing specialists clearly took place sometime before the present day, with specialist families surviving when generalists did not. It is hypothesized that this occurred during the Cenozoic, when crabs with heterotrematous body forms were diversifying into generalist niches. Such a transition may point to competition between decapod groups being the most important factor in faunal progression. Alternatively, if a transition between generalist and specialist families occurred near a mass extinction event or during a time of rapid climactic change, environmental factors may have been the main drivers of faunal progression. In addition to these hypotheses, the data were explored for other patterns, such as the survival of the back-burrowing families Raninidae and Lyreididae to the present, but not Palaeocorystidae.

Overall, findings from this project will help us better understand long-term trends in extinction, faunal progression, and adaptation. Specialization and geographic range are concepts that are already applied to modern day marine species in evaluating their risk of extinction (Finnegan et al., 2015; Knope et al., 2020). Better understanding the impacts of these factors in the fossil record can help us to apply them to the conservation of our extant species. Looking back in time, we may find trends and explanations that help us understand the past and predict the futures of our extant taxa.

METHODS

Data Collection:

The original dataset used in this study contained each species within section Raninoida. It was compiled from within the *Systematic List of Fossil Decapod Crustacean Species* by Schweitzer et al., 2010. Species added to section Raninoida after 2010 were added to the dataset using the publications in which the species was named. Rock type, age, location, and rock formations were compiled along with species names and taxonomic placements. Geographic coordinates and carapace morphology were added over the course of this project. Extant species were determined and added to the dataset using the World Register of Marine Species (WoRMS).

Stratigraphy:

Ages of fossil occurrences were most often reported by a stage or epoch in original publications. Due to limited stratigraphic data, species were ranged through the entire age or epoch of formations in which they occurred. The IUGS International Commission on Stratigraphy's Chronostratigraphic chart v 2020/03 was used to determine the duration of each age in millions of years.

Rock type data was present in the original dataset. This data is important in determining the original depositional environment the fossil formed in, and by extension the paleoenvironment inhabited by each species. In species with missing rock type data, the data was retrieved from the original paleontological publication or collection log where possible. Rock type data was not limited to type specimens and was reported for any specimen with confirmed taxonomic placement.

For ease of analysis, rock types were standardized and organized into the following categories: Fine Siliciclastic, Coarse Siliciclastic, Mixed Siliciclastic, Carbonate, Reef Carbonate, Marl, and Multi-Environment. Fine Siliciclastics include mudstones, siltstones, and shales. Coarse Siliciclastics include sandstones. Mixed Silicilastics include rock types that contain multiple grain sizes. Carbonates include limestones. Reef carbonates include limestones with evidence of coral, sponge, and/or bryozoan fossils. Marls include any type of marl. Multi-Environment includes species with specimens that have been found in more than one distinct category listed above.

Species found in volcaniclastic rocks were marked as such; however, most were also found in or alongside at least one other rock type, either in that same occurrence or in different occurrences. These specimens likely inhabited environments characterized by non-volcaniclastic rocks, with the formation of volcaniclastics constituting a catastrophic event (Schweitzer and Feldmann, 2015). However, the original environment these species inhabited is difficult to determine. Therefore, species found in volcaniclastic rock, and no other rock type were given the volcaniclastic tag and marked as ‘unknown’ for their main environment.

Extant species were assigned to rock types based on the substrate in environments the species is known to inhabit. In some cases, species only had specimens reported by the depth at which they were collected, and substrate type was unknown. These species have been marked as ‘Shallow Subtidal’ or ‘Deep Water’ with respect to the depth at which they were collected.

Location:

In order to create maps of species occurrences, location data was compiled for each type specimen for fossil species and added to the dataset. Exact latitude and longitude coordinates for each type specimen were obtained from the Paleobiology Database and species-naming publications where this information was available. In cases where latitude and longitude data were not available from either source, coordinates were estimated using the names and locations of localities, geographic features, cities, or other geographic information provided by the publication from which the species was named. Google maps was used to obtain latitude and longitude coordinates for these features. Coordinate data was collected for extant species in a similar way. Where available, locations and coordinates from species-naming publications were used. For remaining species, museum specimens from the United States Smithsonian National Museum of Natural History and Muséum national d'Histoire naturelle, Paris collection logs were used to estimate a central location within the species' range.

Paleocoordinates for fossil species were obtained from type specimen listings on the Paleobiology Database, where possible. For remaining specimens, paleocoordinates were calculated from modern latitude and longitude. These calculations were performed using the Paleobiology Database's interface for listing new species. To facilitate these calculations, a private species listing was created in the database. Then, the modern occurrence coordinates and age for each species was entered into the listing and saved. The listing's preview was updated with palecoordinates calculated from the most recently entered information, and these coordinates were copied into an external spreadsheet. This process was repeated for each species that lacked paleocoordinate data.

Carapace Morphology:

The ongoing Covid-19 pandemic prohibited the direct examination of most specimens. Instead, carapace features were examined using previous publications, images from the Treatise Online (Schweitzer et al., 2018) and available specimens where noted. Carapaces were measured for width and length, and morphological features were examined at the microfeature and microstructure levels, as defined below. Carapace morphology was added to the dataset in order to compare taxa to each other, as well as to examine trends or changes in morphology through time. Due to limited data, carapace features were taken from the type species or examined specimens and ranged up to the genus level. Within each genus, discrete features were coded to a genus as present (1), absent (0), both (2), or unknown (?).

Length and width measurements were obtained using images of type species in Schweitzer et al. (2016). Width was measured in millimeters at the widest point on each carapace, while length was measured in millimeters from the posterior of the carapace to the base of the rostrum. In the case of type species images with missing parts, width was measured to the center of the specimen and multiplied by two. Length was measured as accurately as possible given the most posterior section of carapace, and in some cases omitted for specimens with significant portions of their posterior end missing. Length and width are represented as ratios in this study to display carapace elongation while controlling for the size of individual specimens. Width measurements were divided by length to create a width/length ratio for each type specimen. This ratio was then ranged through the genus of the type species for analysis purposes.

Carapace macrofeatures are features observable without the use of magnification. These features were coded using Schweitzer et al. (2016), and the images therein as reference. Carapace macrofeatures are considered diagnostic at the genus level. When missing data from the type species of a genus, another species of the genus was substituted into the analysis.

Generic placement and type species were determined according to Schweitzer et al. (2016). Carapace macrofeatures examined included: **Transverse Ridges**, defined as repeating ridges arranged transversely across the carapace, which may be smooth or slightly serrate. **Grooves**, which are long depressions or lines of pits separating large regions of the carapace. **Keels**, defined as raised ridges or lines of nodes separating large regions of the carapace. **Macronodes**, which are any large nodes or bumps on the surface of the carapace. **Node Clusters,** or groupings of macronodes on the carapace. **Straps**, defined as raised platforms or tightly packed clusters of microfeatures arranged into linear platforms (Waugh et al., 2009). **Complex Pitting**, or large depressions in the surface of the carapace which are often irregularly shaped. **Posterolateral Spines**, which are any spines present on the posterior or lateral margins of the carapace. **Serrate Crest**, which is a serrated ridge just before the anterior margin of the carapace but separate from the margin itself. **Bifid Spines**, defined as any spines with two points at their distal end. **Trifid Spines**, which are any spines with three points at their distal end. Bifid Rostrum, which is a rostrum with two points at its distal end. **Trifid Rostrum**, which is a rostrum with three points at its distal end. **Projecting Orbital Spines**, defined as spines around the orbital margins that extend to or beyond the length of the rostrum.

Carapace microstructures are textural features of the carapace, visible only under magnification. Microstructure data for Palaeocorystidae, Lyreididae, and Raninidae was obtained from Waugh et al. (2009). Carapace microstructures were found to be generally stable at the genus level (Waugh et al., 2009). Microstructures from Necrocarcinidae, Paranecrocarcinidae, Orithopsidae, and Camarocarcinidae were obtained by examining available specimens under a Wild M5-52936 binocular microscope. These were not necessarily type species of their genera. Generic placement was determined according to Schweitzer et al. (2016). Carapace microstructures examined included: Inclined Nodes, High Density Nodes, Inclined Nodes in Pits, Nodes in Depression, Upright Nodes, Fungiform Nodes, Pits, Steep Sided Nodes, Setal Pits, Perforations, High Density Perforations, and Pit Node Perforations. Definitions for these structures are available within Waugh et al. (2009).

Data Analysis:

Microsoft Excel:

Microsoft Excel was used for most of the data management, calculations, and analysis. Graphs showing diversity through time, taxon longevity, and environment types were generated from these calculations within Excel. Python code was used to augment and manage larger calculations across the dataset. Namely, it was used to convert stratigraphic data given in species occurrences as Stage and Age names into numerical data in the format of millions of years ago. Modified versions of this code were used to calculate the time (in millions of years) each species existed before and after specific boundaries, such as the K/T, end-Paleocene, and end-Eocene.

Presence/absence data for each species, genus, and family in each geologic age was used to generate stacked area graphs illustrating changes in familial and generic diversity through time. Families were given a corresponding color, utilized in Figure 1. Genera were given sub-shades of their familial color, determined by modifying the lightness of the base shade. In cases of families with many genera, multiple hues (such as bright red and orange-red in family Raninidae) were used to create enough distinguishable but unified shades of the family-level color.

PAST:

Carapace feature data was analyzed with a Principal Components Analysis at the generic and familial levels using the Paleontological Statistics Software Package (PAST). A Principal Components Analysis was run on the data. Varimax rotation was attempted using SPSS. However, due to missing data, the percent variance values within the first two axes of these analyses turned out the same or worse than the original Principal Components Analysis. Since the goal of this analysis was simply to determine the similarities of carapace features between genera, the original PCA analyses were kept.

At the generic level, hulls were drawn around the genera belonging to each family. Genera were assigned to each hull or overlapping area of hulls they fell within. Genera that were missing significant portions of carapace feature data were omitted from this analysis. Because of the need for one common column for multivariate analysis, specimens that had some data but did not have a W/L ratio were also omitted.

ArcGIS:

To analyze data geospatially, taxonomic categories, geographic coordinates and paleo coordinates, environmental data, W/L ratios, PCA hulls, and first and last appearances of each species were added to a new spreadsheet and formatted for ArcGIS. Species with missing location data were omitted from this analysis. Once in ArcGIS, the Excel data was converted to a shapefile using the 'Display XY data' function. For modern coordinates, modern longitude was assigned to the x coordinate field, and modern latitude was assigned to the y coordinate field. For paleo coordinates, this method was repeated by substituting paleolatitude and paleolongitude data into these fields. The CSGS WGS 1984 coordinate system was used in both cases, to match the basemaps on which these data would display.

To display data from specific time ranges, the Time Slider feature of ArcGIS was utilized. The Time Slider is intended for a wide range of uses, most of them dealing with modern or near-modern periods of time. Because of this, ArcGIS expects dates to be formatted with a month, day, and four-digit year. This is understandably not useful for paleontologists who work on timescales consisting of millions of years. Roelofs (2021) has recently developed a methodology by which non-modern timescales can be converted into a standard date format, and a Python code that can be run in an ArcGIS notebook to convert data into this format. Roelofs' code and detailed instructions for running it, as well as publishing the resulting files to ArcGIS Online, if desired, can be found on GitLab.

Using this code, the ~144mya timescale of fossil raninoid occurrences was converted into a 144-year timescale, ranging from 1900 to 2044. This was repeated for the shapefile generated by the paleo coordinates. The Time Slider was activated in Layer Properties using the option to enter start fields and end fields and selecting the newly-scaled columns for first and last appearance. To view the data in chronological order, it is necessary to reverse the playback direction in the Time Slider controls.

The use of paleo coordinates and data in specific paleontological time intervals necessitated the use of appropriate paleogeographical basemaps on which to overlay the data. Shapefiles for this type of data that were compatible with ArcGIS proved difficult to find, as much available paleogeography data is created for GPlates. Furthermore, ArcGIS does not contain a feature for moving basemaps through time. It is necessary to manually toggle each basemap at the appropriate point in the time slider. Despite this, ArcGIS was chosen over GPlates due to its better functionality in generating static maps and analyzing data.

Paleogeographical data was obtained in the form of .TIFF maps from Cao et al. (2017). These files were originally intended for use in GPlates but can be opened in ArcGIS. Furthermore, they were coded to a coordinate system that ArcGIS can read and contained additional data about shallow marine environments and ice sheets.

Basemaps for 6 mya, 14 mya, 22 mya, 33 mya, 45 mya, 53 mya, 76 mya, 90 mya, 105 mya, 126 mya, and 140 mya were selected from the larger dataset for their relevancy to raninoid fossil occurrences. These maps are .TIFF files, which ArcGIS reads as raster layers. The Raster to Polygon tool was used to convert these maps to shapefiles for ease of modification and use in ArcGIS. The option to create multipart features was selected, allowing all cells of one color, for example landmass color, to transform into a single feature. After converting the maps to shapefiles, appropriate symbology was assigned to each feature type. Using these basemaps, occurrences of fossil Raninoids converted to their paleolocations appear in the approximate locations that they would have inhabited when they were alive, rather than the locations the fossils have been found at in the present day. The 6 mya basemap is nearly identical to the present day, and is used as a modern map for comparison, with modern fossil occurrence coordinates.

RESULTS

Excel Analysis:

Familial diversity in Section Raninoida changed through time (Figure 1). The section was most diverse in the Cretaceous, when all eight families were present. There are two distinct peaks of diversity, with a dip in the early Late Cretaceous. During the first peak, the Palaeocorystidae were the most diverse family, containing 15 species. Cenomanocarcinidae, Necrocarcinidae, and Orithopsidae also comprised significant portions of the fauna, with 5, 6, and 8 species respectively. Raninidae and Lyreididae were the two smallest families during this first peak, containing only 2 raninid species and 4 lyreidid species.

Starting in the Cenomanian, Cenomanocarcinidae, Necrocarcinidae, Paranecrocarcinidae, Palaeocorystidae and Orithopsidae all experienced sharp declines in diversity. Most families had their numbers of species halved. By the Coniacian, there were 2 species in the Cenomanocarcinidae, 3 in the Necrocarcinidae, and 8 in the Palaeocorystidae. Only 2 species within Orithopsidae and 1 within Paranecrocarcinidae remained at the lowest point of this decline. Lyreididae and Raninidae gained some species between the Cenomanian and Coniacian, but by the Coniacian had returned to similar levels of diversity to those in the Early Cretaceous, with 1 and 4 species respectively.

The second peak in raninoidan diversity occurred in the Late Cretaceous. Cenomanocarcinidae, Necrocarcinidae, Paranecrocarcinidae, and Orithopsidae regained diversity on the order of one or two species but did not return to the levels of diversity from the Early Cretaceous. Camarocarcinidae originated during this peak in the Campanian, but with only one species. Lyreididae and Raninidae diversified greatly during this time, both reaching 11 species during the Maastrichtian and becoming the two largest families in the section. Despite consistent declines since the Early Cretaceous, Palaeocorystidae was still the third largest family in the section during the Maastrichtian, with 7 species remaining.

Between the Maastrichtian and Danian all families experienced a sharp decline, likely related to the K/T mass extinction event. The Paranecrocarcinidae and Palaeocorystidae both became extinct at this boundary, while the last remaining species within Necrocarcinidae did not survive past the Danian. Camarocarcinidae diversified after the K/T boundary but remained at low diversity through the Paleocene with a plateau of 4 species. Lyreididae and Raninidae survived the K/T boundary with 4 and 6 species respectively. Both families had small gains in diversity through the Paleocene on the order of 1-3 species, but diversity remained relatively constant until the Eocene.

Camarocarcinidae and Cenomanocarcinidae both became extinct by the beginning of the Eocene. Few species from Orithopsidae remained. Lyreididae diversified slightly in the Eocene, reaching a high of 11 species during the Lutetian before the family declined slowly but survived to the present day. Meanwhile, Raninidae began to diversify rapidly during the Eocene. While there were 7 species in this family during the Thanetian, there were 40 in the Ypresian, and 66 in the Lutetian. Raninid diversity declined sharply in the middle of the Eocene, falling to 32 species in the Bartonian, before it rose back to 45 species in the Priabonian. In the Rupelian, diversity in this family dropped sharply to 22 species, then remained constant throughout the

Miocene before falling again to 10 species after the end of the Miocene. Post-Miocene, the diversity of Raninidae fell slightly, but the family survives through to the present day.

Generic diversity throughout section Raninoida also changed through time (Figure 2). Genera are grouped and color coded by family in this figure, but peak size is still based on the number of species within each genus. As mentioned previously, there was high familial diversity in this section throughout the Cretaceous (Figure 1). Families were also generically diverse during this time, with the exceptions of the Cenomanocarcinidae, Camarocarcinidae, which only contained 1 to 2 genera at once (Figure 2). Necrocarcinidae and Paranecrocarcinidae both contained 2 to 3 genera throughout most of the Cretaceous, though the Paranecrocarcinidae declined to just one genus during the Late Cretaceous. Orithopsidae started with 5 genera in the Early Cretaceous, then declined to just 3 genera during the mid-to-Late Cretaceous. Palaeocorystidae was one of the most generically diverse families, containing 5-6 genera throughout the Cretaceous. Raninidae and Lyreididae contained nearly as many genera as they did species during this time.

At the K/T boundary, generic level diversity fell in all families. After this decline, generic level diversity remained at constant, low levels through the Paleocene in all families except the Raninidae, which saw a slight rise from 5 to 7 genera by the Thanetian. Notably, there were still nearly as many genera as species in both the Raninidae and Lyreididae throughout the Paleocene.

As seen previously, Cenomanocarcinidae and Orithopsidae were represented by few species at the beginning of the Eocene, and only 1 to 2 genera occurred among these species. Lyreididae, while it diversified in species, did not gain many new genera during the Eocene. Instead, the existing lyreidid genera speciated. Lyreididae maintained a diversity of 2 to 4 genera until the Pleistocene, where the family dropped to a single fossil genus. Following familial trends, Raninidae diversified sharply at the generic level in the Ypresian, rising to 16 genera. However, much of the familial level gain in diversity appeared to follow a similar trend to Lyreididae. A few speciose genera, including *Lophoranina*, *Raninoides*, and, in the Oligocene, *Ranina*, accounted for a large portion of diversity within the family. These speciose genera within Lyreididae and Raninidae survived the subsequent losses in diversity after the Eocene and include extant species or species that survived nearly to the present day.

The average generic longevity for each family changed after major geological boundaries (Figure 3A, Figure 3B, Figure 3C). Average generic longevity is recorded in millions of years and calculated from the stratigraphic ranges of every genus within a particular family. Longevities are averaged before and after the End Cretaceous, end-Paleocene, and end-Eocene boundaries. In the case of genera that cross these boundaries, their longevity is split across boundary, and the appropriate portions are incorporated into each familial average.

Paranecrocarcinidae and Palaeocorystidae became extinct at the K/T boundary (Figure 3A). The average time genera within these families survived after the Cretaceous is displayed as 0. Necrocarcinidae survived this boundary, but there was a clear jump from being the family with the highest generic longevity during the Cretaceous at 37.28 million years, to the family with the lowest generic longevity after the End Cretaceous at 4.4 million years. Indeed, the few surviving members of Necrocarcinidae went extinct shortly into the Paleocene. Orithopsidae, Cenomanocarcinidae, and Camarocarcinidae all showed reductions in generic longevity after the end-Cretaceous. Lyreididae showed slightly increased generic longevity after the end-Cretaceous, from 20.6 million years to 25.02 million years. Raninidae showed greatly increased generic longevity, from 11.24 million years before the end-Cretaceous, to 24.49 million years after the end-Cretaceous.

Necrocarcinidae and Camarocarcinidae became extinct by the end of the Paleocene (Figure 3B). Cenomanocarcinidae showed a great reduction in generic longevity after this epoch as well, going from an average of 18.75 million years per genus, to an average of 8.2 million years. The reduction in generic longevity (Figure 3A) is also reflected by the average longevity before the end-Paleocene being slightly lower than the average longevity before the end-Cretaceous, which was 10.2 million years (Figure 3A). Orithopsidae did not show a marked change in generic longevity in this figure from the last, meaning that the drop in longevity occurred largely after the end-Paleocene. Likewise, Raninidae and Lyreididae showed little change in generic longevity from the previous period.

All families but Orithopsidae, Raninidae, and Lyreididae became extinct by the end of the Eocene (Figure 3C). Orithopsidae showed a large decrease in generic longevity after the end-Eocene, and as displayed by other figures, went extinct shortly after this boundary. After showing increasing longevity in figures 3A and 3B, Lyreididae shows a small decrease in generic longevity after the end-Eocene, going from 25.01 million years to 20.12 million years. Raninidae shows nearly identical averages in generic longevity before and after the end-Eocene, at 18.18 million years and 18.89 million years respectively.

Overall, there are very few species found in multiple rock types across the entire section (Figure 4A, Figure 4B). Rock types are indicative of depositional environments, and consequently the paleoenvironment fossil species likely inhabited. Species appeared to specialize in one environment over others, regardless of family. Notably, Raninidae have a smaller percentage of species found in siliciclastic environments than other families, at a total of 38.08%. 32.65% of species in Raninidae were found in carbonates. Lyreididae have a significantly higher percentage of species living in siliciclastic environments, at 84.6%. This indicates more varied environmental preferences in Raninidae, with slightly more preference towards carbonates than siliciclastics.

Lyreidids appear to be heavily specialized for siliciclastic environments. Between Orithopsidae, Paranecrocarcinidae, and Cenomanocarcinidae, there were similar percentages of species found in siliciclastics, ~50-60%, and smaller percentages of species in carbonates, <30%. Palaeocorystidae, Orithopsidae, and Necrocarcinidae have species found within multiple rock types while Paranecrocarcinidae and Cenomanocarcinidae do not. Paranecrocarcinidae and Cenomanocarcinidae have species inhabiting marls, which the Palaeocorystidae, Orithopsidae, and Necrocarcinidae lack. Camarocarcinidae appears equally divided between four different environment types. However, in referencing Figure 4A, it becomes clear that there are only four species in this family included in this study. With such little information, it is difficult to draw comparisons between this family and the others. Rather, the only conclusion that can be made is that camarocarcinids seem able to inhabit a variety of environments and potentially showed a preference for siliciclastics over carbonates and marls.

PAST Analysis:

A Principal Components Analysis of carapace features at the familial level shows Necrocarcinidae, Cenomanocarcinidae, Paranecrocarcinidae, and Camarocarcinidae present in one cluster, while Lyreididae, Palaeocorystidae, and Raninidae are contained within another, looser cluster (Figure 5A). All families within the first cluster became extinct by the beginning of the Eocene and were largely in decline after the K/T boundary. Within the second cluster, all but Palaeocorystidae are extant. The Palaeocorystidae go extinct at the K/T boundary. Orithopsidae is far from both clusters, but closer to the first cluster than the second. This family survived until shortly after the Eocene albeit with low diversity.

The array of carapace features used to produce the arrangement of families within the R-mode PCA analysis is displayed in the associated Q-mode PCA analysis (Figure 5B). In some cases, the absence of a carapace feature in a family impacts the location rather than the presence of that feature in that family. The locations of carapace features in the Q-mode analysis confirms that round and heavily ornamented or spined carapaces were shown by generalist families, while flattened, elongate, and more finely textured carapaces were characteristic of back-burrowing families (Figure 5A, Figure 5B).

The proximities of families in the familial level PCA are echoed in the clusters produced in an R-mode PCA at the generic level (Figure 5A, Figure 6A). Lyreididae are clustered more closely with the bulk of genera from Raninidae than with genera from the other families. Meanwhile, genera from Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae, and Paranecrocarcinidae are clustered very closely together. Genera from Orithopsidae overlap with this group of families, but also show significant similarities to many genera from Palaeocorystidae. Raninidae is by far the most diverse family in terms of carapace features, which is represented by the large hull. Some genera are unique outliers, such as *Ranilia* and *Raniliformis*, extending the shape of the hull. However, the majority of genera within Raninidae are present near the center of the chart. There is significant overlap between the densest cluster of raninid genera, the area genera from Lyreididae occupy, and the area genera from Palaeocorystidae occupy. There is significant overlap between the hulls of Raninidae and Orithopsidae as well.

Interestingly, nearly all genera that occur in recent or near-recent rocks are in areas that do not overlap with the hulls of other families, with the exceptions of *Ponotus* and *Notopus*. *Ponotus* overlaps with both Lyreididae and Palaeocorystidae. However, this genus is a singleton that is only found in the Miocene (Langhian). *Notopus* also overlaps with the Palaeocorystidae and is on the edge of the hull representing Orithopsidae. This genus has one extant species but has remained at low diversity with one or no fossil species reported from the Lutetian when it originated to the modern day. In the Lyreididae, this pattern does not hold true. Only *Lyreidus* and *Lyreidina* are present in the family's hull with no overlaps. The remaining near-recent lyreidid genera all overlap with the hull for Raninidae.

Points in the Q-mode PCA correspond to the carapace features used to ordinate the generic level analysis (Figure 6B). Width/Length ratio weighs heavily on the data. Trifid rostrum also weighs heavily on the points in the lower left quadrant as a diagnostic feature of family Lyreididae, and a feature some other genera share. Posterolateral spines, macronodes, and projecting spines appear to weight importantly on the lower right quadrant, which contains Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae, and Paranecrocarcinidae, as well as portions of Orithopsidae and Palaeocorystidae. Carapace microstructures appear to be most important to the left half of the graph, where genera within Raninidae and Lyreididae plot most frequently. Bifid spines and rostrum, keels, and grooves appear to weight the upper right quadrant where a few, outlying genera of Raninidae are present.

ArcGIS Analysis:

In total, 317 fossil species have been mapped using the location of their type specimens (Figure 7). Note that there is a large overprint of data from North America and Europe, with less data elsewhere in the world. This is likely due to biases in collection rather than the actual paleontological ranges of these organisms. Each point represents the occurrence of a type specimen from one species.

Raninidae is the most diverse and widespread family on the map with 147 species, and Lyreididae is a distant second with 51 species. Other families are interspersed throughout the map in smaller numbers, including 4 Camarocarcinidae, 24 Cenomanocarcinidae, 16 Necrocarcinidae, 17 Paranecrocarcinidae, 20 Orithopsidae, and 38 Palaeocorystidae. Species distributions are displayed as paleo coordinates and divided into the epochs and ages in which the fossils occurred in the figures below.

There are 78 raninoid fossil type specimen occurrences dated to the Early Cretaceous (Figure 8A). The basemap these points are displayed on dates to 105 mya. In comparison to all fossil occurrences through time, there were proportionally fewer species belonging to Raninidae and Lyreididae in the Early Cretaceous. Both families were only represented by 5 species each during this epoch. Instead, the most diverse and widespread family during the Early Cretaceous was Palaeocorystidae with 24 species. Other families during this epoch included Cenomanocarcinidae, Paranecrocarcinidae, and Orithopsidae, all with 12 species each. Necrocarcinidae contained 7 species during this epoch. Camarocarcinidae did not originate until the Late Cretaceous and is not represented on this map

The majority of species present in the Early Cretaceous, 48, did not fall within the raninid or lyreidid carapace hulls generated during carapace feature analysis (Figure 6A). Of the 30 species that did display an overlap in carapace features with raninids and lyreidids, 22 were present in the palaeocorystid carapace hull. Only 4 lyreidid species and 3 raninid species showed no overlap with any other hull during the Early Cretaceous. 1 species was present in the overlap between raninid and lyreidid hulls.

Species inhabited a wide variety of environments in the Early Cretaceous (Figure 8B). Over half of the total species during this epoch, 44, inhabited siliciclastic environments. Of these species, 22 species inhabited fine siliciclastics, 18 species inhabited coarse siliciclastics, and 4 inhabited mixed siliciclastics. Twenty-two species occurred in carbonates, but only one species was confirmed to occur in a reef carbonate. During the Early Cretaceous, 8 species occurred in multiple rock types, indicating multiple paleoenvironments. However, as seen in figure 4, there are not many species that inhabit multiple types of environments in section Raninoida.

There were 119 fossil raninoid occurrences dating to the Late Cretaceous (Figure 9A). The basemap these points are displayed upon is dated to 76 mya. Lyreididae and Raninidae became more diverse during this time and were represented by 20 and 22 species respectively. This put the diversity of Raninidae on par with that of Palaeocorystidae, which also contained 22 species over the course of this epoch. Cenomanocarcinidae was also very diverse and contained 19 species. Necrocarcinidae and Paranecrocarcinidae made up the second tier of diversity during this epoch and contained 12 and 13 species respectively. Orithopsidae only contained 7 species during the Late Cretaceous, a slight fall from the previous epoch. Camarocarcinidae originated during this epoch and contained 4 species, making it the smallest family. Overall, the Late Cretaceous had a high evenness of diversity between raninoid families.

Nearly 2/3 of species, 74, had carapace features that caused them to group within the hulls of families Raninidae and Lyreididae (Figure 6A). This represented a slight increase proportionally of species with these carapace features. Fifteen species of Lyreididae did not overlap with any other hull, as did 15 species of Raninidae. Five species were present in the overlap between Raninidae and Lyreididae. Only 8 Palaeocorystidae had carapace features that caused them to cluster with Raninidae. However, majorities of other families did show significant overlap in carapace features with Raninidae. Five species from Orithopsidae, the majority of species within the family, also had raninid-like carapace features. All but 1 cenomanocarcinid shared carapace features with both Raninidae and Palaeocorystidae.

Remaining species had carapace features characteristic of Necrocarcinidae, Orithopsidae, or Palaeocorystidae in various combinations. In general, camarocarcinids had unique carapace features that did not overlap with other families' hulls (Figure 6A).

In the Late Cretaceous, there were a total of 66 species found in siliciclastics, with 18 in fine siliciclastics, and 21 in coarse siliciclastics (Figure 9B). Twenty-seven species were found in mixed siliciclastics, which was a marked increase from the Early Cretaceous. Only 34 species occurred in carbonates during this epoch, with 4 of those being reef carbonates. Eleven species inhabited multiple environments, which was a marked increase, but still a small proportion of all species. These species were spread out among many families, with only 2 in Raninidae and Lyreididae respectively. Four multi-environment species were from Palaeocorystidae, and the remaining species were necrocarcinids and orithopsids.

There were 67 fossil raninoid occurrences during the Paleocene, which occurred after the K/T mass extinction event dated to 66 mya (Figure 10A). There is a visual shift between this map and the last, from multicolored points to predominantly red and pink ones. This indicates a change in family level diversity. Raninidae was the most diverse family by far after the K/T boundary, with 44 species. Lyreididae was the second most diverse family, though it was represented by only 14 species throughout the Paleocene. There were only 9 total species across the remaining families in the section across this age. Three orithopsids, 3 camarocarcinids, 2 cenomanocarcinids, and a single necrocarcinid species persisted. Palaeocorystidae and Paranecrocarcinidae went extinct before the Paleocene and are not represented on this map.

Most persisting species outside of Raninidae or Lyreididae did not cluster closely with these two families in the carapace feature analysis (Figure 6A). The two exceptions are *Cristella* *hastata*, an orithopsid and *Arcticocarcinus insignis*, the last remaining necrocarcinid. The Raninidae and Lyreididae of this epoch are present almost entirely in their own carapace feature hulls, or within the overlap between the raninid and lyreid hulls. Three species from Lyreididae overlap with the raninid hull, while the rest are present only within their own hull. Thirty-seven raninid species are present only within their own hull, with 2 of the remaining species overlapping with Lyreididae, and the remaining 5 overlapping with the now-extinct Palaeocorystidae. Two species also overlap with the orithopsid hull, and one also overlaps with cenomanocarcinids.

Over half of species during the Paleocene, 35, occur in siliciclastics (Figure 10B). Seven of these are in fine siliciclastics, 14 are in coarse siliciclastics, and the remaining 14 are in mixed siliciclastics. This appears to follow a similar trend to the previous epoch, where similar numbers of species occurred in coarse and mixed siliciclastic environments, while slightly fewer occurred in fine siliciclastic environments. Also similarly to the Late Cretaceous, many fewer species, 19, occurred in carbonates. Five of the carbonate-dwelling species were found in reef carbonates. Five species, all from Raninidae, occurred in multiple environment types.

There were 120 fossil type specimen occurrences in the Eocene, nearly doubling diversity from the previous epoch (Figure 11A). By the beginning of the Eocene, only 4 species outside of Raninidae and Lyreididae remained. These include a single necrocarcinid, and three species from Orithopsidae. Of these, only one species originated in the Eocene: *Cherpiocarcinus rostratus* from family Orithopsidae. A total of 19 species of Lyreididae lived throughout the Eocene, but the most diverse family by far was Raninidae with 97 species. This is the same sharp rise in diversity seen in Figures 1 and 2.

Though increasing in diversity, raninids and lyreidids appeared not to develop many carapace features similar to each other, or to other extant families in the section. No lyreidid species for which there was carapace feature data clustered with any other family's carapace feature hull during this epoch. The large majority of raninid species, 75, were also present solely within their own area of the analysis (Figure 6A). The remaining species had carapace features similar to the now-extinct Palaeocorystidae (22 species) and Orithopsidae (5 species). Only 1 species from Raninidae had similar carapace features to Lyreididae, despite it being the second most successful family. Interestingly, *Cherpiocarcinus rostratus* overlapped with the raninid carapace hull, unlike the other two orithopsid species in this Epoch.

In the Eocene, a total of 54 species appeared in siliciclastics, with 10 species in fine siliciclastics, 20 species in coarse siliciclastics, and 24 species in mixed siliciclastics (Figure 11B). A dense cluster of species occurred in mixed siliciclastics in what would be considered the northwestern United States in the modern day. Thirty-one species appeared in carbonates. Notably, *Cherpiocarcinus rostratus* lived in carbonates, rather than siliciclastics as the other surviving orithopsids did. Nine species appeared in marls, a more significant number than other ages or epochs. Ten species appeared in multiple environments, which is a similar proportion to the previous age. It must also be noted that 16 species occurred in unknown environments during this epoch. Nearly all of these species have the volcaniclastic tag. It is likely these species were living near volcanic activity, but not in solely volcaniclastic sediments.

There were 42 fossil type specimen occurrences in the Oligocene (Figure 12A). This is a sharp decrease in diversity from the Eocene. No species outside Raninidae and Lyreididae remained by the beginning of this Epoch, with the exception of *Cherpiocarcinus rostratus.* However, this species went extinct before the end of the epoch. Eight lyreidids and 33 raninids lived throughout the Oligocene.

Only 1 lyreidid species had similar carapace features to raninids. The remaining species were clustered only within their own hull. Twenty-nine Raninidae were present only within their own hull. Similar to the Eocene, the remaining 4 species overlapped with the palaeocorystid carapace hull, and one of these overlapped with the orithopsid hull. Only one of these species with palaeocorystid-like carapace features originated in the Oligocene.

A total of 25 species occurred in siliciclastics during the Oligocene, with 7 species occurring in fine siliciclastics, 10 species occurring in coarse siliciclastics, and 8 species occurring in mixed siliciclastics (Figure 12B). Only 8 species occurred in carbonates, with 1 of those being in reef carbonates. Five species occurred in multiple rock types during this age. Three of these species were also present in the Eocene, but 2 originated in the Oligocene.

There were 25 fossil type specimen occurrences dated to the Miocene (Figure 13A). This map is largely similar to that of the Eocene, with continuing losses in diversity. Only Raninidae and Lyreididae remained in this epoch. Lyreididae was represented by 5 species, while Raninidae was represented by 20 species.

There were 2 lyreidid species within their carapace feature hull, and 2 within the overlap with Raninidae. All but 2 Raninidae were present in their own hull with no overlaps. The two species that had carapace features similar to other families both shared features with Palaeocorystidae, and one species also had carapace features similar to lyreidids.

In the Miocene, a total of 15 species occurred in siliciclastics, with 5 in fine siliciclastics, 7 in coarse siliciclastics, and 3 in mixed siliciclastics (Figure 13B). Almost all specimens in carbonates disappeared, aside from those in the southern Pacific, which consisted of 4 species. None of these species appeared in reef carbonates. Proportionally, there are many more multi-environment species left in this age at 5 species. Three of these species were present in the Oligocene, while 2 originated in the Miocene.

Nine fossil type specimens occurred in the Pliocene or later (Figure 14A). This map is largely similar to the Miocene, but once again with losses of diversity. Two Lyreididae occurred in this age, and 7 Raninidae. Only 1 lyreidid displayed similar carapace features to raninids. All other species were present exclusively within their own family's hulls (Figure 6A).

In the Pliocene, a total of 5 species appear in siliciclastics, with 1 in fine siliciclastics, 1 in coarse siliciclastics, and 3 in mixed siliciclastics (Figure 14B). Two species appear in reef carbonates. Two species occur in multiple environments, and both species were raninids that survived from the previous epoch.

There are 47 extant raninoidan species (Figure 15A). These species primarily come from Raninidae, but 8 representatives from Lyreididae persist. Specimens are found almost exclusively in the tropics, with a preference for the Eastern Pacific. While there appear to be many more modern raninoids than those from the Pliocene, it is unclear if this is due to recent speciation, or preservational biases. The two modern genera from Lyreididae are *Lyreidus*, which is reported in the fossil record, and *Lysirude*, which is not. Modern Raninidae include the genera *Cyrtorhina*, *Cosmonotus*, *Notopus*, *Ranilia*, *Umalia*, *Ranina*, *Notopoides*, *Notosceles*, *Raninoides*, and *Symethis*. Of these, *Cyrtorhina* and *Symethis* do not appear in the fossil record.

There appear to be many more raninoidan species, 12 total, inhabiting carbonates and reef environments than in the Oligocene, Miocene, or Pleistocene (Figure 14B). There are 11 extant species inhabiting siliciclastic environments, creating a relatively even split. This is a change from previous epochs where siliciclastic environmental preferences were dominant. However, due to differences in fossil and modern species collection, many extant species were reported from deep water environments with unknown substrates. This makes it difficult to draw conclusions about whether these species may be inhabiting deep water siliciclastic or carbonate environments. Four extant species are known to inhabit multiple environment types.

DISCUSSION

Summary:

Section Raninoida shows a trend of decreasing familial and generic diversity through time. This corresponds with the general decline of podotremes from the Late Cretaceous to the present day. All raninoid families experienced large declines in diversity at the end-Cretaceous, from which only Lyreididae and Raninidae recovered. Though high in diversity in the Late Cretaceous, and similar in overall morphology to the two extant families, Palaeocorystidae ultimately went extinct at the end-Cretaceous boundary. This may have been due to the family's geographic distribution, which was less widespread than the other diverse families, or morphology, which showed combinations of back-burrowing adaptations and macrofeatures not seen in other families in the section.

Of the surviving families after the end-Cretaceous mass extinction event, only Raninidae and Lyreididae appear to have successfully adapted to the Cenozoic. These families gained in average generic longevity and diversified sharply in the Eocene while other families failed to recover. During this diversification, Raninidae and Lyreididae also began to differentiate from each other in carapace morphology.

Raninoids were not found to have strong preferences for environment types overall, and only Raninidae and Lyreididae showed significantly different preferences for certain environment types within families. Species inhabiting multiple environment types were not common in this section, nor did they appear to survive longer than species found in only one kind of environment. Modern species inhabit environments similar to those that species of the same family in the fossil record inhabited. However, modern geographic ranges are much more restricted to the tropics when compared to fossil species in warmer epochs.

Excel and PAST Analyses:

Diversity through time:

During the Cretaceous, all raninoid families were generically diverse and contained many genera with few species (Figure 2). This indicates that a variety of different forms and lifestyles may have been successful for raninoids during this time. Many families in this section declined in diversity during the late Early Cretaceous. The exceptions were Raninidae and Lyreididae. These two families originated in the Early Cretaceous and displayed low diversity throughout the epoch. They did not gain or lose much diversity at the end of the epoch as other families declined, however. It is possible that whatever factor caused other families to lose diversity did not affect early raninid and lyreidid species, which were uniquely adapted to survive. When other families regained some diversity in the Late Cretaceous, Raninidae and Lyreididae experienced significant diversification. They became the two largest families in the section by the Maastrichtian.

A sharp decline in both generic and familial diversity for the section took place at the K/T boundary (Figure 1, Figure 2). Palaeocorystidae notably became extinct, as did Paranecrocarcinidae. However, Paranecrocarcinidae was one of the smallest families in the section up to the end of the Maastrichtian, making its extinction unsurprising, given that less speciose taxa are less diverse and less likely to be widespread. Palaeocorystidae was the third most diverse family in the Late Cretaceous, only surpassed by Raninidae and Lyreididae, and was relatively successful through the Cretaceous as a whole. The difference that caused Lyreididae and Raninidae to survive through the mass extinction, but not Palaeocorystidae, is not apparent from diversity alone. Other factors that may have led to the extinction of Palaeocorystidae will be discussed shortly.

Throughout the Paleocene, Raninidae and Lyreididae persisted in low numbers while the species from other families continued to go extinct (Figure 1, Figure 2). However, in the Eocene, Raninidae experienced a huge radiation in diversity. Lyreididae underwent a much smaller but still notable diversification. Interestingly, diversification in both families included many speciose genera, rather than large numbers of genera containing few species as in the Cretaceous. Perhaps environmental conditions in the Eocene were favorable for raninids and lyreidids, but in narrower parameters than those of the Cretaceous. This would have facilitated the evolution of many species that were highly similar to each other, and which would be grouped into the same genus rather than named to new ones. The climate during the Eocene would have been very warm, in conditions that were similar to those of the Cretaceous (Zachos et. al, 2001). Given that the Cretaceous was a time in which section Raninoida previously thrived, it is likely that raninoids found these warm climates favorable. There is a break in the peak of diversity during the Lutetian and Bartonian ages, where diversity appears to decline sharply before rising again (Figure 1, Figure 2). However, this may be an artifact of less rock being recovered from these ages (Schweitzer and Feldmann, 2014).

At the end of the Eocene, raninids and lyreidids faced extremely sharp loses in diversity, similar to the losses at the end-Cretaceous. Many of the speciose genera survived, while numerically smaller ones went extinct. Global climate would have been cooling during this time, punctuated by the Early Oligocene Oxygen Isotope Increase as a sudden, severe global cooling event (Zachos et al., 1993; Zachos et al., 2001; Sotak, 2010). While not considered a mass extinction event, this change in climactic conditions may have had a large effect on raninoids if they preferred warmer climactic conditions. Diversity in the surviving genera remained relatively stable until the end of the Miocene, when it fell again. This drop in diversity before the Pliocene also corresponded with a time of global cooling (Zachos et al., 2001).

Longevity through Time:

Assuming that genera successfully adapted to their environment will persist longer in the geologic record before going extinct, the average time a genus from a given family survives can be taken as a measure of overall success or environmental fitness. In section Raninoida, the average length of time genera survived falls in families that ultimately became extinct (Figure 3). Necrocarcinidae and Cenomanocarcinidae both experienced sharp drops in generic longevity after the end-Cretaceous and end-Paleocene boundaries, suggesting that these families may have been in decline rather than successfully adapting to new environments. For example, Camarocarcinidae, while newly originated in the Late Cretaceous, had its average generic longevity cut by half after the end-Cretaceous boundary. This family became extinct during the Paleocene. Thus, falling generic longevity combined with low diversity may indicate an inability of this family to adapt to conditions after the end-Cretaceous.

In orithopsids, generic longevity dropped after the end-Cretaceous. Afterwards, it remained constant throughout the Paleocene. Orithopsidae experienced a reduction in average generic longevity after the end of the Eocene, when only one species remained in the family and was soon to go extinct. Given the consistent generic longevity of this family, it is possible orithopsids were relatively successful until the Oligocene, despite low levels of diversity.

For lyreidids and raninids, a pattern emerges in which these families gained generic longevity after the end-Cretaceous, rather than losing longevity as did every other family in the section. Average generic longevity stabilized in the Paleocene for these two families, remaining roughly the same as it was after the end-Cretaceous. After the end-Eocene, average generic longevity rose slightly in raninids to the present day and dropped by a small amount in lyreidids. These trends may indicate that these two families became overall more successful over time. The fact that Lyreididae and Raninidae not only survived but diversified, suggests that they continued to adapt to environments throughout the Cenozoic.

Environments:

In total, very few raninoid species, even in extant families, inhabited multiple environment types, and there did not seem to be a clear preference for any type of environment in families that survived for longer periods of geologic time (Figure 4). Families considered to have 'generalist' or 'specialist' body forms do not appear to show marked preference between environment types either. All families except Raninidae and Lyreididae had similar percentages of species in each environment type. When all grain sizes are combined, there is a general preference for siliciclastics across the section. Raninoids inhabited carbonates in smaller numbers, with very few species overall being reported in reef carbonates. However, this may be due to the fact that reef carbonates are a subtype within the broader carbonate rock type that requires the presence of extra fossils, such as corals, sponges, or bryozoans, to confirm. Some publications may have reported raninoid fossils within carbonates but neglected to specify the presence of other taxa.

Raninidae and Lyreididae showed percentages of species per environment type that differed from the other families in the section. Larger percentages of species within Raninidae inhabited carbonates, while smaller percentages inhabited siliciclastics when compared to other families. Species within Lyreididae inhabited siliciclastics in higher percentages than species of other families and inhabited fewer carbonates. The environmental preferences of these two families may indicate more inclination towards specialization into carbonate or siliciclastic environments respectively. Additionally, since these are the two extant families, the fact that they live similar lifestyles in different environments could be a form of niche partitioning. This may have contributed to the success of these two families through time.

Carapace Features:

Carapace features are some of the most important tools in assigning raninoids to families, genera, and species, as they are some of the most readily preserved features of raninoid specimens (Schweitzer et. al, 2018). From the familial-level analysis, it is apparent that two main clusters exist within section Raninoida (Figure 5A). One cluster includes the more generalist families Necrocarcinidae, Paranecrocarcinidae, Cenomanocarcinidae, and more distantly Camarocarcinidae. The transposed PCA reveals that features shared among these families are round, ornamented carapaces and a lack of microstructures for the generalist cluster (Figure 5B). These features would not have lent themselves to burying behavior and instead indicate these families had lifestyles less specialized than those of the other cluster. The carapace morphology of Orithopsidae is closer to Necrocarcinidae, Paranecrocarcinidae, and Cenomanocarcinidae than to others but is still distant from the core group of other ‘generalist’ families. In fact, it is closer to Raninidae than the rest of the cluster. This appears to be due to carapace microstructures such as pits and micronodes which are present in some, but not all, orithopsids. The functions of these specific microstructures are not well known (Waugh et al., 2009). This gap in understanding makes it hard to determine whether this similarity in morphology indicates any similarity in lifestyle between certain orithopsids and the back-burrowing families. The second cluster contains Lyreididae and Palaeocorystidae, with Raninidae more distant but closer to these two families than others (Figure 5A). The features weighing most heavily on this side of the chart are length/width ratio, bifid or trifid rostrum, and a general lack of posterolateral spines and macronodes (Figure 5B). Many of these features seem to be adapted to back-burrowing behavior. Elongate carapaces are suited for rapid burial, and microstructures in general are thought to grip sediment and make the animal harder to remove by predators (Waugh et al., 2009; van Bakel et al., 2012). The lack of large spines and nodes likely streamlines the body for burial, while decreasing the defensive capabilities of these families on the surface of the sediment. This would lead to specialization in back-burrowing lifestyles for members of families with these traits. Overall, the family level analysis largely confirms carapace features thought to be diagnostic of each of these families and allows them to be compared to each other.

At the generic level, similar clusters to the familial level can be observed (Figure 6A). Areas of overlap indicate areas of similar morphologies shared by each family. The fact that hulls overlap so heavily in this analysis reveals that genera and families share similar characteristics throughout the section. However, a gradient can still be observed moving from very round, ornamented families such as the Necrocarcinidae and Cenomanocarcinidae near the right end of the chart to elongate, specialist families such as the Lyreididae and Raninidae near the left end of the chart (Figure 6B). Palaeocorystidae is present near the center of this gradient as a morphologically intermediate family. Some palaeocorystid genera displayed similar characteristics to raninids and lyreidids, while others had characteristics similar to those of orithopsids and necrocarcinids. While seemingly similar in the family level analysis, the generic level analysis reveals some key differences between palaeocorystids and other back-burrowing families. *Ferroranina* and *Cenocorystes* were the two genera of palaeocorystids most similar to raninids and lyreidids in the Late Cretaceous. However, these two genera retained carapace macrofeatures such as keels, macronodes, and projecting orbital spines which are rare in the other two back-burrowing families. Given that these features may have made the carapace less streamlined for burying, their presence may indicate that palaeocorystids were less specialized for the lifestyle than raninids and lyreidids, or otherwise specialized to the lifestyle in a different manner. Regardless, the morphology of Palaeocorystidae demonstrates key differences from the other back-burrowing families.

Areas where hulls share no overlap indicate areas of unique morphologies within a family. The most tightly clustered groups of raninid and lyreidid genera are in areas where their morphologies do not overlap with that of other families. Additionally, few surviving raninids share hulls with any other family. Surviving lyreidids share hulls with raninids and no other family. Much like the environment types, it is possible these families, while specialized for similar lifestyles overall, have specialized further to partition niches.

ArcGIS Analysis:

Paleogeographic Diversity:

In mapping all fossil species by type specimen occurrences in modern coordinates, it is clear there is a large overprint of fossils from North America and Europe (Figure 7). This is a known issue in decapod paleontology and is likely not indicative that species from this section largely lived in these two areas (Schweitzer and Feldmann, 2015). It also means that drawing conclusions about worldwide locations or dispersal of species from this study may be tenuous.

However, these locations may still provide a general sense of the diversity and distribution at the family level.

Geographic range was a great predictor of survival through the end-Cretaceous mass extinction event (Jablonski, 1986). Raninidae and Lyreididae were the most diverse and widespread families in section Raninoida during the Late Cretaceous, with species all over the globe (Figure 9A). By contrast, the Palaeocorystidae, while comparable in diversity at the time, were present in a few clusters around the world, including in the present-day Gulf of Mexico and nearby interior seaways, Madagascar, central Europe, and northeastern China. Indeed, two of these clusters of palaeocorystid diversity were in proximity to the Chicxulub impact site and Deccan traps, which are areas at which decapods experienced high rates of extinction (Schweitzer and Feldmann, 2022). The wide distribution of Raninidae and Lyreididae may have given these families a better chance of survival during the end-Cretaceous than other families in the section. This is especially apparent when compared to the disadvantageous distribution of the Palaeocorystidae.

After the end-Cretaceous, surviving raninoids appear to move from a global distribution into the tropics as climate cools. Species persist near the poles during the Paleocene and Eocene (Figure 10A, Figure 11A). However, these species disappear during the Oligocene as climate cools sharply (Figure 12A). After the Oligocene, type specimen occurrences begin to disappear from northern European, North American, and Chinese locations, but persist closer to the equator where temperatures would remain warm, even in cooler climates (Figure 13A, Figure 14A).

Carapace features through time:

Raninid and lyreidid carapace features started out as uncommon throughout the section in the Early Cretaceous. This changed in the Late Cretaceous, when there was an increase in the number of species with carapace features more similar to those of raninids and lyreidids (Figure 9A). Strangely, few palaeocorystids had features that were highly similar to those of raninids and lyreidids in either epoch. A retention of macrofeatures such as keels and macronodes, which most raninids and lyreidids lacked, may have been responsible for this difference. Additionally, the most speciose genera of Palaeocorystidae, *Eucorystes*, *Cretacoranina*, and *Joeranina,* showed unique combinations of carapace features within the section. *Eucorystes* and *Cretacoranina* displayed microstructures and straps like those of back-burrowing families, along with features uncommon to these families such as keels and bifid spines. *Joeranina* in particular displayed traits most similar to more generalist families such as grooves, keels, and bifid rostrum, but also had pits and high-density microstructures. It may be possible that other families had outcompeted palaeocorystids with highly similar morphologies, and thus occupied similar niches during the Cretaceous. By the Late Cretaceous, most palaeocorystids diverged morphologically from other families.

After the end-Cretaceous, Palaeocorystidae became extinct (Figure 9A, Figure 10A). While this initially seemed to be a paradox given the family's high diversity and overall similarity to back-burrowers that survived this event, the pattern in carapace features for palaeocorystid genera during the Late Cretaceous offers an explanation. The family was characterized by species with unique morphologies, which differed from other back-burrowing families in ways that may not have been conducive to survival during the mass extinction event. Combined with limited geographic distribution, this may begin to explain why Palaeocorystidae did not survive the end-Cretaceous, despite being similar to other surviving families, and the third most diverse family at the time.

During the Paleocene, no raninids or lyreidids were present in the overlapping hulls of any family but one another's (Figure 6A, Figure 10A). Previously, around two-thirds of raninids and lyreidids had shared carapace features with other families. This might indicate that the features unique to these two families particularly helped them survive the extinction event, or that features similar to those of other families were detrimental. In the other surviving families, all but two species also shared similar carapace features to raninids and lyreidids, further supporting this hypothesis.

In the Eocene, lyreidids and raninids continued to lack morphological similarities to other families in the section (Figure 11A). They also begin to differentiate from each other, with only 1 raninid present in the zone of morphological overlap between Raninidae and Lyreididae. Lyreidid genera inhabiting Eocene rocks displayed generally similar carapace features to those of previous epochs but had carapaces that were slightly more elongate. Raninids during the Eocene maintained a greater diversity of carapace shapes and features, but overall trended to be less elongate than Eocene lyreidids. Many Eocene raninids shared carapace features that Eocene lyreidids lacked, such as inclined nodes and trifid spines (but not trifid rostrums). Some raninids also began to exhibit keels during their diversification in the Eocene. In combination with their elongate and microstructured carapaces, this made them notably similar to the extinct Palaeocorystidae. Raninid species with similar traits to palaeocorystid species mostly became extinct in the Oligocene and disappeared by the Miocene. Selective pressures may have pushed raninids back to more specialized morphology.

Other species remained largely differentiated from raninids and lyreidids from the Paleocene on. *Cherpiocarcinus rostratus* was the single exception, and yet survived into the Oligocene when species rapidly became extinct again. While carapace microstructure data was unavailable for this species, it displayed a notable lack of carapace macrofeatures that other orithopsids displayed. This difference likely caused *Cherpiocarcinus rostratus* to be grouped closer to palaeocorystids and less specialized raninids and may have indicated a similarity in lifestyle.

Environments through time:

Raninoids inhabited siliciclastic environments much more consistently through time than carbonates. Their presence in carbonate environments waxed and waned through specific epochs. The Paleocene and Oligocene were two notable periods where proportionally fewer Raninoid species appeared in carbonate environments than in previous or subsequent epochs. Oddly, coral reefs were not greatly affected by the end-Cretaceous mass extinction and were overall more sensitive to periods of warming climate than cooling climate (Pandolfi and Kiessling, 2014). The lack of raninoid fossils in carbonate environments during these times clearly had more to do with the diversity or environmental tolerances of raninoids themselves than the corals facilitating these environments. Notably, the Paleocene was a time of low diversity for the section, and the Oligocene was a time of falling diversity and low sea levels.

Raninid and lyreidid species inhabiting multiple environment types from this family did not appear until the Oligocene or later. This refutes the hypothesis that these families may have survived by having broader environmental tolerances at the species level despite their specialized lifestyles. In fact, in the Late Cretaceous, several palaeocorystid species inhabited multiple environments, and yet the family still became extinct, likely due to aforementioned factors. At the end-Cretaceous boundary, species inhabiting multiple environment types did not appear to have much advantage in persisting into the Paleocene, or else this advantage was not enough to overcome disadvantages related to location and morphology. From the Paleocene to the Eocene, species inhabiting multiple environments persisted through a few ages, but did not live notably longer than species in more specialized environment types. From the Oligocene to the Pliocene, as the section was largely in decline, more species inhabiting multiple environment types began to appear and survive multiple ages. However, this pattern did not persist into the modern day, and very few extant raninoid species inhabit multiple environment types (Figure 15B).

While many modern raninoids are present in deeper water environments with unknown substrates, the family has not appeared to migrate into deep water environments over time as lobsters have (Schweitzer & Feldmann, 2015). It is likely this is more a symptom of the types of data that can be collected from fossil specimens more readily, such as rock type, and modern specimens more readily, such as water depth. In removing this discrepancy, modern raninoids appear to inhabit largely similar environments to fossil raninoids.

CONCLUSIONS

Raninoids:

Raninoid families with rounder, more ornamented carapaces display greater longevity before, but not immediately after the end-Cretaceous. In fact, families with morphology specialized for back-burrowing preferentially survived the end-Cretaceous mass extinction event, solidifying the transition from generalist to specialist families within the section. The timing of this transition suggests that environmental factors may have had the most important impact on the decline of the section as a whole. While the majority of raninoidan families survived the event, mostly located in the more sheltered regions of northern Europe, these groups failed to diversify even as orithopsids survived into the Oligocene.

In examining raninoids alone, it is difficult to say whether back-burrowing conferred an advantage during the end-Cretaceous mass extinction event in and of itself. Certainly, burying behavior may help brachyurans escape temporarily unfavorable conditions (Lee, 2015). It also appears that families most specialized for back-burrowing survived preferentially to those that were not, as is the case between Raninidae, Lyreididae, and the extinct Palaeocorystidae. However, given that the extinction event was likely prolonged beyond just the Chicxulub impact, it is more likely that a combination of factors helped back-burrowing families survive, rather than just lifestyle. Certainly, Raninidae and Lyreididae were the two largest families heading into the mass extinction and had the widest geographic distributions. Given that these are known factors that can confer survival to taxa through mass extinctions, they may offer the more likely explanation (Jablonski, 1986). This is especially supported by the fact that Palaeocorystidae did not share the same geographic distribution as the surviving specialist families.

Unlike geographic distribution, less specialized morphology and tolerance for a wide range of environments did not appear to enhance the survival of raninoids either through mass extinction events, or through time. In fact, tolerance for multiple environment types was not common in the section, nor did it appear to contribute differentially to survival, especially across the end-Cretaceous. It's possible that factors mentioned above helped specialist families survive, while tolerance for a wide range of environments was simply not a trait that was able to be selected for in this section, since very few raninoids inhabited multiple environments at any point in time.

One environmental tolerance is apparent, which is that raninoids as a section appear to prefer warm climates. This is supported by the diversification of the section in warm epochs, as well as shifts in their distribution that confined them to the tropics as global climate cooled after the Eocene. Modern raninoids are present almost exclusively in tropics and warmer areas of the globe. This preference for warmer environments may have contributed to general declines in the section in the Late Cretaceous as well, since the Maastrichtian featured cooling climate (Bralower et al., 2002).

Decapods:

The failure of generalist raninoid families to recover after the end-Cretaceous mass extinction event, despite surviving it, may indicate a lack of open niches for these decapods to diversify into. Heterotrematous crabs became the largest component of decapod fauna during the Cenozoic and may have already occupied them (Schweitzer & Feldmann, 2015). This may have allowed specialist families occupying unique niches, such as Raninidae and Lyreididae, to diversify when conditions became favorable in the Eocene, while keeping orithopsids from recovering.

Additionally, the diversification of heterotrematous crabs may begin to explain patterns of raninoid diversity in the Late Cretaceous. Heterotremes originated in the Early Cretaceous and began to diversify in the Late Cretaceous, reaching nearly ¼ of total decapod fauna (Schweitzer & Feldmann, 2015). This coincides with the first decline in raninoid familial diversity and offers a possible explanation as to why diversity might have been falling in more generalist families in this section, even before the end-Cretaceous mass extinction. It's possible that the end-Cretaceous event sped up the inevitable, that heterotrematous body forms would replace podotremes occupying similar, generalist niches. As the most specialized of the raninoids, Raninidae and Lyreididae seemed positioned to survive this competition.

Faunal Progression:

Overall, analysis of extinction and survival within Section Raninoida indicates that environmental changes may be most important to patterns of faunal turnover, with competition as an important secondary factor. In mass extinctions and times of cooling climate, raninoids sharply declined in diversity. If other podotrematous crabs shared similar environmental tolerances, their precipitous declines likely freed up niches perfect for diversifying heterotremes to exploit. However, the role of competition cannot be discounted. Given that generalist raninoid families did not go fully extinct at the end-Cretaceous boundary, and indeed persisted through the Cenozoic in low numbers, the question of why these families were not able to recover and diversify in periods of warmth, as raninids and lyreidids were able to, remains. Given the dominance of heterotrematous crabs in the fauna by this point in time, it is likely that competition at the very least prohibited the recovery of generalist raninids, and potentially generalist podotremes. Whether heterotremes would have inevitably outcompeted generalist raninoids and other podotremes in the absence of changing environmental factors is hard to say for sure. All that can be said is that the two factors seem to operate in tandem during this particular faunal turnover. Future studies on other decapod taxa may explain these trends more clearly or offer insight into whether the primary importance of environmental factors and secondary importance of competition holds true across other faunal turnovers.

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FIGURES

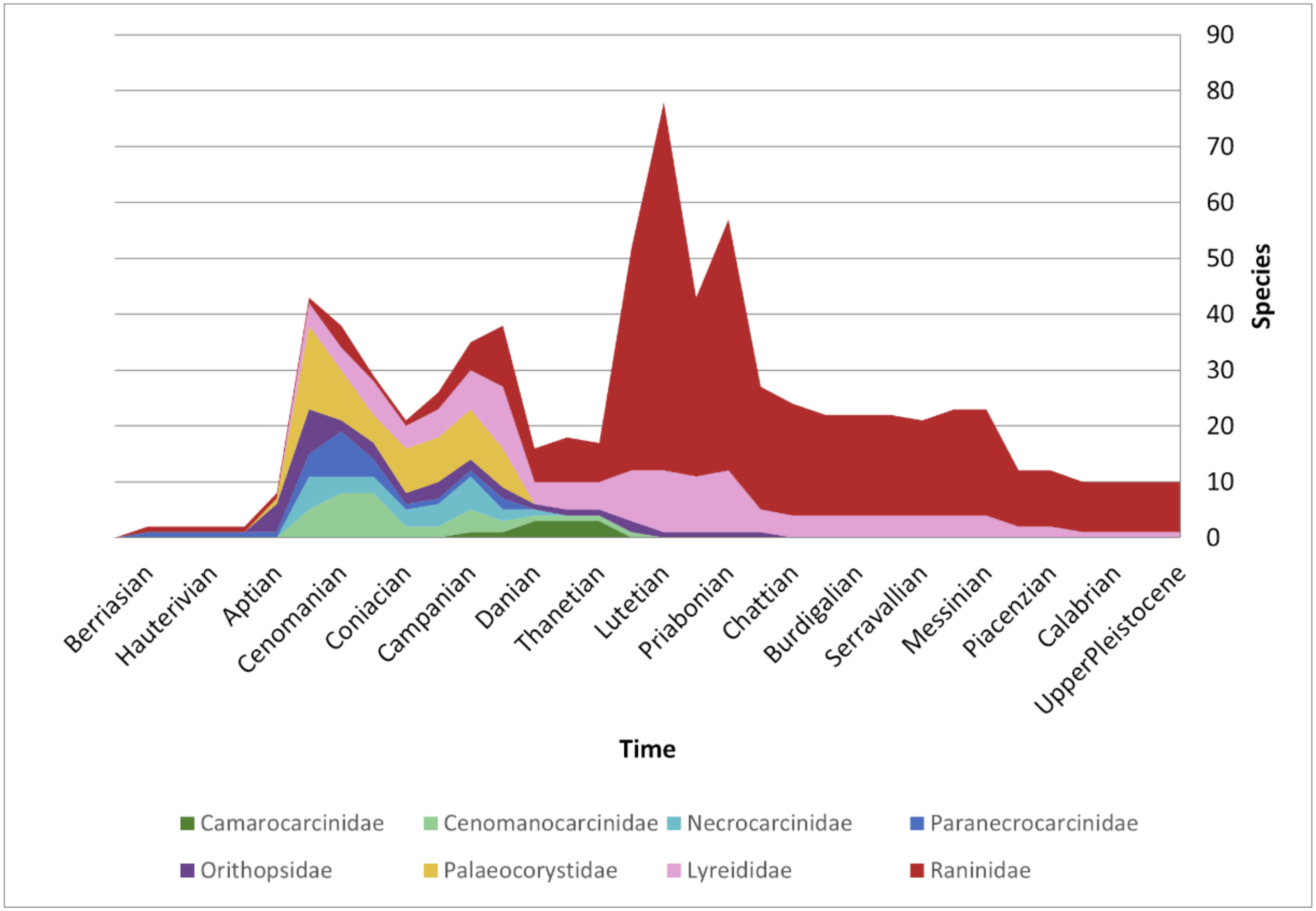


Figure 1: Familial diversity based on number of species in Section Raninoida through geologic time.

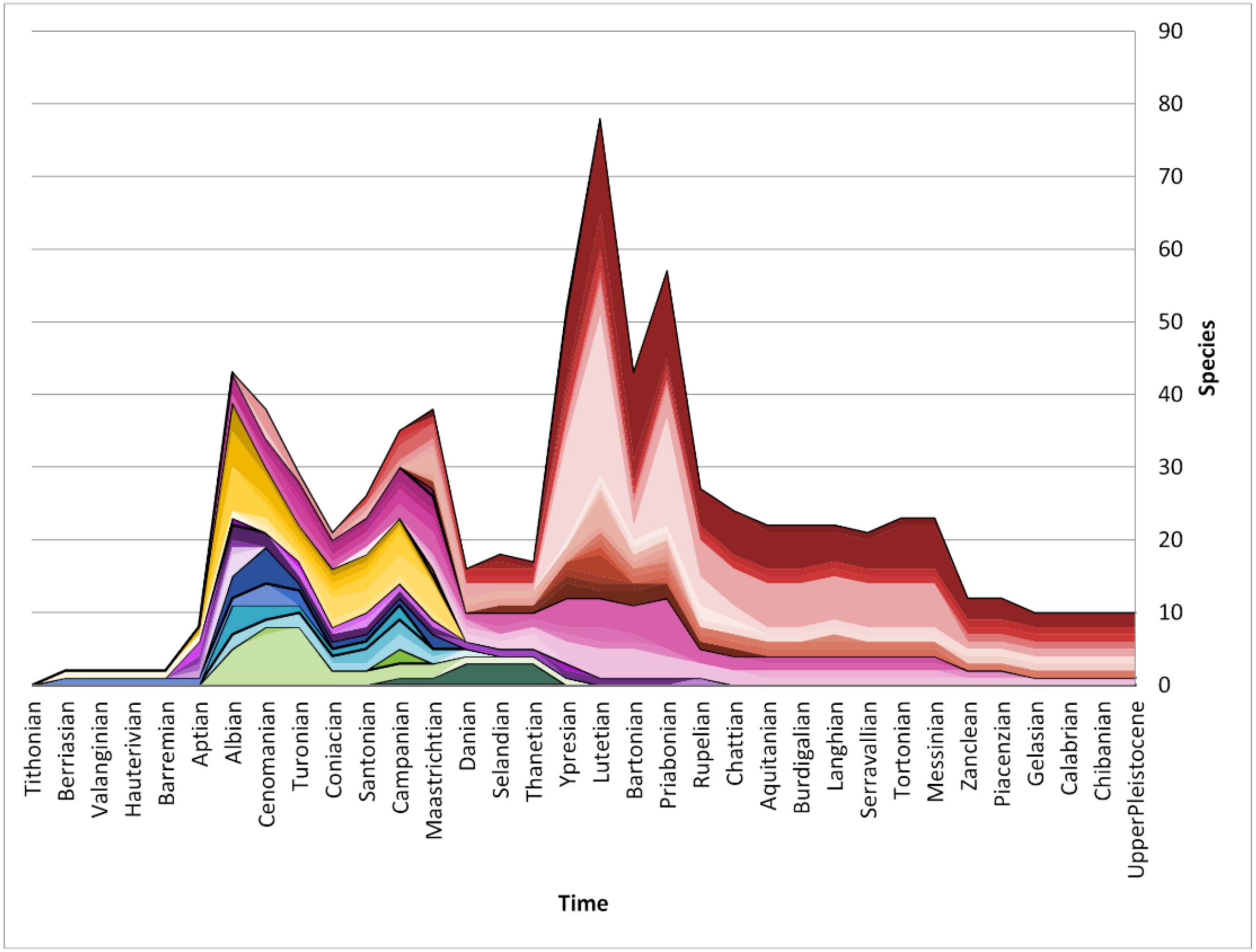


Figure 2: Generic diversity in Section Raninoida through geologic time. Following the color scheme of Figure 1, Camarocarcinidae is shown in dark green, Cenomanocarcinidae is shown in light green, Necrocarcinidae is shown in teal, Paranecrocarcinidae is shown in dark blue, Orithopsidae is shown in purple, Palaeocorystidae is shown in yellow, Lyreididae is shown in pink, and Raninidae is shown in red. See Appendix H for color ke

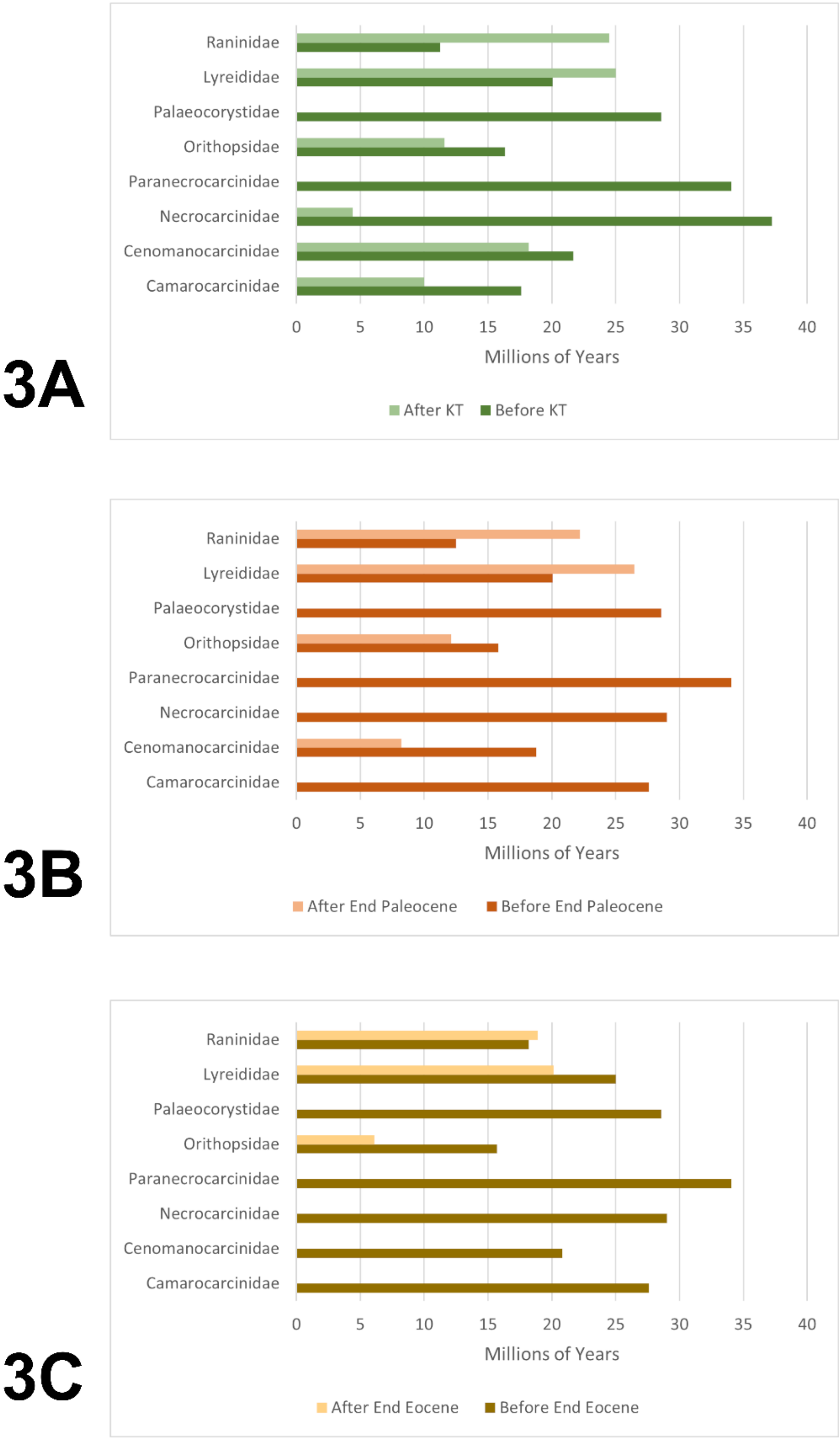


Figure 3: Average generic longevity in millions of years by family. A: Before and after the K/T Boundary, B: Before and after the end-Paleocene, C: Before and after the end-Eocene

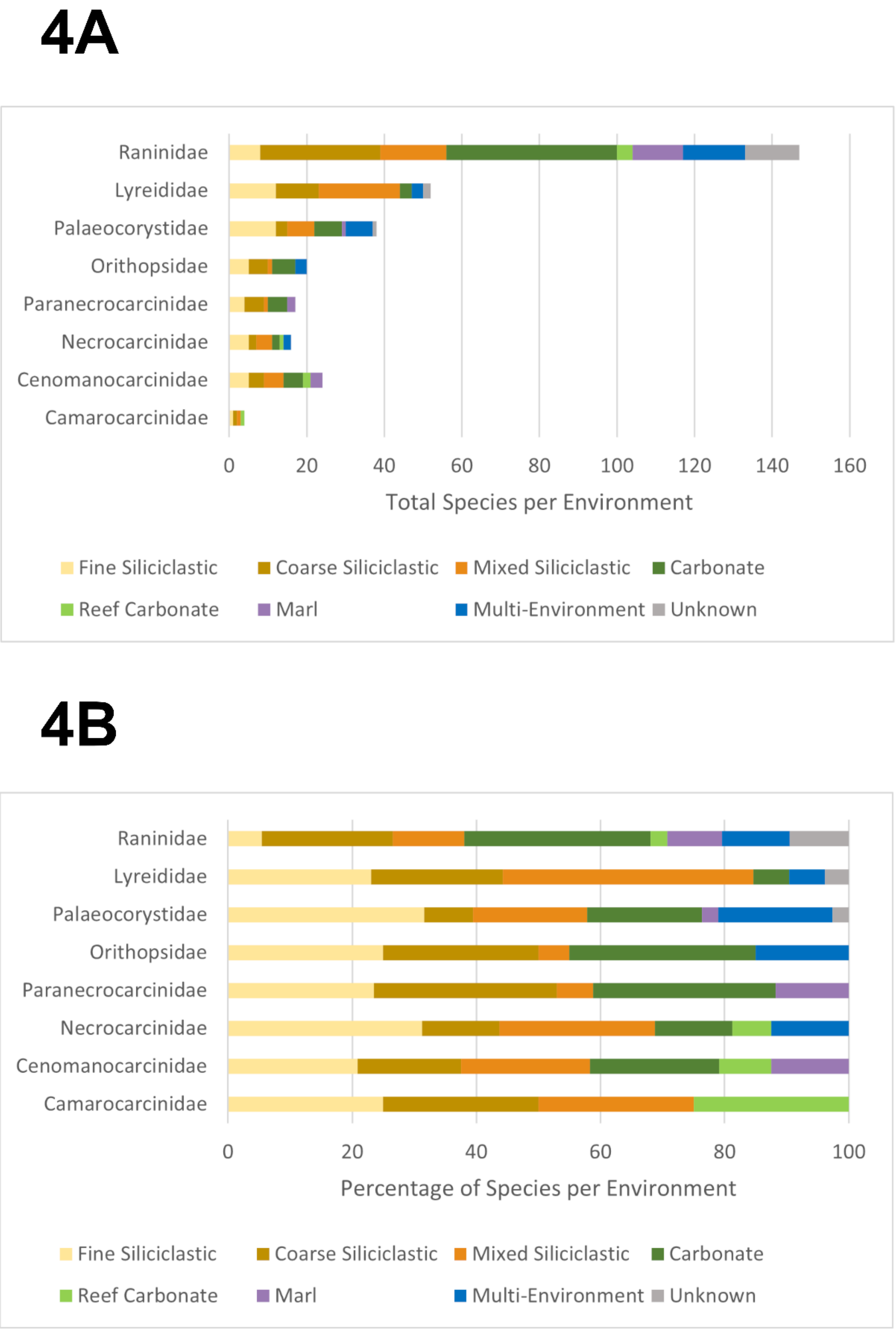


Figure 4: Rock types by family. A: In total, B: As percentages.

5A

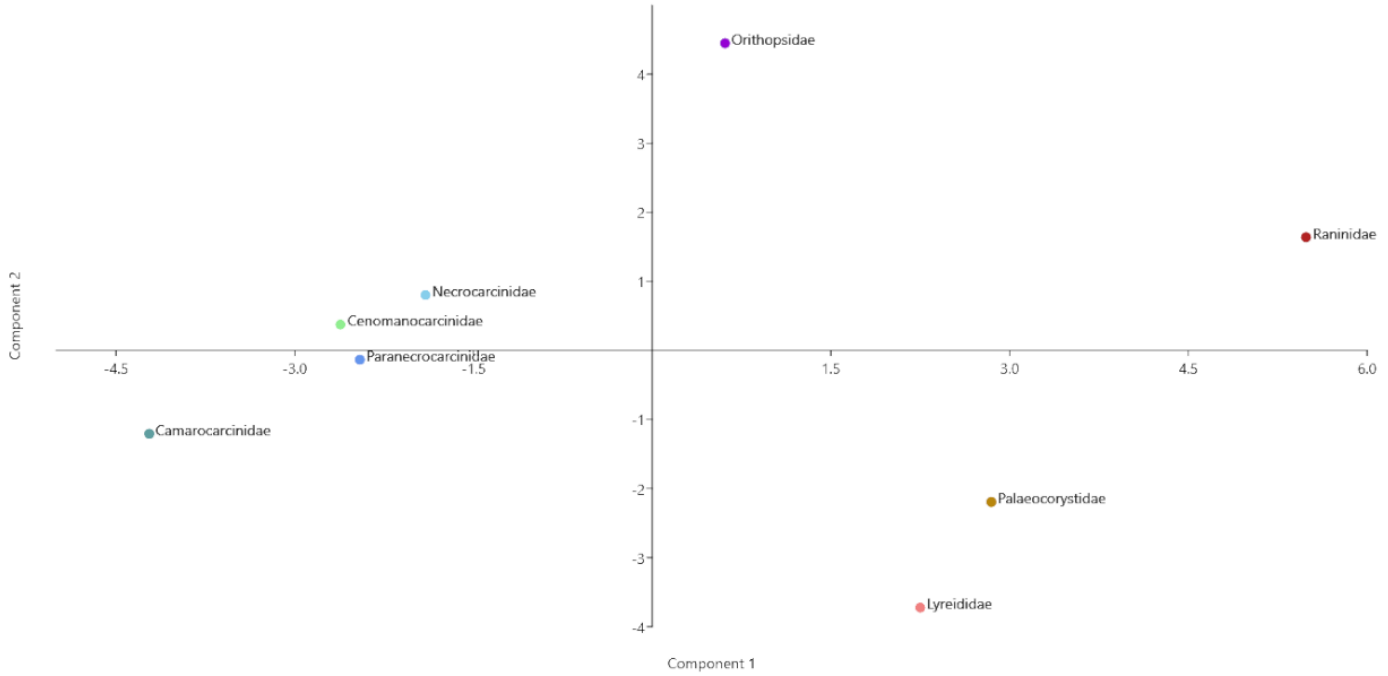


Figure 5A: R-mode PCA Analysis of carapace features ranged through to the familial level. Camarocarcinidae is shown in dark green, Cenomanocarcinidae is shown in light green, Necrocarcinidae is shown in teal, Paranecrocarcinidae is shown in dark blue, Orithopsidae is shown in purple, Palaeocorystidae is shown in yellow, Lyreididae is shown in pink, and Raninidae is shown in red. See Appendix D for data, and Appendix E for loadings and scores.

5B

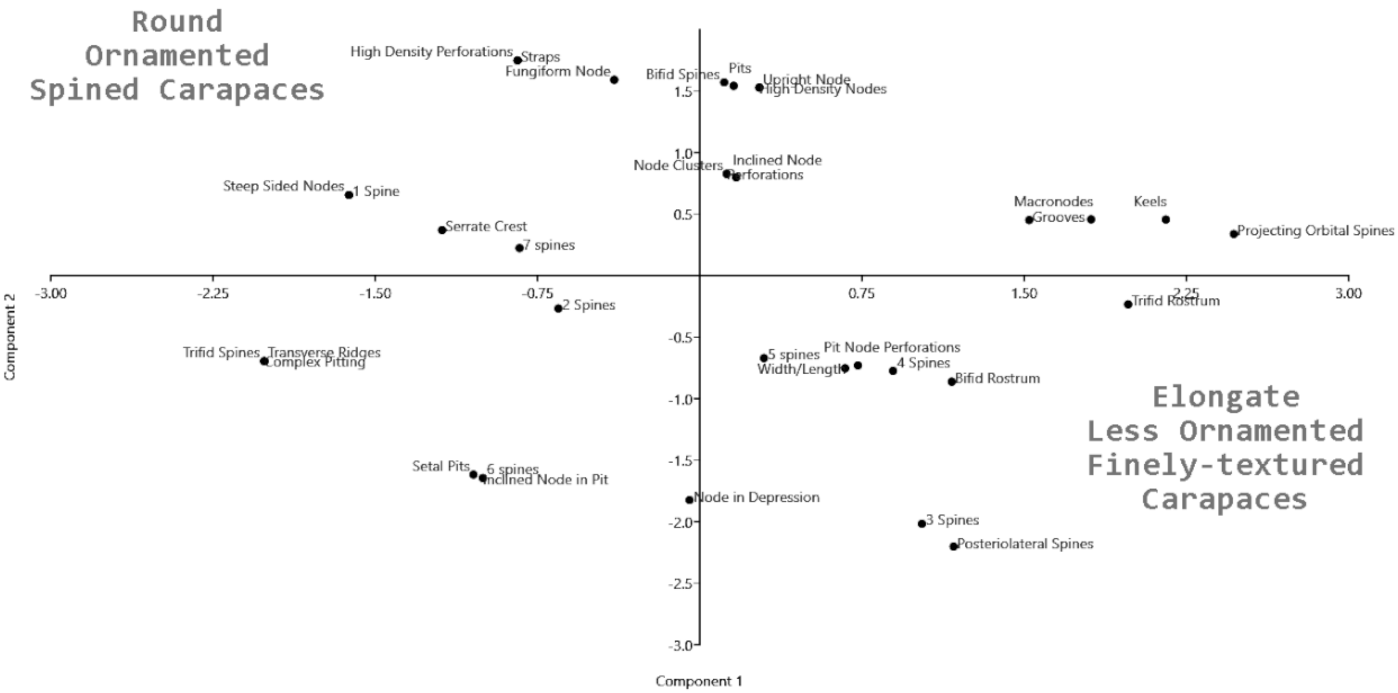


Figure 5B: Q-mode PCA Analysis of carapace features ranged through to the familial level. See Appendix D for data, and Appendix E for loadings and scores.

6A

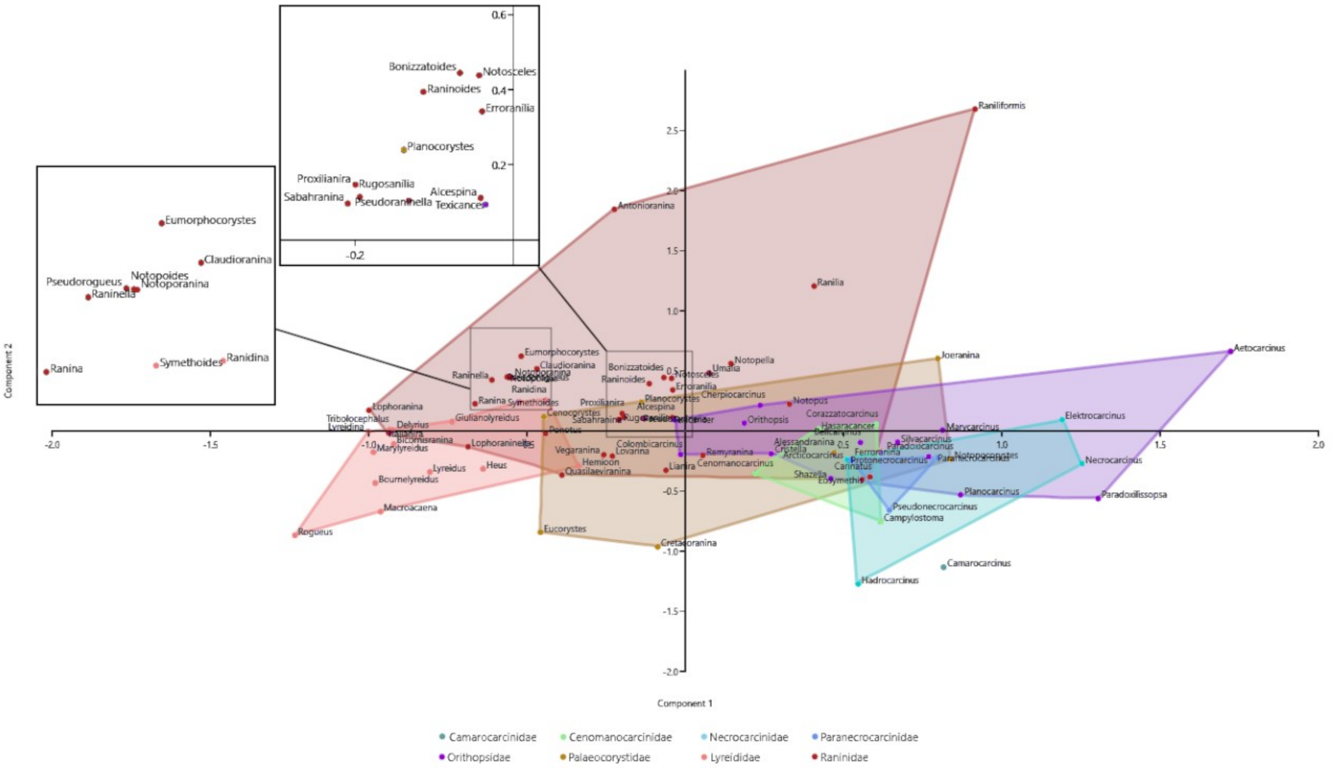


Figure 6A: R-mode PCA analysis of carapace features ranged through to the generic level. Hulls have been added around each family. Camarocarcinidae is shown in dark green, Cenomanocarcinidae is shown in light green, Necrocarcinidae is shown in teal, Paranecrocarcinidae is shown in dark blue, Orithopsidae is shown in purple, Palaeocorystidae is shown in yellow, Lyreididae is shown in pink, and Raninidae is shown in red. Insets of cluttered areas of the chart have been added to increase legibility. See Appendix F for data, and Appendix G for loadings and scores.

6B

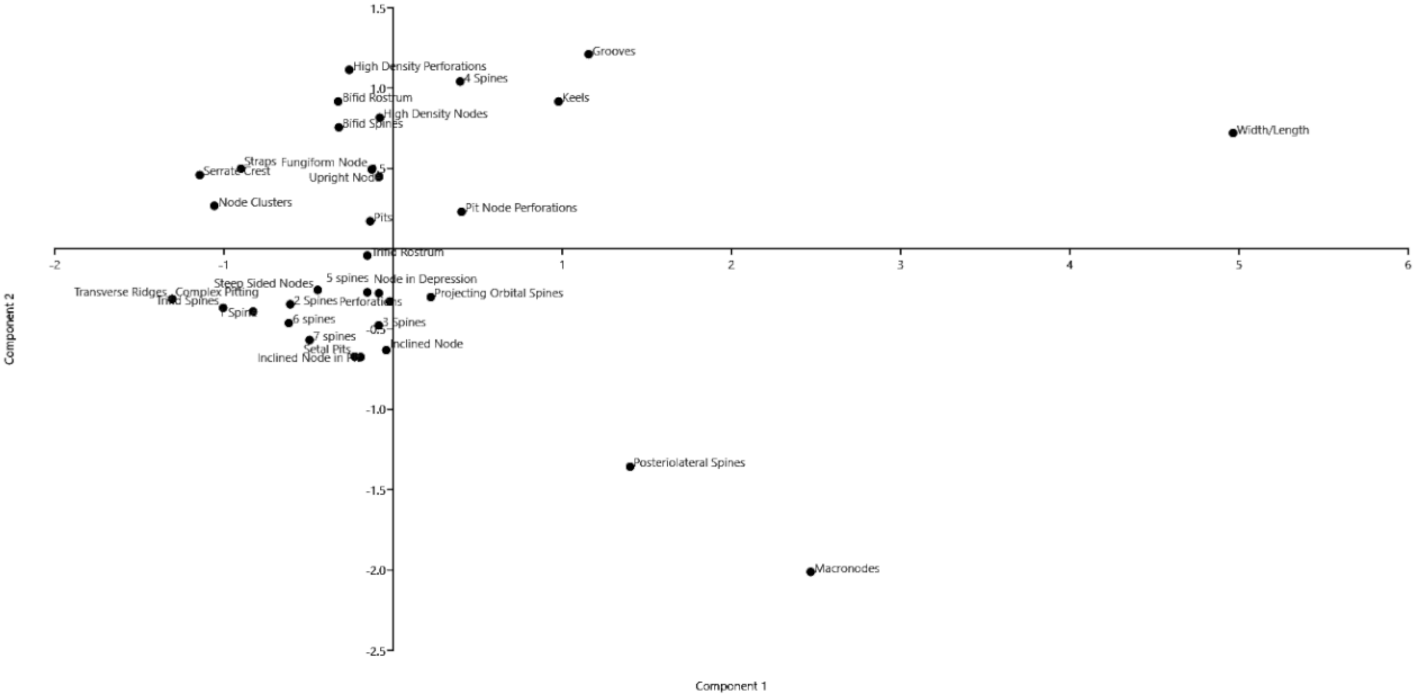


Figure 6B: Q-mode PCA Analysis of carapace features ranged through to the generic level. See Appendix F for data, and Appendix G for loadings and scores.

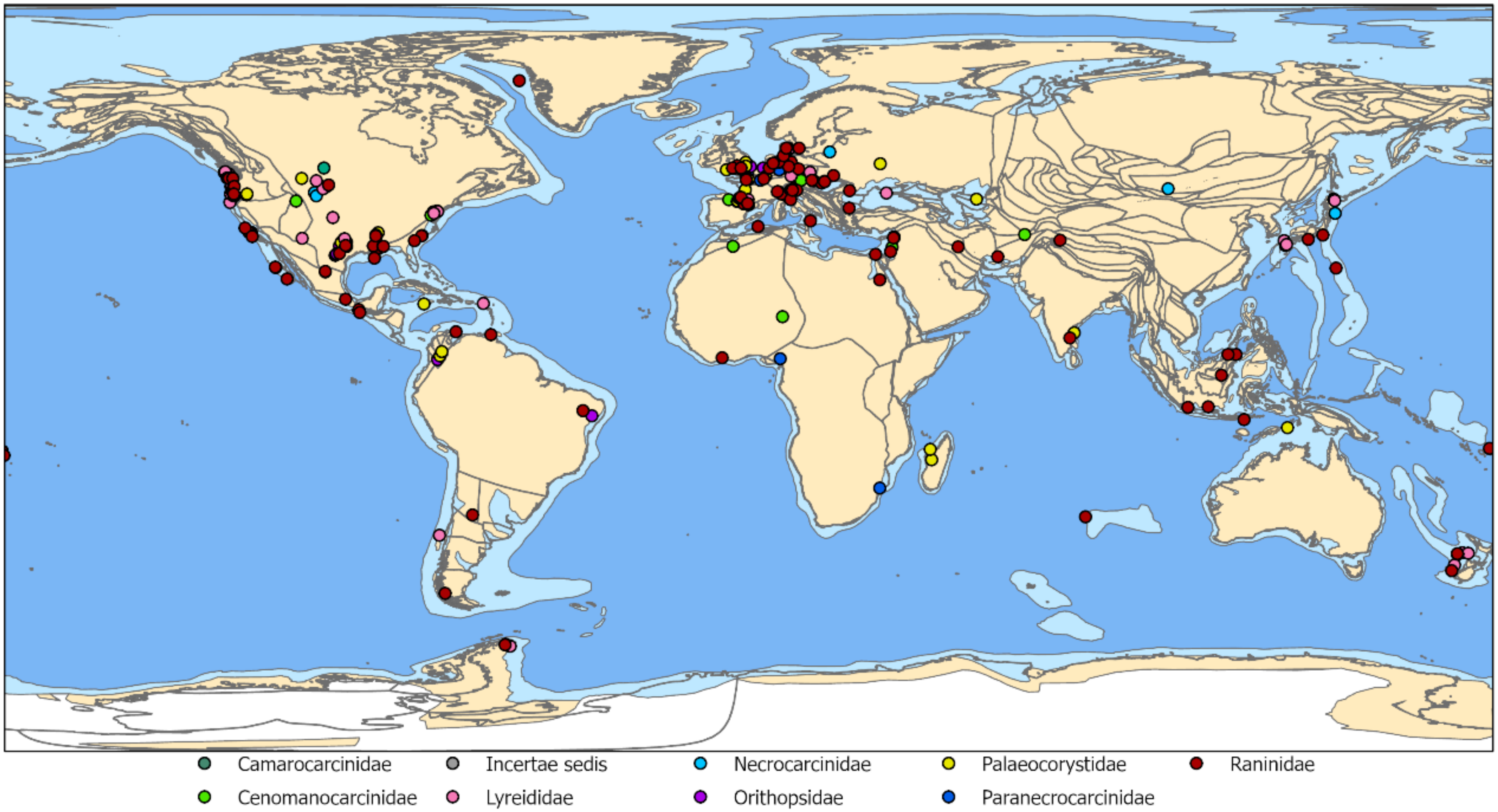
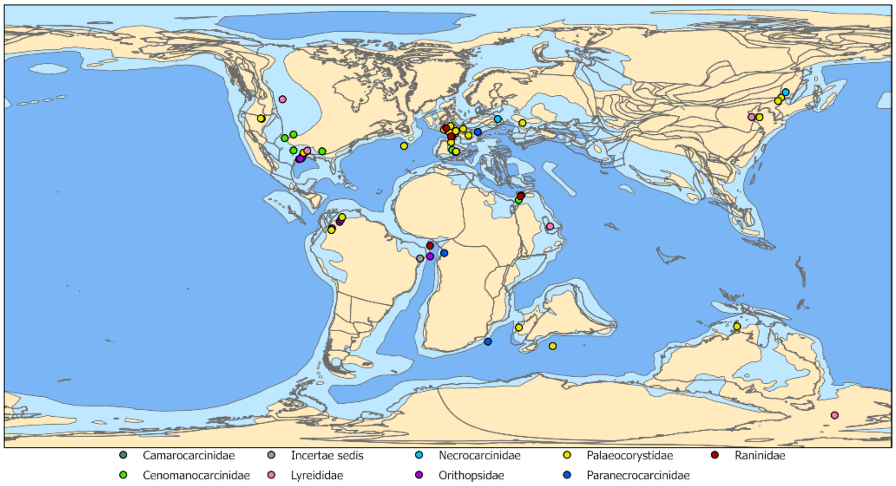


Figure 7: Map of all fossil raninoid occurrences. Basemap: 6 mya

8A



8B

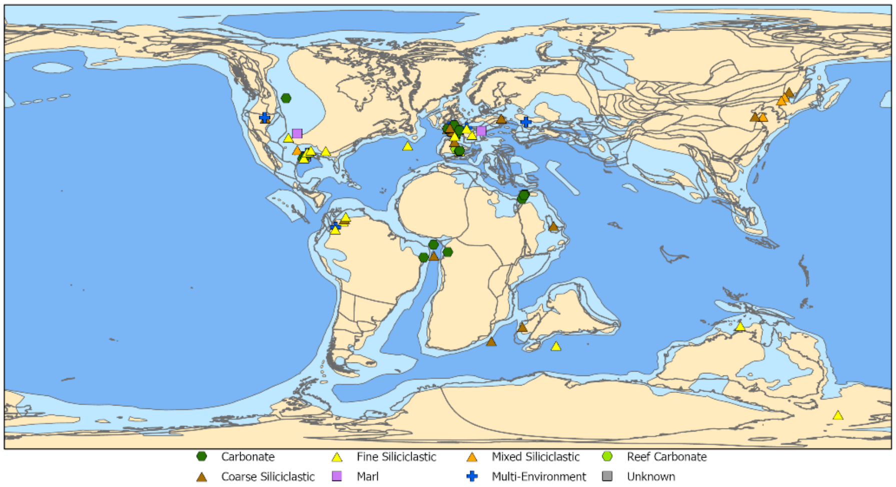
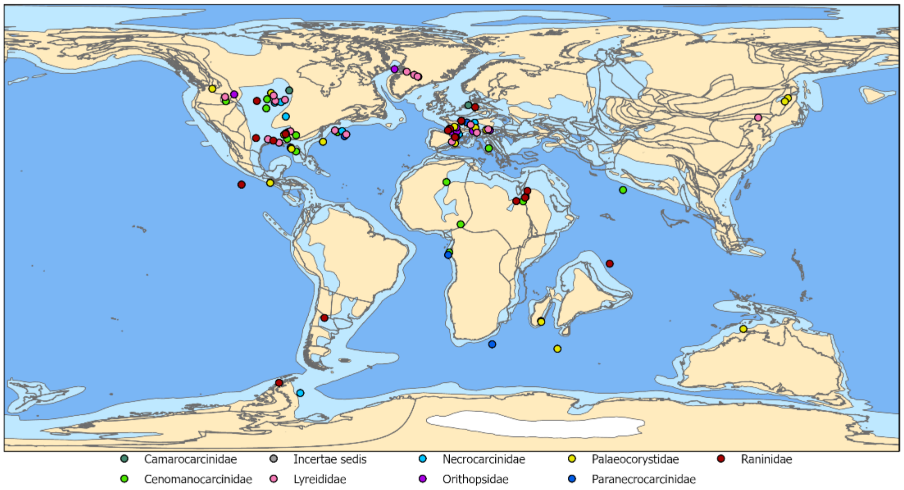


Figure 8A: Paleomap of occurrences of type specimens of species colored by family in the Early Cretaceous (145mya - 100.5mya). Basemap: 105mya

Figure 8B: Paleomap of type specimens, displayed by rock type for the Early Cretaceous (145mya - 100.5mya). Basemap: 105mya

9A



9B

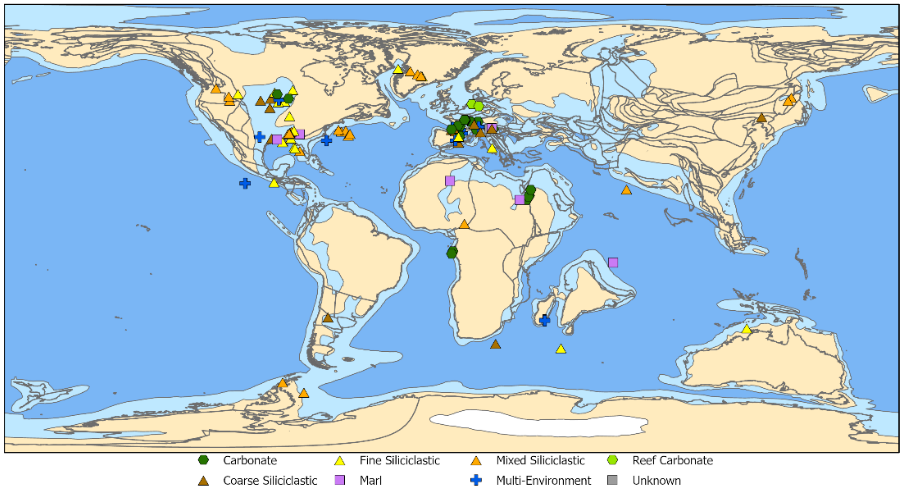
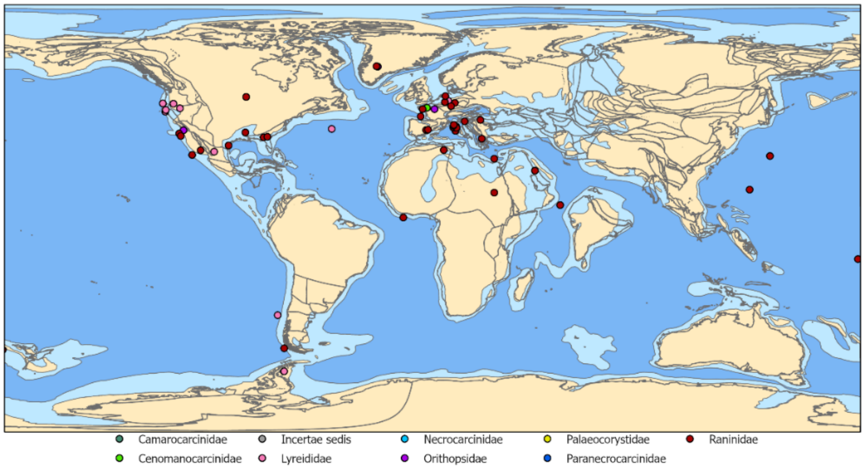


Figure 9A: Paleomap of occurrences of type specimens of species by family in the Late Cretaceous (100.5mya to 66mya). Basemap: 76mya

Figure 9B: Paleomap of type specimens, displayed by rock type for the Late Cretaceous (100.5mya to 66mya). Basemap: 76mya

10A



10B

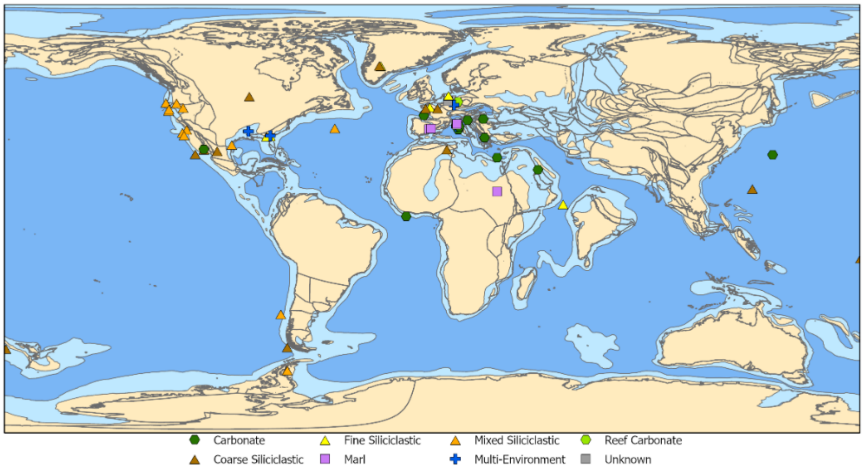
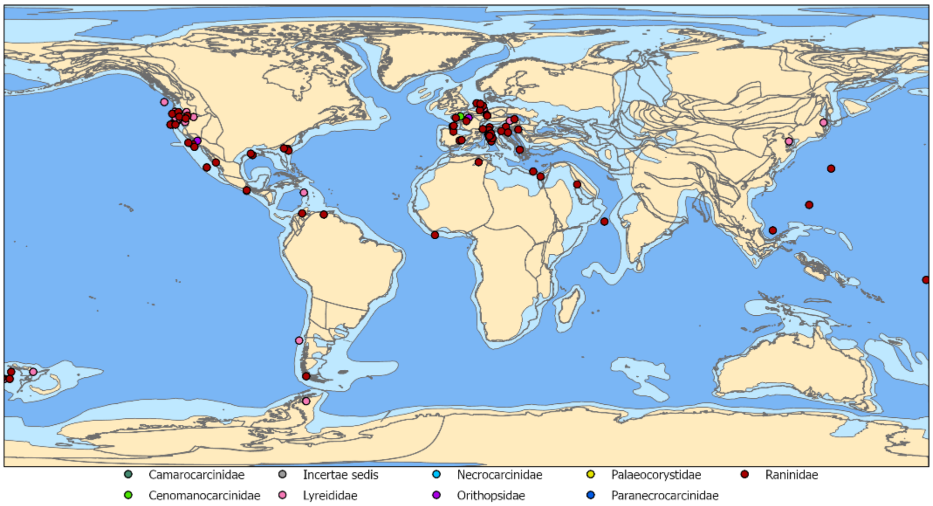


Figure 10A: Paleomap of occurrences of type specimens of species by family in the Paleocene (66mya to 56mya). Basemap: 53mya

Figure 10B: Paleomap of type specimens, displayed by rock type for the Paleocene (66mya to 56mya). Basemap: 53mya

11A



11B

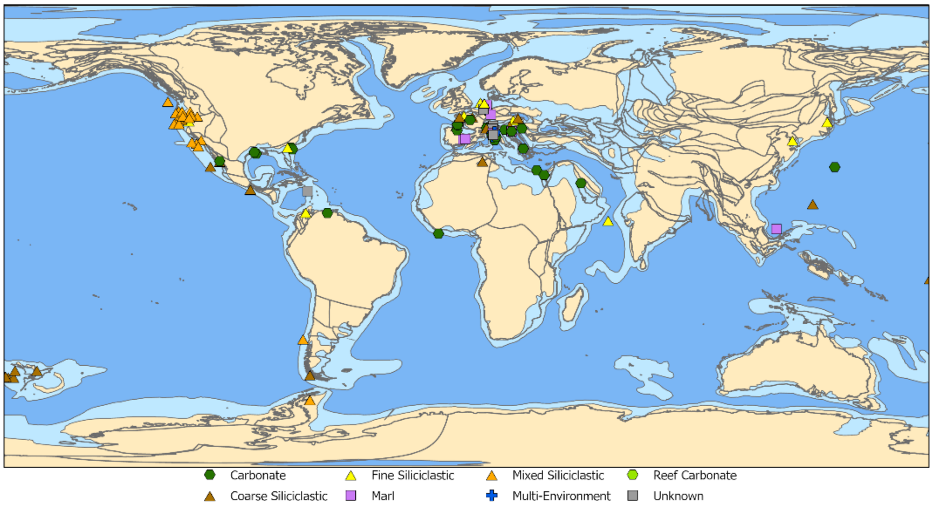
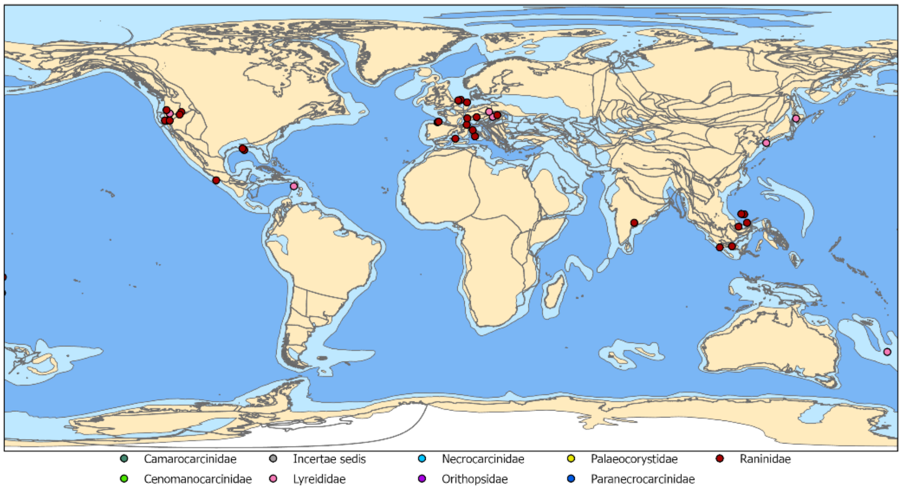


Figure 11A: Paleomap of occurrences of type specimens of species by family in the Eocene (56mya to 33.9mya).

Basemap: 45mya

Figure 11B: Paleomap of type specimens, displayed by rock type for the Eocene (56mya to 33.9mya). Basemap: 45mya

12A



12B

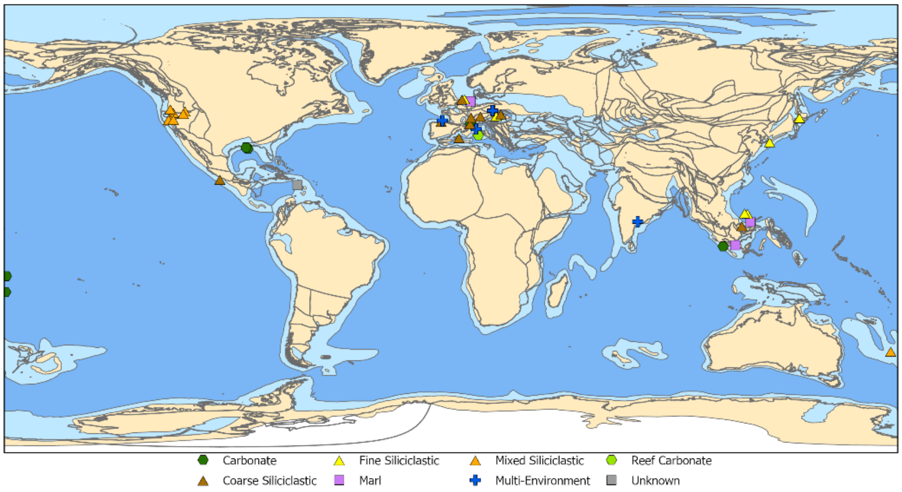
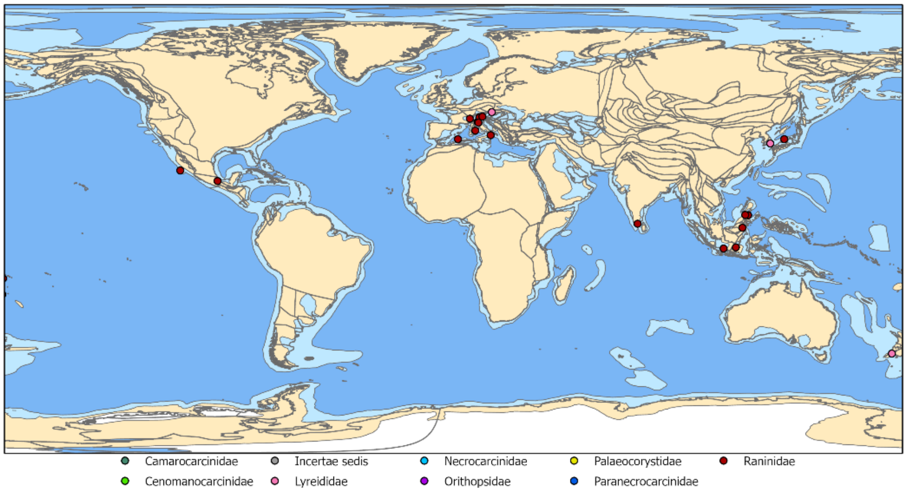


Figure 12A: Paleomap of occurrences of type specimens of species by family in the Oligocene (33.9mya to 23.03mya). Basemap: 33mya

Figure 12B: Paleomap of type specimens, displayed by rock type for the Oligocene (33.9mya to 23.03mya). Basemap: 33mya

13A



13B

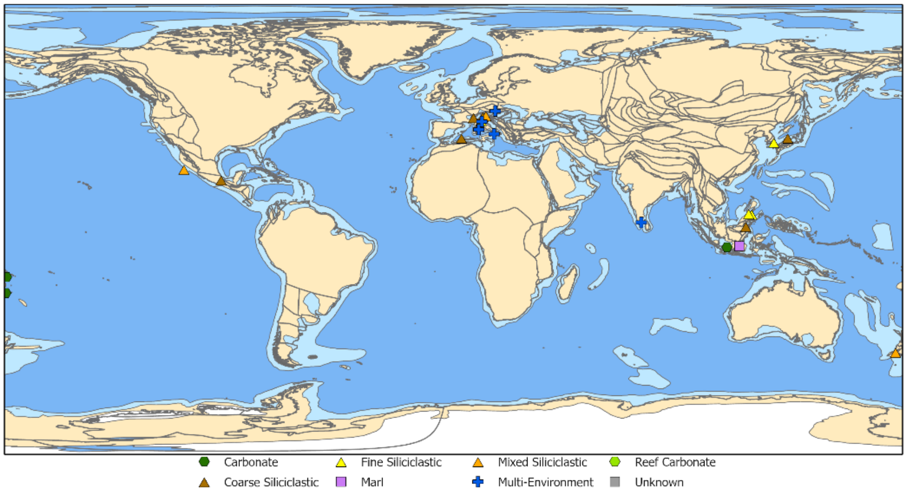
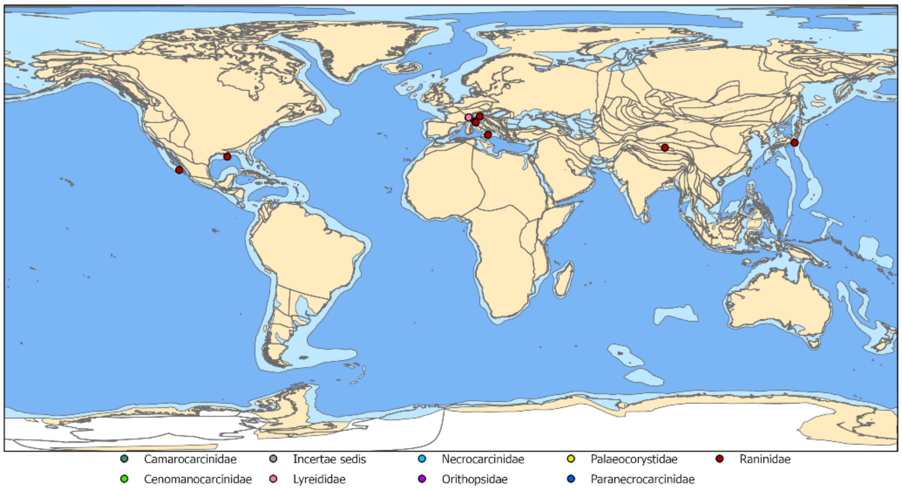


Figure 13A: Paleomap of occurrences of type specimens of species by family in the Miocene (23.03mya to 5mya). Basemap: 14mya

Figure 13B Paleomap of type specimens, displayed by rock type for the Miocene (23.03mya to 5mya). Basemap: 14mya

14A



14B

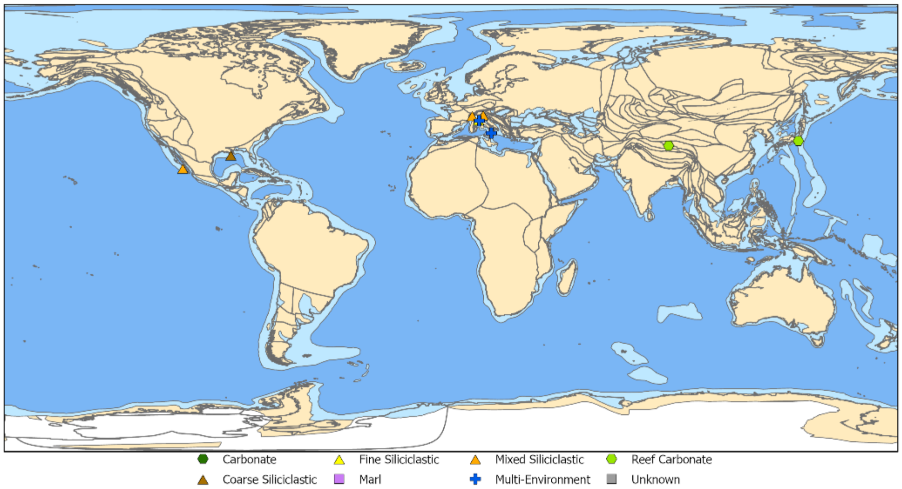
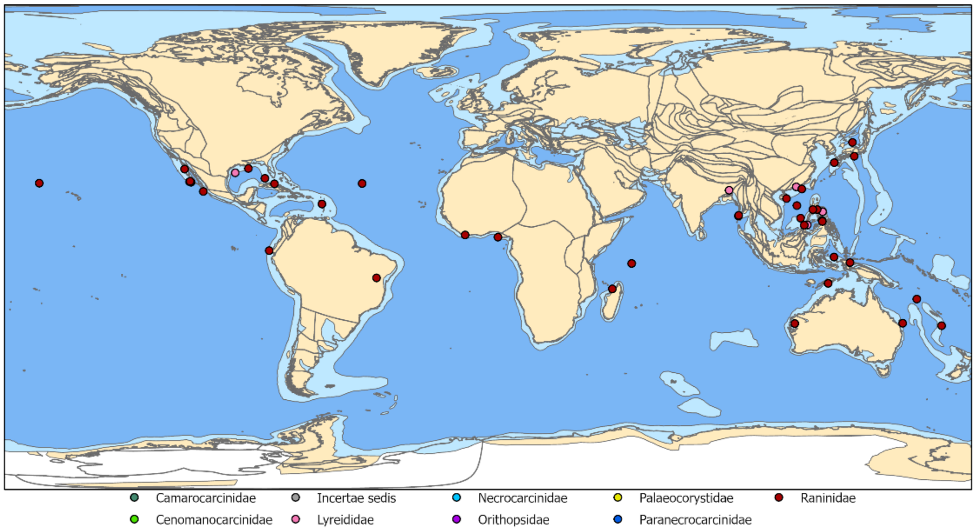


Figure 14A: Paleomap of occurrences of type specimens of species by family in the Pliocene to Pleistocene (5mya to 0mya). Basemap: 6 mya

Figure 14B: Paleomap of type specimens, displayed by rock type for the Pliocene to Pleistocene (5mya to 0mya) Basemap: 6 mya

15A



15B

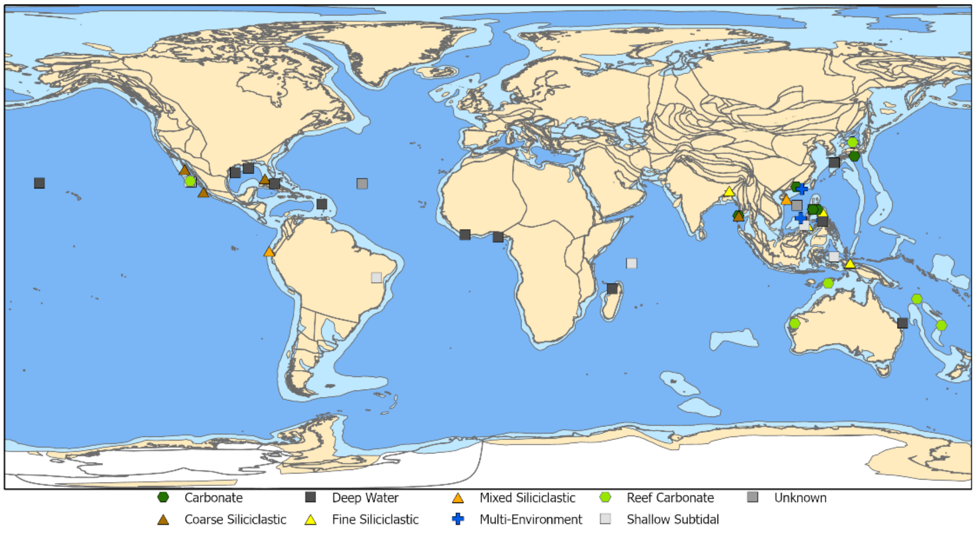


Figure 15A: Map of all extant type specimens or representative specimens of species by family, Basemap: 6mya.

Figure 15B: Map of all extant species, displayed by rock type, Basemap: 6mya

■ Camarocarcinus	■ Campylostoma	■ Cenomanocarcinus	■ Corazzatocarcinus
■ Hasaracancer	■ Arcticocarcinus	■ Elektrocarcinus	■ Hadrocarcinus
■ Necrocarcinus	■ Paranecrocarcinus	■ Protonecrocarcinus	■ Pseudonecrocarcinus
■ Aetocarcinus	■ Anoplocarcinus	■ Bellcarcinus	■ Cherpiocarcinus
■ Colombicarcinus	■ Cristella	■ Exucarcinus	■ Marycarcinus
■ Orithopsis	■ Paradoxicarcinus	■ Paradoxilissopsa	■ Planocarcinus
■ Shazella	■ Silvacarcinus	■ Texicancer	■ Araripecarcinus
■ Alessandranina	■ Cenocorystes	■ Cretacoranina	■ Eucorystes
■ Ferroranina	■ Joeranina	■ Notopocorystes	■ Planocorystes
■ Ripleycorystes	■ Bicornisranina	■ Giulianolyreidus	■ Lyreidus
■ Ranidina	■ Symethoides	■ Tribolocephalus	■ Doraranina
■ Rogueus	■ Macroacaena	■ Adinagenus	■ Bournelyreidus
■ Delyrius	■ Hemioon	■ Heus	■ Marylyreidus
■ Lyreidina	■ Antonioranina	■ Claudioranina	■ Eumorphocorystes
■ Italianira	■ Lianira	■ Lovarina	■ Notopella
■ Notoporanina	■ Notopus	■ Ponotus	■ Proxilianira
■ Pseudoraninella	■ Raniliformis	■ Rugosanilia	■ Ranilia
■ Umalia	■ Alcespina	■ Lophoranina	■ Lophoraninella
■ Pseudoranina	■ Ranina	■ Raninella	■ Remyranina
■ Tethyranina	■ Vegaranina	■ Bonizzatoides	■ Cristafrons
■ Notopoides	■ Notosceles	■ Pseudorogueus	■ Quasilaeviranina
■ Raninoides	■ Sabahranina	■ Carinatus	■ Eosymethis

Figure 16: Generic color key for Figure 2

APPENDICES

Appendix A:

Taxonomic list of all species in section Raninoida. See Excel document.

Appendix B:

Stratigraphic, Location, and Environmental data for all fossil species in section Raninoida. See Excel document.

Appendix C:

Location and Environmental data for all extant species in section Raninoida. See Excel document.

Appendix D:

Carapace feature data at the familial level, used in PCA Analysis. See Excel document.

Appendix E:

Loadings and Eigenvalues generated by the familial level PCA analysis on carapace features. See Excel document.

Appendix F:

Carapace feature data at the generic level, used in PCA Analysis. See Excel document.

Appendix G:

Loadings and Eigenvalues generated by the generic level PCA analysis on carapace features. See Excel document.

Appendix H:

Generic color key for Figure 2 (Figure 16).