Fall 1990

Danian (Paleocene) Molluscan Paleoecology in the Aftermath of the Cretaceous-Tertiary Extinctions, East-Central Texas

Benjamin R. Farrell
Western Washington University

Recommended Citation

Farrell, Benjamin R., "Danian (Paleocene) Molluscan Paleoecology in the Aftermath of the Cretaceous-Tertiary Extinctions, East-Central Texas" (1990). *WWU Graduate School Collection*. 809.
https://cedar.wwu.edu/wwuet/809

DANIAN (PALEOCENE) MOLLUSCAN PALEOECOLOGY IN THE AFTERMATH OF THE CRETACEOUS-TERTIARY EXTINCTIONS, EAST-CENTRAL TEXAS

by

Benjamin R. Farrell

Accepted in Partial Completion
of the Requirements for the Degree of
Master of Science

[redacted]
Dean of Graduate School

Advisory Committee

[redacted]
Chair

[redacted]

[redacted]

Master's Thesis

In presenting this thesis in partial fulfillment of the requirements for a master's of science degree at Western Washington University, I agree that the Library shall make its copy freely available for inspection. I further agree that extensive copying of this thesis is allowable only for scholarly purposes. It is understood, however, that copying or publication of this thesis for commercial purposes, or for financial gain, shall not be allowed without my written permission.

Signature ____________________

Date February 20, 1991

MASTER'S THESIS

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Western Washington University, I grant to Western Washington University the non-exclusive royalty-free right to archive, reproduce, distribute, and display the thesis in any and all forms, including electronic format, via any digital library mechanisms maintained by WWU.

I represent and warrant this is my original work and does not infringe or violate any rights of others. I warrant that I have obtained written permissions from the owner of any third party copyrighted material included in these files.

I acknowledge that I retain ownership rights to the copyright of this work, including but not limited to the right to use all or part of this work in future works, such as articles or books.

Library users are granted permission for individual, research and non-commercial reproduction of this work for educational purposes only. Any further digital posting of this document requires specific permission from the author.

Any copying or publication of this thesis for commercial purposes, or for financial gain, is not allowed without my written permission.

Name: Benjamin R Farrell

Signature:

Date: 5/18/18

DANIAN (PALEOCENE) MOLLUSCAN PALEOECOLOGY IN THE AFTERMATH OF THE CRETACEOUS-TERTIARY EXTINCTIONS, EAST-CENTRAL TEXAS

A Thesis Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Benjamin R. Farrell
December 1990

ABSTRACT

Danian shelf sediments from the Brazos River region of east-central Texas span approximately the first two million years after the Cretaceous-Tertiary (K-T) extinctions with only minor changes in lithofacies. Study of these virtually continuous stratigraphic sections reveals the nature and timing of the molluscan faunal rebound in the wake of the K-T extinction event. Diverse Late Maastrichtian molluscan faunas were dominated by epifaunal suspension-feeders, primarily oysters. Immediately above the K-T extinction horizon, low-diversity molluscan assemblages were characterized by a bloom in the abundance of the pelagic herbivore family Litiopidae, which were rapidly replaced by a low diversity assemblage dominated by a deposit-feeding bivalve of the family Nuculanidae (Upshaw, 1989; Hansen and Upshaw, 1990). This low diversity assemblage persisted for approximately 300,000 years after the K-T extinctions and may have been caused by the low productivity of the hypothesized "Strangelove" ocean of Hsu (1986).

Diversity rapidly increased to nearly pre-extinction levels within the *Globigerina pseudobulloides* zone (P1b), roughly 300,000 years after the K-T extinctions. Coinciding with this diversity increase was a change in the composition of the fauna from a roughly even mixture of Cretaceous, Paleocene, and undescribed species to a fauna composed primarily of Paleocene species. The relative proportions of

deposit-feeders and suspension-feeders also return to roughly Late Cretaceous levels within this biozone. Above the base of the *G. pseudobulloides* zone (P1b), the molluscan assemblages were characterized by increased stability. Diversity and trophic proportions of these assemblages persisted at nearly pre-extinction levels for the remainder of the studied interval, a period of at least 1.6 million years. In contrast to the large amount of faunal turnover apparent in the earliest Paleocene, molluscan assemblages within and above the *G. pseudobulloides* (P1b) biozone are characterized by increased species longevity in the studied sections.

Some faunal constituents were affected more permanently by the K-T extinctions. Epifaunal soft-bottom suspension-feeders such as oysters were a prominent component in local Late Cretaceous faunas, but they never regained their former levels of diversity and abundance in the studied Paleocene stratigraphic sections. Infaunal burrowing carnivorore-scavengers such as Naticidae and various opistobranchs became much more abundant in the Paleocene than they were in the Cretaceous.

ACKNOWLEDGEMENTS

Special thanks goes to my committee members Dr. Thor Hansen, Dr. Chris Suczek, and Dr. Dave Schneider for their considerable help and advice.

Dr. Tom Waller and Mr. Warren Blow provided me with access to systematic collections at the United States National Museum. Dr. Norm Sohl of the U.S.G.S. kindly helped identify some of my mollusks. Dr. Warren Allmon verified identifications for mollusks of the family Turritellidae. Planktonic foraminiferal biostratigraphy for the Danian stratigraphic sections was worked out by Dr. Gerta Keller. Dr. Erle Kauffman, Richard Farrand, and Banks Upshaw III shared data.

Financial assistance for this project was provided by Sigma Xi Grants-in-Aid-of-Research, a Geological Society of America Student Research Award, and a Western Washington University Geology Departmental Grant.

Many people in Bellingham have made my stay here enjoyable. I'd particularly like to thank Dr. Russ Burmester and Gary Hurban for a fantastic, adventurous summer of field-mapping in the Idaho wilderness. The boys of 1420 Ellis St. provided me with an entertaining temporary home during the end of this drawn-out process. This thesis was substantially improved through numerous discussions with Banks Upshaw. Administrative assistants Patty Combs and Vicki Critchlow helpfully answered my many questions and steered me past the school-bureaucracy. Lastly, I’d like to thank my family and friends for encouraging me during the course of this project. Thanks!

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The theory that extraterrestrial bodies such as comets or meteorites struck the Earth at the end of the Cretaceous Period causing wide-scale environmental changes and mass extinctions (Alvarez et al., 1980) has generated a great deal of scientific research and debate. Most of this research has centered on precisely recording the mass extinction while very little research has focused on the paleoecological and evolutionary consequences of this event. Only recently have such topics as the dynamics of species survivorship and faunal rebound begun to be assessed. The purpose of this study is to carefully document how molluscan communities restablished themselves after the Cretaceous-Tertiary (K-T) mass extinctions based on local stratigraphic sections in east-central Texas.

It has been estimated that approximately 15% of marine families and 50% of marine genera went extinct during the K-T mass extinction (Sepkoski, 1986). Diverse terrestrial groups such as dinosaurs, pterosaurs, and plants were also adversely affected. Yet, despite the profound effect the K-T extinction had on the world's biota, the cause of this event is still extensively debated. Some researchers have proposed a bolide impact to explain it. The effects of a bolide impact should include a period of temporary global darkness and temperature changes (Alvarez et al., 1980; Toon et al., 1982; Wolbach et al., 1985), acid rain (Lewis et al., 1982; Prinn and Fegley, 1987), and meteoritic contamination of surface waters, which would become enriched in trace elements originally contained in the bolide (Erickson and Dickson, 1987). These environmental disturbances should lead to rapid extinction in a short period of days to years. Other researchers have embraced an extinction scenario of a world-wide massive increase in volcanism with ensuing global cooling and concomitant sea-level regression as the mechanism of extinction (Officer and Drake, 1985; Hallam, 1987). Still others have proposed a combination of both hypotheses, with the bolide impact causing flood-basalt volcanism in the Deccan Traps leading to extinction (Alt et al.,1988; Rampino and Strothers, 1988).

While the causes of the K-T extinctions remain unresolved, some interesting facts concerning the evolutionary dynamics of these extinctions have come to light. Jablonski (1986a; 1986b) in his study of Late Cretaceous marine bivalves and gastropods found that traits which enhanced species longevity during background times were inconsequential during the K-T transition, suggesting that the K-T mass extinction did not result only from an acceleration of normal neo-Darwinian processes. During background times in the Late Cretaceous, planktotrophic larval dispersal, high species richness, and broad geographic range of the constituent species of a clade enhanced survivorship. In contrast, during the end-

Cretaceous extinction, broad geographical distribution of a clade regardless of the ranges of its constituent species was the only trait found to increase survivorship. A study of Late Cretaceous diatoms found that a life-history strategy of alternating planktonic and nonplanktonic stages may have increased the survivorship of diatoms during the K-T exinctions (Kitchell et al., 1986). The contrasting results of the above two studies show the uncertain role biologic adaptations play in the survivorship of mass extinctions.

Sheehan and Hansen (1986) suggested that there was a selectivity to the K-T extinctions in the marine realm, with marine animals that lived in or fed directly from the water column being more affected than marine benthic scavengers and deposit-feeders. The period of global darkness associated with the K-T bolide impact would have cut off photosynthesis for a period of months, causing food chains that were dependent on living plant matter to collapse. Food chains based on detritus would have been insulated from the extinction at least temporarily since there was still a food supply for these organisms. The K-T extinction pattern at the Brazos River shows this selectivity, with carnivorous and deposit-feeding molluscs preferentially surviving the end-Cretaceous extinction event (Hansen et al., 1987). This interpretation has been challenged by Upshaw (1989), who concluded that the most abundant deposit-feeder found in the earliest Paleocene of the Brazos River localities did not occur in the local Cretaceous stratigraphic sections.

Adaptive radiation is a term introduced by Simpson (1953) to describe rapid evolution within a taxonomic group. Adaptive radiations may arise in two fundamental ways. A morphologic breakthrough can create competitive superiority within a taxonomic group and subsequent rapid speciation. Alternately, ecospace may be emptied by a large-scale environmental disturbance, with surviving groups rapidly speciating to fill environmental niches vacated by the extinction. Recently, it has been shown that the displacement of a group by a competitively superior one is not as common as was generally supposed (Jablonski, 1986c). Indeed, it has been suggested that the world evolutionary system would greatly slow down in the absence of large scale environmental perturbations which remove large numbers of species (Gould, 1984). The rapid proliferation of species in the wake of a mass extinction has been termed faunal rebound (Jablonski, 1986c).

Patterns of faunal rebound have only begun to be evaluated. Based on stratigraphic sections in the Mediterranean, Smit (1982) documented a recovery sequence for earliest Paleocene planktonic foraminifera. Relatively diverse assemblages of Cretaceous planktonic foraminifera suffered an abrupt extinction in an iridium-rich clay layer at the K-T boundary in the studied sections. This layer contains microspherules interpreted as microtectites (Smit, 1982) and is overlain by a very low diversity zone of planktonic foramifera consisting of local Cretaceous survivors, the *Guembelitria cretacea* zone (P0). According to Smit, the P0 zone represents recovery of the fauna on an ecological time scale shorter than post-extinction speciation, which lasted approximately 50,000 years. This zone in turn was followed by the more diverse *Globigerina eugubina* zone (P1a), which is characterized by a pioneering stock of newly evolved planktonic foraminifera. The assemblage stabilized and the rate of evolutionary turnover slowed in the *Globigerina pseudobulloides* zone (P1b), approximately 500,000 years after the K-T extinction.

Hansen (1988) modeled the recovery of molluscan fauna after an impact-generated K-T mass extinction. He predicted an initial ecological recovery phase which should consist of a very low diversity fauna composed of local survivors. This phase should be followed by a secondary ecological recovery phase in which other Cretaceous survivors migrated into the area. Both of the ecological recovery phases represent responses of the fauna adjusting to the disturbance within a relatively short time, and therefore no newly evolved Paleocene species should be found in these phases. The ecological recovery phases were followed by an initial radiation phase in which particular families underwent rapid speciation apparently filling ecospace emptied by the K-T mass extinction. These families, termed "bloom taxa", were considered by Hansen to be analogous to ecologically opportunistic species, and either were members of speciose families not greatly affected by the extinction or were families that rapidly diversified after the extinction. According to Hansen, the initial radiation phase was followed by a long secondary radiation phase of approximately 25 million years, in which landscape diversity gradually increased to pre-extinction levels, and the assemblage stabilized and assumed a more normal Tertiary aspect. The initial radiation phase was correlated by Hansen with the *G. pseudobulloides* zone (Plb) and the molluscan families Turritellidae, Cucullaeidae, Ostreidae, and Carditidae were designated as "bloom taxa" based on Danian molluscan occurrences on the Gulf Coast coastal plain. Because these organisms evolved directly from genera which originated in the Cretaceous, Danian molluscan faunas have a notably Cretaceous character.

Upshaw (1989) examined the molluscan fauna immediately above the K-T boundary at two localities along the Brazos River in east-central Texas. His results do not match the recovery model of Hansen (1988) exactly. The diversity of the molluscan fauna immediately above the boundary was quite low. Instead of being composed of solely Cretaceous survivors, the earliest Danian molluscan fauna consisted of an even mixture of Cretaceous survivors, unnamed species, and Paleocene species. This result suggests that the stratigraphic resolution at the Brazos River localities was not fine enough to capture the short-term, survivors-only, ecologic recovery phase or that ecologic and evolutionary recovery did not occur as seperate discrete phases. The number of species in the assemblage increases rapidly upsection and reaches a maximum of 20-25 species in the upper portion of the P1a and lower P1b planktonic foraminiferal biozones. The failure of these earliest Danian assemblages to rebound to pre-extinction diversity levels and ecologic structure suggest unstable environmental conditions for the duration of the P0 and P1a zones, representing a period of about 300,000 years.

The study by Upshaw (1989) examined the molluscan fauna from the K-T boundary to the base of the Littig Glauconite Member (P1a/P1b boundary) at two localities along the Brazos River. My study documents the course of evolutionary recovery for molluscs, the initial radiation phase of Hansen (1988), from the base of the Littig Glauconite Member upward. The objective of this study is to describe the molluscan paleoecology and depositional environments of local Danian stratigraphic sections of east-central Texas in an effort to assess paleoecological and evolutionary patterns in the wake of the K-T mass extinction. More specifically, fulfillment of this objective involves description and interpretation of local stratigraphy, creation of species lists and range charts, quantitative measurement of molluscan diversity, and paleoecological interpretations.

REGIONAL GEOLOGY

The Cretaceous-Tertiary contact trends to the Northeast from Eagle Pass on the Rio Grande River toward San Antonio, Austin, and the Texas-Oklahoma-Arkansas border (Figure 1). The latest Cretaceous and earliest Tertiary strata of east-central Texas are composed predominately of terrigenous shelf sediments derived from the southern Rockies, which were uplifted during the Laramide Orogeny, and from the Ouachita Mountains (Stanton, 1982). Deltaic deposition was concentrated in the northeastern portion of the East Texas Embayment near the Arkansas/Texas border (McGowen and Lopez, 1983) and in the eastern part of the Rio Grande Embayment in southwestern Texas (Weise, 1979). Fine-grained terrigenous sediments were deposited between these depocenters on the continental shelf of east-central Texas. Paleogeographic reconstructions indicate that the continental shelf was extremely wide in east-central Texas during the Cretaceous-Tertiary transition (Winker, 1984).

In east-central Texas, three well-known localities encompass the Cretaceous-Tertiary boundary: the Littig Quarry stratigraphic section near Austin, the Walkers Creek section near Cameron, and the Brazos River sections near Rosebud (Figure 1). At all of these localities the latest Cretaceous is represented by the Corsicana Formation, the uppermost member of the Navarro Group. This formation is predominately composed of structureless clays with

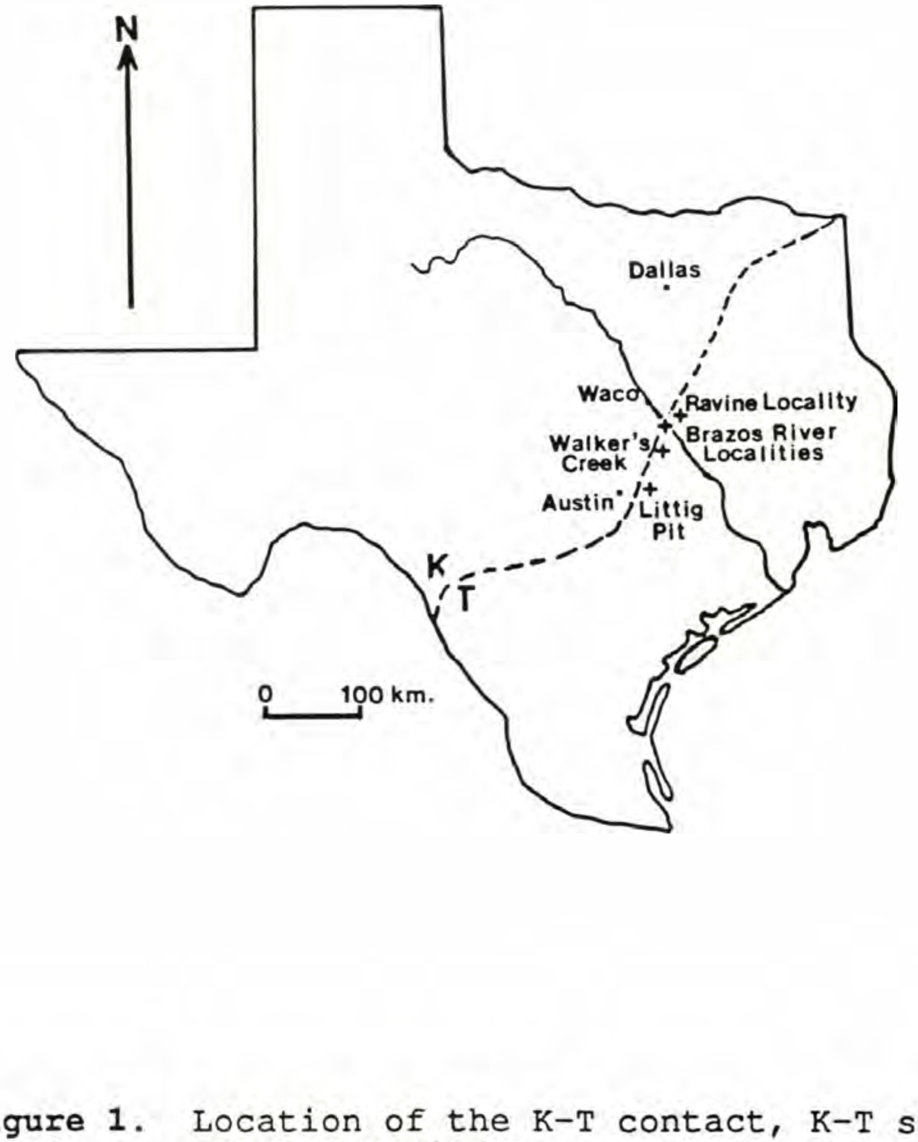


Figure 1. Location of the K-T contact, K-T stratigraphic sections, and the studied Danian stragraphic sections in east-central Texas.

occasional interspersed sands and has been interpreted as representing deposition in a mid to outer shelf environment with water depths ranging between 75 and 200 meters (Farrand 1984; Bourgeois et al., 1988). The Corsicana Formation is unconformably overlain by the Paleocene Littig Glauconite Member of the Kincaid Formation in most of the region. A composite stratigraphic section showing the latest Cretaceous and earliest Tertiary strata of east-central Texas is shown in Figure 2.

The Kincaid Formation comprises the oldest portion of the Paleocene Midway Group and has been divided into three members: the lower Littig Glauconite Member, the middle Pisgah Member, and the upper Tehuacana Creek Member. Sediments of the Midway Group are dominately composed of terrigenous shelf sediments and represent the most extensive Tertiary marine transgression in Texas (Kellough, 1959). The type locality of the Littig Glauconite Member in Travis County, Texas, consists of greenish-black calcareous glauconite weathering to a yellowish-green or buff color and containing phosphate nodules, small pebbles, shark's teeth, casts of fossils, and spherical calcareous concretions (Plummer *in* Gardner, 1933). Portions of the Littig Glauconite Member at Walkers Creek and Littig Quarry are thought to have formed as a condensed zone during a rapid transgression that produced starved conditions on the continental shelf (Kocurek and Hansen, 1982).

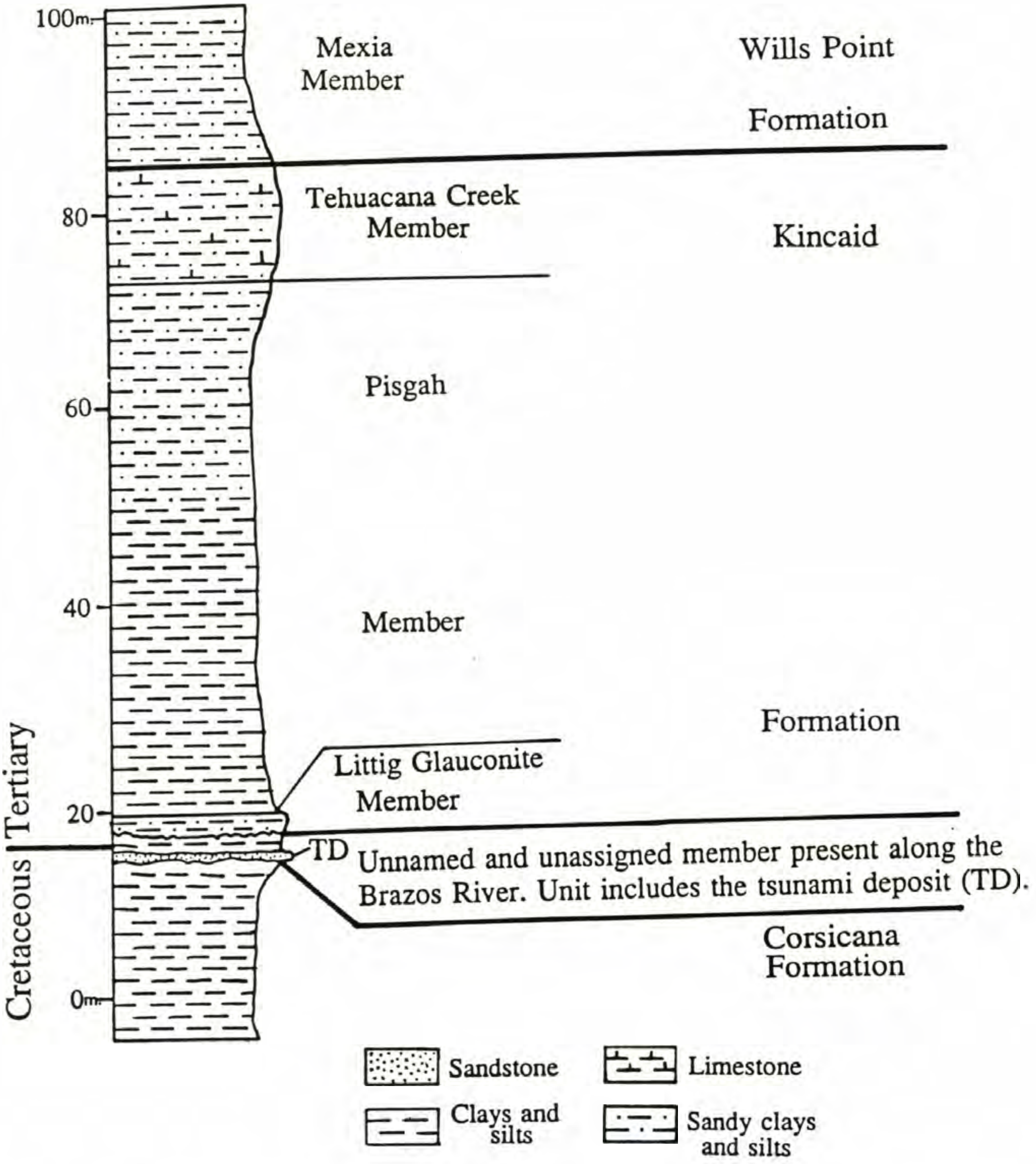


Figure 2. Composite outcrop section of the Late Cretaceous and early Tertiary strata of east-central Texas.

The Pisgah Member of the Kincaid Formation conformably overlies the Littig Glauconite Member and is composed predominately of clays and sandy clays (Gardner, 1933). The environment of deposition for the Pisgah Member is interpreted as being mid to outer shelf based upon paleoecological analysis of foraminifera (Kellough, 1959). The Pisgah Member is conformably overlain by the Tehuacana Creek Member which is mostly composed of calcareous, glauconitic, and commonly indurated sands (Gardner, 1933). Locally, the Tehuacana Creek Member consists of lenses of sandy limestone (Gardner, 1933). Based upon analysis of foraminiferal and molluscan assemblages, Kellough (1959) reported that the Tehuacana Creek Member was deposited in a shallower depositional environment than the Pisgah Member of the Kincaid Formation.

The Kincaid Formation is conformably overlain by the Wills Point Formation of the upper Midway Group that has been divided into the lower Mexia Member, middle Kerens Member and upper Solomon Creek Member. The Mexia Member consists of glauconitic, shales and sandy shales and represents deposition in an open marine environment (Kellough, 1965). The Kerens and Solomon Creek Members are not considered in this report.

The Cretaceous-Tertiary Contact

At both Littig Quarry and Walkers Creek, there is a significant uncomformity between the Cretaceous Corsicana

Formation and the overlying Paleocene Kincaid Formation. The duration of this hiatus is approximately 1 to 2 million years (Jiang, 1980). These unconformable sections contrast with the Brazos River stratigraphic sections, which are among the most complete and best preserved K-T boundary sequences in the world (Jiang and Gartner, 1986; Bryan and Jones, 1989; Keller, 1989; Hansen and Upshaw, 1990). At the Brazos River localities of Bourgeois et al. (1988), the K-T interval consists of underlying Cretaceous clay of the Corsicana Formation, which is capped by an approximately .75 meter thick iridium-rich sandstone complex interpreted as a tsunami deposit (Bourgeois et al., 1988). This in turn is covered by earliest Paleocene clays distinct from the Littig Glauconite Member of the Kincaid Formation. The tsunami deposit and earliest Paleocene clays were argued to be distinctive enough to warrant formal stratigraphic designation as a new member (Hansen et al., 1987) and will be referred to as the unnamed member present along the Brazos River (Figure 2). This unnamed member is unconformably overlain by the heavily burrowed Littig Glauconite Member of the Kincaid Formation.

The biostratigraphy of the Cretaceous-Tertiary boundary has been extensively studied at the Brazos River. Based on calcareous nannofossils, the Brazos River locality (B-1) was found to be virtually complete, containing both the latest Maastrichtian *Micula murus* zone as well as the characteristic "disaster" nannofossil fauna of the earliest Danian (Jiang and Gartner, 1986). The earliest Paleocene clays also contain the complete earliest Paleocene planktonic foraminifera succession of the *Guembelitria cretacea* zone (PO), the *Globigerina eugubina* zone (P1a), and the *Globigerina taurica* zone (P1b) (Keller, 1989). The latest Maastrichtian *Abathomphalus mayaroensis* zone is missing at the Brazos River locality (Keller, 1989). However, it has been suggested that this index fossil may be facies controlled, being limited to facies deeper than continental shelf deposits. For this reason the *Pseudotextularia deformis* zone has been proposed for the latest Maastrichtian and this species is present at the Brazos River localities (Keller, 1989). Since there is obvious evidence of erosion at the base of the tsunami deposit, a portion of the upper Cretaceous must be missing. Paleomagnetic analysis of a core drilled near the Brazos River localities places the K-T boundary low in magnetozone 29r, while in undisturbed K-T intervals the boundary appears high in magnetozone 29r, indicating a stratigraphic gap. (Hansen and Upshaw, 1990). Estimates for the amount of time missing from the boundary interval at the base of the tsunami deposit range from 200,000 (Hansen and Upshaw, 1990) to 300,000 years (Keller, 1989).

Outcrop Stratigraphy

The study area encompasses seven collecting sites within the Kincaid and Wills Point Formations in east-central Texas. Five of these are located along the western bank of the Brazos River 21 kilometers northeast of Rosebud (Figures 1 and 3). One, informally named the Ravine, is situated approximately 12 kilometers north-east of Reagan (Figure 1 and 4), and the last locality is located 7.25 kilometers north of the town of Mexia where Texas Highway 14 crosses Tehuacanna Creek. Stratigraphic sections for each locality are shown in Figure 5.

Brazos-2

The Brazos-2 (B-2) locality (Hansen et al., 1987) is located approximately 50 meters downstream from the confluence of the Brazos River and the informally named Cottonmouth Creek, an ephemeral stream that drains into the Brazos River approximately two kilometers south of the Texas Farm Road 413 bridge (Figure 3). The lower portion of the section consists of approximately one meter of moderately fossiliferous blue-gray clay of the Cretaceous Corsicana Formation. This is covered by a 20-cm.-thick indurated silty limestone unit. The Cretaceous-Tertiary boundary lies approximately 12 cm. below the base of the limestone unit as determined by biostratigraphic analysis of planktonic foraminifera and the first increase in iridium (Hansen et al., 1987). The silty limestone unit is covered by an approximately .5-meter-thick sequence of Paleocene clays virtually identical in appearance to the underlying

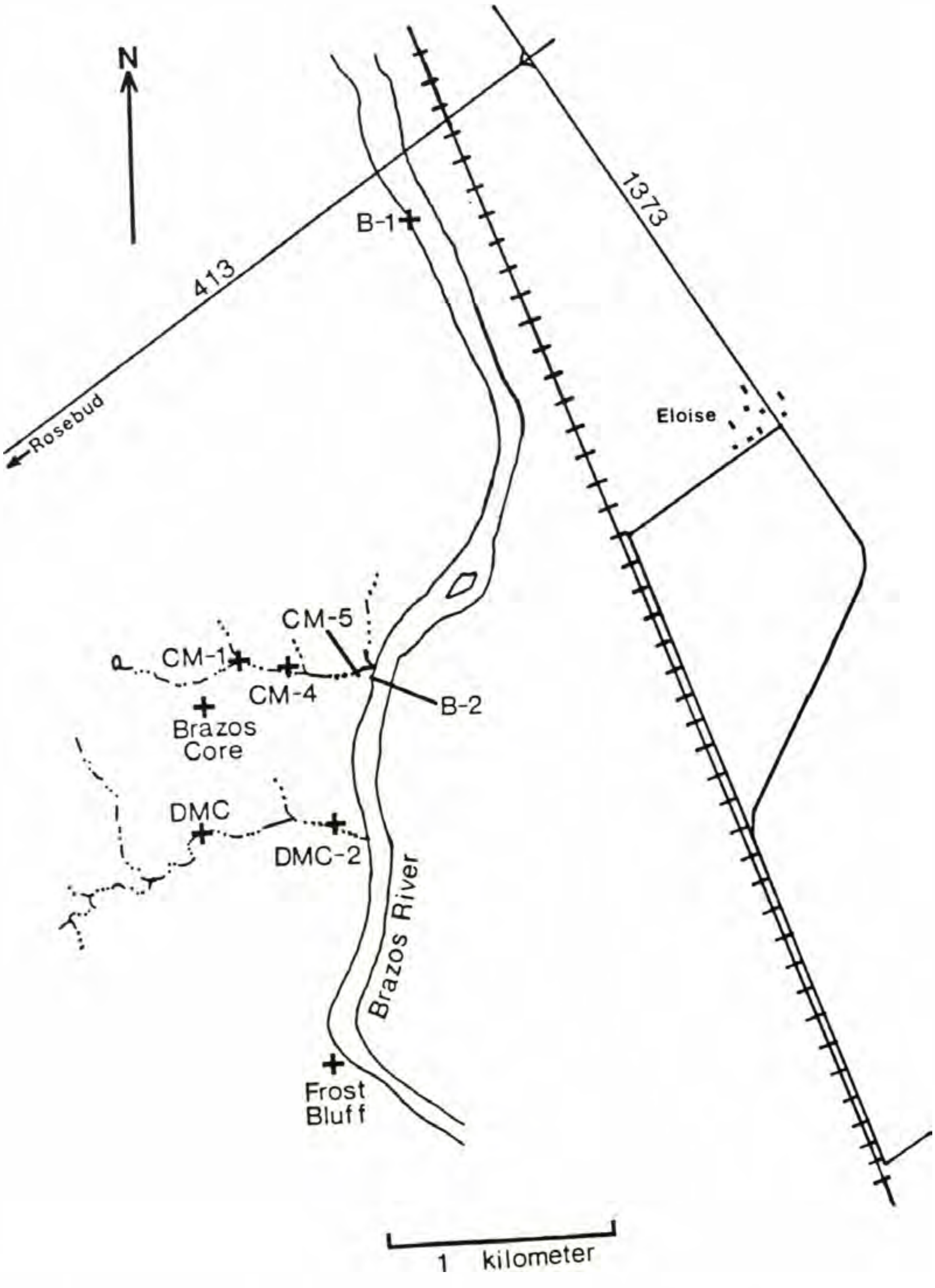


Figure 3. Location of sampled sites along the Brazos River.

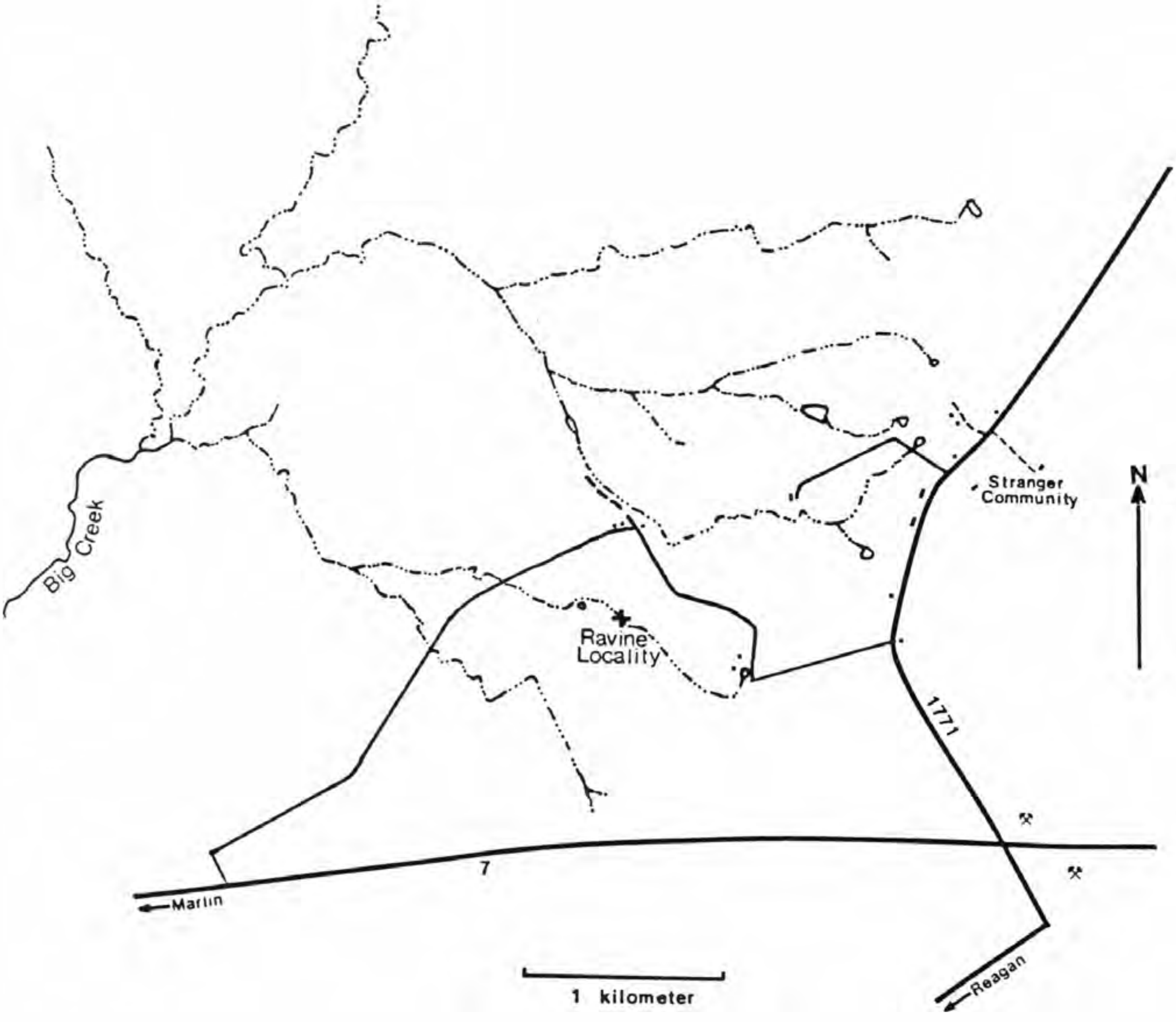


Figure 4. Location of the Ravine stratigraphic section in east-central Texas.

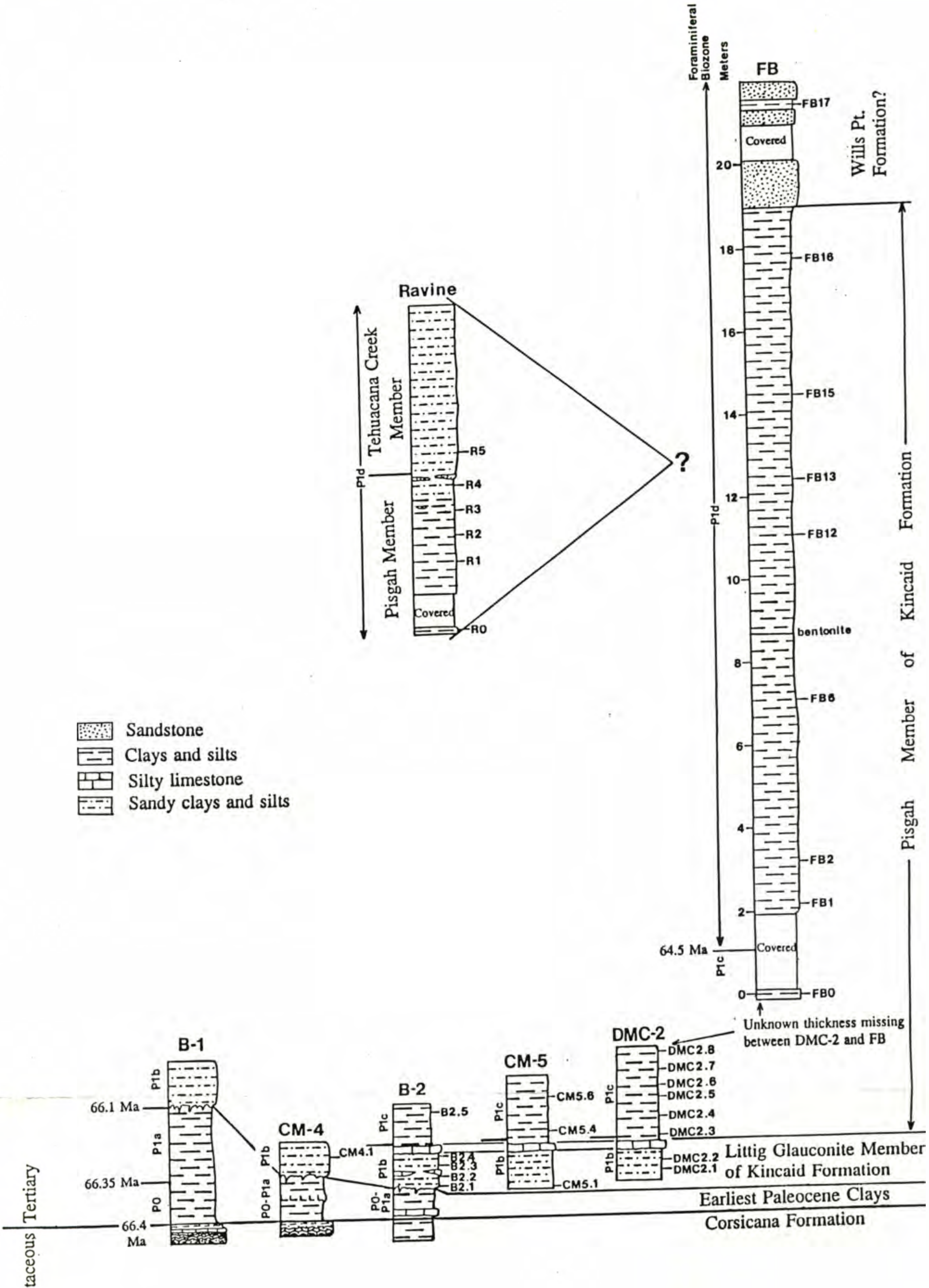


Figure 5. Lithostratigraphic and biostratigraphic correlation of the studied earliest Tertiary stratigraphic sections.

Cretaceous clays. Above these Paleocene clays lies the Littig Glauconite Member of the Kincaid Formation. In the Brazos River region, the Littig Glauconite Member is a heavily burrowed, gray, sandy clay, with common phosphatized molluscan molds visible in outcrop. The unit may also be recognized by the presence of two thin laterally persistent limestone layers. At B-2, the lower of these indurated units is located about 30 cm. above the base of the Littig Glauconite Member. This unit is more irregular in thickness and less laterally persistent than the 15 cm. thick upper silty limestone unit, which is located about one meter above the base of the Littig Glauconite Member at B-2. The Littig Glauconite Member is approximately 1.25 meters thick at B-2, and the contact between the underlying clays and the Littig Glauconite member is extensively burrowed. Approximately one meter of Pisgah clays overlies the Littig Glauconite member at this locality with the contact between the two units being gradational.

Cottonmouth Creek

Localities in the vicinity of Cottonmouth Creek have been thoroughly studied with an eye towards boundary events (Bourgeois et al., 1988; Keller, 1989; Hansen and Upshaw, 1990). A new locality, CM-5 (Figure 3), is situated on the southern side of Cottonmouth Creek, approximately 100 meters upstream from its junction with the Brazos River. The section consists of one meter of heavily burrowed Littig

Member capped by the upper Littig silty limestone layer and 1.5 meters of Pisgah clays. A single sample was was also collected from low in the Littig Glauconite Member at the CM-4 locality of Upshaw (1989) (Figure 3).

Darting Minnow Creek

Darting Minnow Creek is another small informally named creek located approximately .6 kilometers south of Cottonmouth Creek (Figure 3). The sampled section (DMC-2) consists of one meter of Littig Glauconite Member covered by the upper silty limestone and over two meters of Pisgah clays.

Frost Bluff

One of the best exposures of the Kincaid Formation in east-central Texas occurs at Frost Bluff (Figure 3). The section here consists of more than 18 meters of moderately fossiliferous, homogeneous, gray clays of the Pisgah Member of the Kincaid Formation. A glauconitic sandstone approximately 1.3 meters thick may mark the top of the Pisgah Member at this locality (Gardner, 1933). This sandstone is probably overlain by the Mexia Member of the Wills Point Formation (Gardner, 1933). At this locality, the Mexia Member (?) occurs as a series of silty sands and clays that are mostly covered by vegetation.

Ravine

The Ravine stratigraphic section (Figures 1 and 4) consists of three meters of gray silty clays of the Pisgah

Member that are covered by more than two meters of buff colored sandy clays of the Tehuacana Creek Member (Gardner, 1933). A number of indurated shell stringers and lenses occur within approximately one meter of the contact between the Pisgah and Tehuacana Creek members. Very common shells of the molluscan family Turritellidae are arranged linearly within these stringers suggesting sorting by currents.

Tehuacana Creek

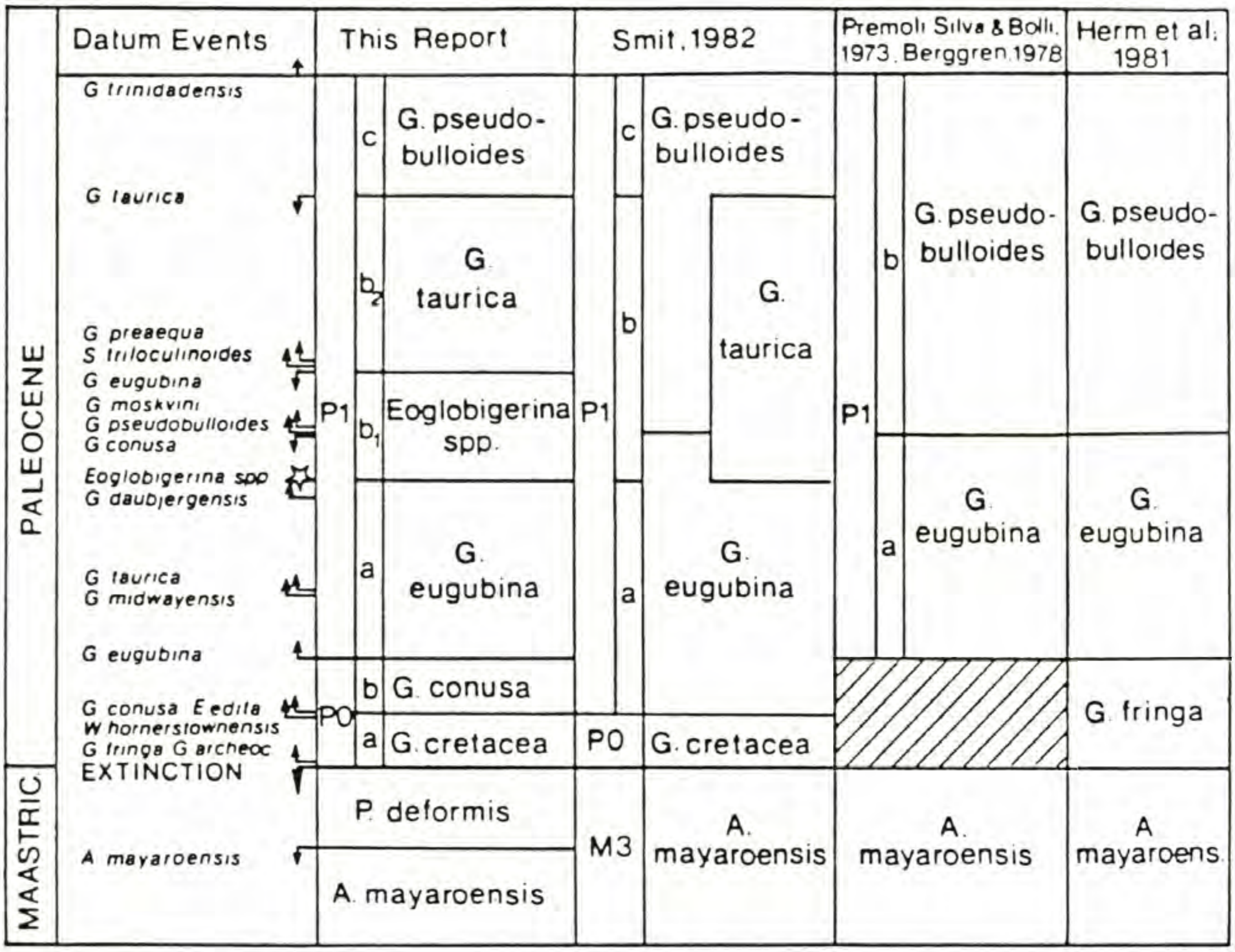
A single stratigraphic level was sampled from a silty shale horizon at the base of the Mexia Member of the Wills Point Formation (sample WPTC) located approximately .4 kilometers west of the Texas Highway 14 bridge along Tehuacana Creek. At this locality, the Tehuacana Creek Member is composed of clay-rich sands and sandy limestone capped by a resistant sandy limestone layer. These are overlain by fossiliferous, glauconitic sands and clays of the Mexia Member (Kellough, 1959).

Lithostratigraphic and Biostratigraphic Correlations

Correlations between the different outcrops were made on the basis of both lithology and the biostratigraphy of planktonic foraminifera. The tsunami deposit, the base of the Littig Glauconite Member, and the upper silty limestone bed in the Littig Glauconite Member all provide readily identifiable marker beds for local correlations of the early Danian strata. A composite stratigraphic section was constructed of Frost Bluff using a bentonite marker bed for correlation. Lithostratigraphic and biostratigraphic correlations between the studied sections are shown in Figure 5.

The biostratigraphy of earliest Paleocene planktonic foraminifera has undergone considerable revision since the publication of the controversial impact hypothesis by Alvarez et al. in 1980. The earliest Paleocene was first divided into the *G. eugubina* zone (P1a), the *G. pseudobulloides* zone (P1b), and the *G. trinadadensis* zone (P1c) (Premoli Silva and Boli, 1973; Berggren, 1978). This basic zonation was subdivided into further zones and subzones by Smit (1982) and Keller (1989), beginning with zone P0 at the K-T boundary (Figure 6). In this report, the zonation of Keller (1989) is adopted with the exception that foraminiferal biozones P0 and P1b were not subdivided.

The sampled stratigraphic section extends from the base of the Littig Glauconite Member upward to the base of the Mexia Member of the Wills Point Formation and spans the P1b, P1c, and a portion of the P1d foram zones (Keller, personal communication, 1989). Zone P1b corresponds to the Littig Glauconite Member fairly closely. The P1a/P1b boundary apparently coincides to a small hiatus of 80,000 years in duration, located approximately 30 cm. below the base of the Littig Glauconite Member of the Kincaid Formation at the CM-4 and B-1 localities (Keller, 1989). The above unconformity



(from Keller, 1988)

Figure 6. Comparison of the Late Maastrichtian and early Paleocene planktonic foraminiferal biozonation of this report (Keller, 1988) with other zonation schemes.

was not recognized in the field. An obvious unconformity exists between the earliest Paleocene clays and the extensively burrowed Littig Glauconite Member and is of uncertain duration.

The P1b zone extends from 30 cm. below the base of the Littig Glauconite Member to the top of the upper silty limestone layer at Cottonmouth Creek, Brazos-2, and the Darting Minnow Creek localities (Keller, personal communication, 1989). This zone is defined as ranging from the entry of common *Eoglobigerina spp.* and corresponds to the peak occurrence of *G. taurica*.

Zone P1c is defined as ranging from the last appearance of *G. taurica* to the first appearance of *G. trinadadensis*. The P1c biozone begins 10-20 cm. above the top of the upper silty limestone layer and ranges upward to a covered interval above the base of Frost Bluff. Portions of the B-2, DMC-2, CM-5, and the Frost Bluff localities contain this biozone.

The first appearance of *G. trinidadensis* is used to mark the beginning of the P1d foraminiferal biozone (Keller, 1988). The lowest stratigraphic interval in which *G. trinidadensis* is found is located 2.35 meters above the base of Frost Bluff (FB1) (Keller, personal communication, 1989). The next lowest sample (FB0) is of P1c age. A 2.35 meter covered interval separates the samples and encompasses to the P1c/P1d boundary at this locality. The Ravine stratigraphic section was not found to contain abundant planktonic foraminifera. However, based on the presence of *G. trinidadensis*, *G. pseudobulloides*, *G. moskvini*, *G. daubjergensis*, and *G. trifolia*, the stratigraphic section was placed within biozone P1d (Keller, personal communication, 1989). The single sample from Tehuacana Creek was also assigned to the P1d zone. As can be seen from perusal of Figure 5, the planktonic foraminiferal biostratigraphy confirms correlations based on the lithostratigraphy.

Sedimentation Rates

Berggren et al. (1985) place the K-T boundary at 66.4 Ma, the first appearance of *G. pseudobulloides* at 66.1 Ma, and the first appearance of *G. trinidadensis* at 64.5 Ma. At the Brazos River localities, *G. pseudobulloides* first occurs .2-.3 meters above the base of the Littig Glauconite Member depending on the locality, and *G. trinidadensis* first occurs at 2.35 meters above the base of Frost Bluff (FB1) (Figure 5). This portion of the sampled section therefore spans approximately 1.6 million years. There is a stratigraphic gap between the top of the Darting Minnow Creek section and the bottom of the Frost Bluff stratigraphic section of unknown thickness and duration. The molluscan fauna changes in terms of its diversity, trophic structure, and taxonomic composition between the two localities suggesting an appreciable loss of time. Keller (1989) calculated a sedimentation rate of .4 centimeters per thousand years for the duration of the P0 foram zone at the Brazos River localities. Assuming a similar regional sedimentation rate for the early Danian, one can calculate the amount of time represented by the strata. There are approximately 3.5 meters of existing strata from the base of zone P1b to the base of zone P1d at the Brazos River localities. The amount of time represented by the strata is equal to: (350 cm. *1000 yrs)/.4cm = 875,000 years. By this calculation approximately 725,000 years is missing at the stratigraphic gap between the top of Darting Minnow Creek and the base of Frost Bluff, assuming that the sedimentation rate remained constant during this 1.6 million year time interval and that the sedimentation rate calculated for the P0 zone is representative for later in the Danian. These assumptions are probably inaccurate. For example, the heavily burrowed sediments, large abundance of planktonic foraminifera, and common phosphatized molds in the Littig Glauconite Member suggest a decrease in the sedimentation rate for this portion of the section and a possible increase in water depth. These facts suggest that the above method probably overestimates the amount of time missing from the section.

Using the same approach, the amount of time represented by the strata at Frost Bluff can be calculated. There are approximately 18 meters of strata measured from the P1c/P1d boundary to the top of Frost Bluff. The amount of time represented assuming the same .4 cm/thousand year sedimentation rate is: (1,800 cm. *1000 years)/ .4 cm = 4.5 million years. As the entire duration of the P1d foraminiferal biozone is only 1.5 million years and none of the sampled localities is of P2 age, this estimate of sedimentation rate must be too low. The sediments in the upper portion of Frost Bluff are coarser and planktonic foraminifera are much less abundant in them than in the underlying strata, suggesting either an increase in the sedimentation rate that would dilute the foraminifera, or a shallowing of the continental shelf environment or both.

The calculated amount of time supports the interpretation of an increased sedimentation rate significantly greater for the Frost Bluff portion of the stratigraphic section than for the underlying strata. The amount of time represented in the total stratigraphic section is probably well in excess of 1.9 million years. More precise determinations are not possible without the magnetostratigraphy of the studied sections.

METHODS

Sample Collection and Processing

Collecting localities were chosen so as to give complete sampling through the P1b-P1d foraminiferal biozones. The samples from the Ravine and Tehuacana Creek localities were taken to give a slightly broader geographic perspective to the study. A total of 48 stratigraphic levels was sampled from the seven localities. Samples were taken at 0.3 or 1.0 meter intervals, depending on stratigraphic location. The lowest portion of the section was sampled at 0.3 meter intervals in an effort to capture rapid evolutionary changes hypothesized to occur in this interval, while the Frost Bluff and Ravine stratigraphic sections were sampled at 1.0 meter intervals to provide broader stratigraphic coverage. Irregular sample intervals occurred where there were covered portions of the section or difficulty in accessing the outcrops. The outcrops were cleared off to ensure the collection of unweathered material, and then were sampled by making a horizontal cut and carefully prying out a 10-20 cm. thick piece of the relatively soft sediment. Approximately 7.5 kg. of sediment were taken from each stratigraphic level. Of the 48 stratigraphic levels, 33 were processed for mollusks. Where the stratigraphic sections overlapped at different localities, samples were combined based on stratigraphic position to create composite assemblages, thereby reducing the number of stratigraphic levels analyzed for mollusks to 27. All the samples were sieved for planktonic foraminifera using a 63 micron sieve size and were sent to Dr. Gerta Keller of Princeton University for analysis.

Because the mollusk specimens are extremely fragile and easily fragmented during sieving or ultrasonic disaggregation, the bulk samples were processed by carefully picking apart the moistened sediment with a needle. Molluscan identifications were made to the species level wherever possible. In some cases, due to poor preservation or small size, specimens were identifiable only to family, or occasionally class. Species identifications were made using available literature and by comparison with type material at the United States National Museum. Some of the possible Cretaceous and unidentified mollusks were examined and identified by Dr. Norm Sohl of the U.S.G.S., an expert on Cretaceous mollusks of the Gulf Coast region. Mollusks of the family Turritellidae were identified by Dr. Warren Allmon of the University of South Florida.

Only the beaks of bivalves were counted, and these counts were divided by two. This procedure sometimes yielded one-half individuals and in these cases the bivalve counts were rounded up to the next whole number. For gastropods, specimens with either the apex or aperture intact were counted after carefully checking to see that these didn't match up with other specimens of the same species. Scaphopods were counted only if they were largely complete and solitary corals were counted only if their bases were intact.

Species lists from the latest Cretaceous of the Brazos River localities (CM-1) were made available by Dr. Erle Kauffman of the University of Colorado at Boulder. Portions of the Cretaceous species lists compiled by Farrand (1984) were used in this study. The earliest Danian of the Brazos River was studied in detail by Upshaw (1989) and some of his results are incorporated.

Grain-Size Analysis

Sediments were wet-sieved in order to determine their sand content using sieves in the 0-4 phi size range. Each size-fraction was examined under a low power microscope in order to determine roughly its composition. After dry-weighing, the samples were immersed in a 5% HCl solution in order to dissolve the sand-size carbonate fraction. The samples were then reweighed dry, and the percent carbonate in the sand-size fraction was calculated.

Analytical Methods

Species were assigned to a variety of origination categories following the criterion of Upshaw (1989). Local Cretaceous species (LK) are those species known from the Cretaceous of Texas. Immigrant Cretaceous species (IK) are those species previously found in Cretaceous rocks other than the Corsicana Formation of Texas. Local Paleocene species (LP) are those species known only from sediments of Paleocene age in Texas. Eastern Gulf Paleocene species (EGP) are those species known previously from the Clayton Formation of Alabama. Maryland Paleocene species (MP) are those species previously described from the Brightseat or Aquia Formations of Maryland. North Dakota Paleocene (NDP) species are those species found previously in the Cannonball Formation of North Dakota. Eocene species (E) are those species previously desribed from rocks of Eocene age. Unknown species (UnS) include undescribed species as well as those unique taxa that could not be assigned to the other categories due to poor preservation. Unidentified taxa are those taxa that could not be identified as unique, either because of poor preservation or small size.

Each species was designated to a life-habit category so that changes in the paleoecology through time, and any long-term environmental effects of the K-T extinctions could be assessed. This was achieved by researching the life-habits of modern representatives of the same family.

Cluster Analysis

Cluster analysis was used in an effort to recognize naturally occurring groupings of sites. This technique offers several potential advantages over manual inspection of the data including reproducibility of results, the ability to analyse large quantities of data, and reduction of results to a readily interpretable dendrogram (Everitt, 1974). Q-mode cluster analysis identifies groupings of sampling localities based on their species co-occurrences (Valentine, 1973).

Q-mode clustering was performed on the Paleocene data set using M.V.S.P. version 1.3, a multivariate statistics package written for the IBM PC and compatibles by Warren L. Kovach of Indiana University, and SYSTAT, a system of statistics for the PC (Wilkinson, 1989).

A vast number of similarity and dissimilarity indexes has been developed to aid in the comparison of ecologic data (Clifford and Stephenson, 1975). One commonly used index that has been developed to handle relative abundance data is the Canberra Metric distance coefficient (Lance and Williams, in Sneath and Sokal, 1973) and is given by the equation:

$$\sum_{1}^{n} \frac{|x_{1_i} - x_{2_i}|}{|x_{1_i} + x_{2_i}|}$$

where n = # of species, and x_{1i} and x_{2i} are the values for the ith attribute (site). The Canberra Metric distance coefficient is quite sensitive to the occurrence of rare species (Clifford and Stephenson, 1975). For example, the coefficient would rate a pair of sites with values of 10,000 and 0 for a given species as equally dissimilar as a pair of sites with values of one and 0 for the same species (Clifford and Stephenson, 1975). Because the Paleocene data set does not contain such a large range of values, this undesirable property does not have an overwhelming effect on the analysis.

Data are commonly rearranged through various transformations such as log n or square root n before they are analysed with similarity or distance coefficients, so that the resulting clusters best reflect naturally occurring groupings (Clifford and Stephenson, 1975). These transformations and the large number of similarity coefficients available have given rise to charges that methods are being selected to prove what it is the observer wants to prove anyway (Clifford and Stephenson, 1975). Because of this controversy over data transformation, and because the Paleocene data are relatively low in terms of their abundances (the most abundant species has less than one hundred and fifty individuals at a given site), no transformations were used. However, extremely rare species consisting of a single individual occurring at a single stratigraphic level were excluded from the cluster analysis, as were those individuals which could not be identified as unique taxa. This manipulation reduced the number of species to 84, a manageable number of species for the computer programs to handle.

Clusters are constructed by the computer from a symetric matrix of similarity or dissimilarity coefficients. A large number of methods exist for the fusing of clusters (Sneath and Sokal, 1973; Clifford and Stephenson, 1975). The unweighted pair-group method is commonly used and has generally been found to be satisfactory for ecologic work (Clifford and Stephenson, 1975). In the unweighted pair-group method, the average similarity between the groups that form the clusters is calculated from the original coefficients between all species or sites, so that each member of each cluster has equal weight in all clustering steps (Valentine, 1973). This method is a relatively weakly clustering strategy, producing only moderately sharp clusters (Clifford and Stephenson, 1975). Another commonly used clustering strategy is the weighted pair-group method, in which the average dissimilarity between the members which make up the new cluster is calculated from the previous clustering step (Valentine, 1973). In this method, late-joining groups that are small are more heavily weighted in the clustering than in the unweighted pair-group method (Valentine, 1973). The weighted pair-group method is preferable in circumstances where there is reason to believe that particular species or sites have been undersampled (Valentine, 1973; Pielou, 1984). Both of these methods of clustering were used in the analysis of the Paleocene data set. To check results obtained using the above methods, further cluster analysis was performed using prensence/absence data and Jaccard's coefficient (Clifford and Stephenson, 1975).

Diversity

The number of species and their relative abundances are both important elements of the diversity of an assemblage (Peet, 1974). Four measurements of diversity were employed in this study. The simplest of these is species richness, which is defined as the number of species collected in a given sample (Peet, 1974). A problem with species richness is that it is extremely sensitive to changes in sample size; as the sample size increases, more species are gradually added to the assemblage.

Several analytical methods have evolved to allow comparison of samples with unequal abundances. Species range-richness is defined as the number of species ranges that occur in a given sample. This method alleviates the effects of a patchily distributed fauna, since a species is counted as being present in a stratigraphic level if stratigraphic levels both above and below it contain the species. A commonly used measure of species diversity which is relatively insensitive to changes in sample size is the Shannon-Weaver Index (Sanders, 1968; Clifford and Stephenson, 1974), which is given by the equation,

$$H'=-\sum (p_i)\ln(p_i)$$

where H' = the Shannon-Weaver diversity index, and p_i is the proportion of the i_{th} species in the sample. Unidentified taxa were not included in the calculation of the Shannon-Weaver diversity index because these specimens could not be identified with certainty.

Another approach to describing diversity is rarefaction analysis, in which diversity is portrayed graphically (Sanders, 1968; Hurlbut, 1971; Tipper, 1979). Rarefaction analysis circumvents the problem of sample-size sensitivity of most diversity measures by calculating expected numbers of species at different sample sizes given the total sample size and the relative abundances of the various species for a given assemblage. The algorithm for calculating rarefaction curves is given by Hurlbut (1971) :

$$E(Sn) = \sum_{i=1}^{N} -1 \frac{\binom{N-N_i}{n}}{\binom{N}{n}}$$

E(Sn) = the expected number of species, N = the total number of individuals, N_i = the number of individuals in the i_{th} species, and n = the hypothetical number of individuals.

RESULTS

Ninety-four species represented by 4,847 individuals were collected from the Kincaid and Wills Point Formations during the course of this study. Of these, 45 are unknown species (UnS) and could not be designated as previously described Cretaceous or Tertiary taxa. Thirty-seven are local Paleocene species (LP), five have been previously described from the Paleocene Aquia or Brightseat Formations of Maryland (MP), two are local Cretaceous species (LK), two are described Eocene species (E), one is known previously from Paleocene Clayton Formation of Alabama (EGP), and one has been previously described from the Paleocene Cannonball Formation of North Dakota (NDP). Table 1 contains a complete list of invertebrate macrofossil species found in the Paleocene stratigraphic sections and their origination categories. It includes the 94 taxa found in this study as well as taxa found by Upshaw (1989) for a total of 107 species. A number of specimens could only be identified to higher taxonomic groupings such as class or family and are not considered to be unique taxa. These unidentified taxa are included with the complete species assemblage list for the studied sections (Appendix I). A total of 41 unidentified taxa was differentiated in addition to the identified species.

Cluster Analysis

Q-mode cluster analysis was used to help identify

Table 1. Invertebrate macrofossil species found in the Danian studied sections showing assigned origination categories.

Family	**Species Name**	**Origination Category**
Anthozoa		
Caryophylliidae	1. *Caryophyllia dumblei?* Vaughan and Popenoe	LP
Caryophylliidae	2. *Caryophyllia mediavia?* Vaughan and Popenoe	LP
Caryophyllidae	3. *Platytrochus primaevus* Vaughan and Popenoe	LP
Flabellidae	4. *Flabellum conoideum?* Vaughan and Popenoe	LP
Dendrophylliidae	5. *Balanophyllia ponderosa var. texana?* Vaughan and Popenoe	LP
Scaphopoda		
Siphondentaliidae	6. *Cadulus phoenicea?* Gardner	LP
Dentaliidae	7. *Dentalium mediaviense* Harris	LP
Dentaliidae	8. *Dentalium sp. A*	UnS
Dentaliidae	9. *Dentalium sp. B*	UnS
Gastropoda		
Vitrinellidae	10. *Solariorbis proius* Gardner	LP
Vitrinellidae	11. *Solariorbis sp. A*	UnS
Vitrinellidae	12. *Solariorbis (?) sp. B*	UnS
Vitrinellidae	13. *Solariorbis sp. C*	UnS
Vitrinellidae	14. Vitrinellidae sp. A	UnS
Mathildidae	15. *Promathilda parvula* Sohl	IK
Turritellidae	16. *"Turritella" postmortoni* (Harris)	E
Turritellidae	17. *"Turritella" prehumerosa* (Govonni)*	MP
Turritellidae	18. *"Turritella" premortoni* (Govonni)*	MP
Cerithiidae	19. *Bittium (Bittium) estellense* (Aldrich)	LP
Cerithiidae	20. Cerithiidae sp. A	UnS
Cerithiidae	21. Cerithiidae sp. B	UnS
Cerithiidae	22. *Nudiavagus sp. A* Stephenson	LK
Cerithiidae	23. *Nudiavagus sp. B*	UnS
Litiopidae	24. *Litiopa sp. A*	UnS
Scalariidae	25. Epitoniidae (?) sp.	UnS
Aporrhaidae	26. Aporrhaidae sp.	UnS
Calytraeidae	27. *Calyptraea sp.*	UnS
Strombidae	28. *Calyptrophorus cf. aldrichi* Gardner	LP
Strombidae	29. *Calyptrophorus popenoe* Gardner	LP
Naticidae	30. *Polinices (?) julianna* (Gardner)	LP
Columbellidae	31. Columbellidae sp.	UnS
Nassariidae	32. Nassariidae sp.	UnS
Fasciolariidae	33. *Exilia cf. pergracilis* Conrad	LP
Fasciolariidae	34. *Falsifusus cf. harrisi?* Le Blanc	LP
Fasciolariidae	35. Fasciolariidae sp. A	UnS
Fasciolariidae	36. Fasciolariidae sp. B	UnS
Fasciolariidae	37. Fasciolariidae sp. C	UnS
Fasciolariidae	38. Fasciolariidae sp. D	UnS
Olividae	39. *Agaronia mediavia* (Harris)	LP
Volutidae	40. *Volutocorbis texanus* (Gardner)	LP
Turridae	41. *Amuletum curvocostatum* Stephenson	LK
Turridae	42. *Amuletum sp. d*	UnS
Turridae	43. *Anomalofusus substriata* or *subnosus* Wade; Sohl	IK
Turridae	44. *Beretra aff. ornatula* Stephenson	LK
Turridae	45. Turridae sp. A	UnS
Turridae	46. Turridae sp. B	UnS
Turridae	47. Turridae sp. C	UnS
Turridae	48. Turridae sp. D	UnS
Turridae	49. Turridae sp. R	UnS

Pyramidellidae	50.	*Creonella obscurplica* Govonni*	MP
Acteonidae	51.	*Tornatellaea quercollis?* Harris	LP
Acteonidae	52.	*Tornatellaea texana* Gardner	LP
Acteonidae	53.	Acteonidae sp. A	UnS
Ringiculidae	54.	*Ringicula butleriana?* Aldrich	E
Ringiculidae	55.	*Ringicula dubia* Stanton	NDP
Ringiculidae	56.	*Ringicula sp. A*	UnS
Atyidae	57.	*Atys (Aliculastrum) sp.* Gardner 1933	LP
Retusidae	58.	*Retusa (Cylichnina) emoryi* (Gardner)	LP

Bivalvia

Nuculidae	59.	*Nucula (Nucula) mediavia* Harris	LP
Nuculanidae	60.	*Jupiteria (Ledina) smirna* Dall	LP
Nuculanidae	61.	*Nuculana cf. corpulentoides* (Aldrich)	E
Nuculanidae	62.	*Nuculana saffordana?* Harris	LP
Nuculanidae	63.	*Nuculana sp.* (Gardner 1933)	LP
Nuculanidae	64.	*Saccella sp.* Gardner 1933	LP
Nuculanidae	65.	*Nuculana sp. B*	UnS
Nuculanidae	66.	*Nuculana sp. C*	UnS
Solemyidae	67.	*Solemya bilix* Stephenson	LK
Arcidae	68.	*Striarca webbervillensis* (Stephenson)	LK
Arcidae	69.	*Striarca (?) sp. A*	UnS
Arcidae	70.	*Nemodon eufalensis* (Gabb)	LK
Arcidae	71.	Arcidae sp. B	UnS
Limopsidae	72.	*Limopsis sp.*	UnS
Cucullaeidae	73.	*Cucullaea macrodonta* Whitfield	LP
Mytilidae	74.	*Brachidontes saffordi* (Gabb)	LP
Mytilidae	75.	Mytilidae sp.	UnS
Pectinidae	76.	*Amusium (Propeamussium) alabamense* (Aldrich)	LP
Pectinidae	77.	*Syncyclonema sp.*	UnS
Ostreidae	78.	*Ostrea (Ostrea) pulaskensis* Harris	LP
Ostreidae	79.	*Pycnodonte sp.*	UnS
Lucinidae	80.	*Phacoides julianne* Bretzsky*	MP
Lucinidae	81.	*Lucina (Callucina) cf. ulheri* Clark	MP
Lucinidae	82.	Lucinidae sp. A	UnS
Leptonidae/ Montacutidae	83.	Leptonidae/Montacutidae sp.	UnS
Sportellidae	84.	Sportellidae sp.	UnS
Carditidae	85.	*Venericardia (Baluchicardia) bulla* Dall	LP
Carditidae	86.	*Venericardia (Glyptoactis) eoa* Gardner	LP
Carditidae	87.	*Venericardia (Glyptoactis?) moa* Gardner	LP
Crassatellidae	88.	*Crassatella gabbi* Safford	LP
Crassatellidae	89.	*Crassatella sp. A*	UnS
Astartidae	90.	*Vetericardiella webbervillensis* Stephenson	LK
Cardiidae	91.	Cardiidae sp.	UnS
Tellinidae	92.	*Tellina cf. quihi* Gardner	LP
Tellinidae	93.	*Tellina sp. A*	UnS
Tellinidae	94.	*Tellina sp. B*	UnS
Semelidae	95.	Semelidae sp.	UnS
Kelliellidae	96.	*Kelliella (?) evansi* Gardner	LP
Veneridae	97.	*Pitar sp.*	UnS
Corbulidae	98.	*Caryocorbula coloradoensis* Gardner	LP
Corbulidae	99.	*Caryocorbula kennedyi* Gardner	LP
Corbulidae	100.	*Corbula milium* Dall	LP
Corbulidae	101.	*Corbula subengonata* Dall	MP
Hiatellidae	102.	*Panopea sp.*	UnS
Pholadidae	103.	*Martesia sp.?*	UnS
Cuspidariidae	104.	*Cuspidaria grandis?* Stephenson	LK
Cuspidariidae	105.	*Cuspidaria sp. A*	UnS
Cuspidariidae	106.	*Cuspidaria sp. B*	UnS
Verticordiidae	107.	*Verticordia sp.* Harris 1896	EGP

Key to Origination Categories

UnS = Unknown Species. This category includes previously undescribed taxa as well as those unique taxa not assignable to the other origination categories listed below due to their small size or poor preservation.

IK = Immigrant Cretaceous Species
LK = Local Cretaceous Species
LP = Local Paleocene Species
MP = Maryland Paleocene Species
NDP = North Dakota Paleocene Species
EGP = Eastern Gulf Paleocene Species
E = Eocene Species

* Denotes a species taxonomically described in an unpublished manuscript. *Phacoides julianne* was a species recognized in the Paleocene Brightseat Formation of Maryland by Bretzsky and Kauffman in an uncompleted manuscript. See Govoni (1984) for other species designated with an asterisk. Mollusks of the family Turritellidae originally described by Govonni (1984) were designated "Turritella" because of their uncertain taxonomic placement (Allmon, personal communication, 1990).

Tertiary molluscan species names used in this study are from Palmer and Brann (1965; 1966).

groupings of the sites, and the results of this analysis are shown in Figure 7. Of the methods selected, the Canberra Metric Coefficient coupled with the weighted pair-group method of cluster joining yielded the most reasonable clusters. A total of five groupings of sites may be identified from the dendrogram. The sites generally group in stratigraphic order and correspond closely to the earliest Paleocene planktonic foraminiferal biozones. Assemblage A occurs in a series of earliest Paleocene outcrops along the Brazos River that were studied in detail by Upshaw (1989) and coincides with the occurrence of the P0 and P1a planktonic foraminiferal biozones (Keller, 1989). Assemblage B is found in the sampled sites of the Littig Glauconite Member of the Kincaid Formation and matches the occurrence of the P1b planktonic foraminiferal biozone. The incidence of Assemblage C is limited to the lowermost part of the Pisgah member of the Kincaid Formation, zone P1c. Assemblage D is found at the Frost Bluff and Tehuacana Creek localities in the Pisgah Member of the Kincaid Formation and the Mexia Member of the Wills Point Formation. These rock units belong principally to the P1d biozone. Assemblage E is restricted to the Ravine locality and is in the P1d biozone.

Samples DMC2.6, DMC2.7, and DMC2.8 cluster with the samples from the Littig Glauconite Member, Assemblage B, rather than with the other samples from the lowermost

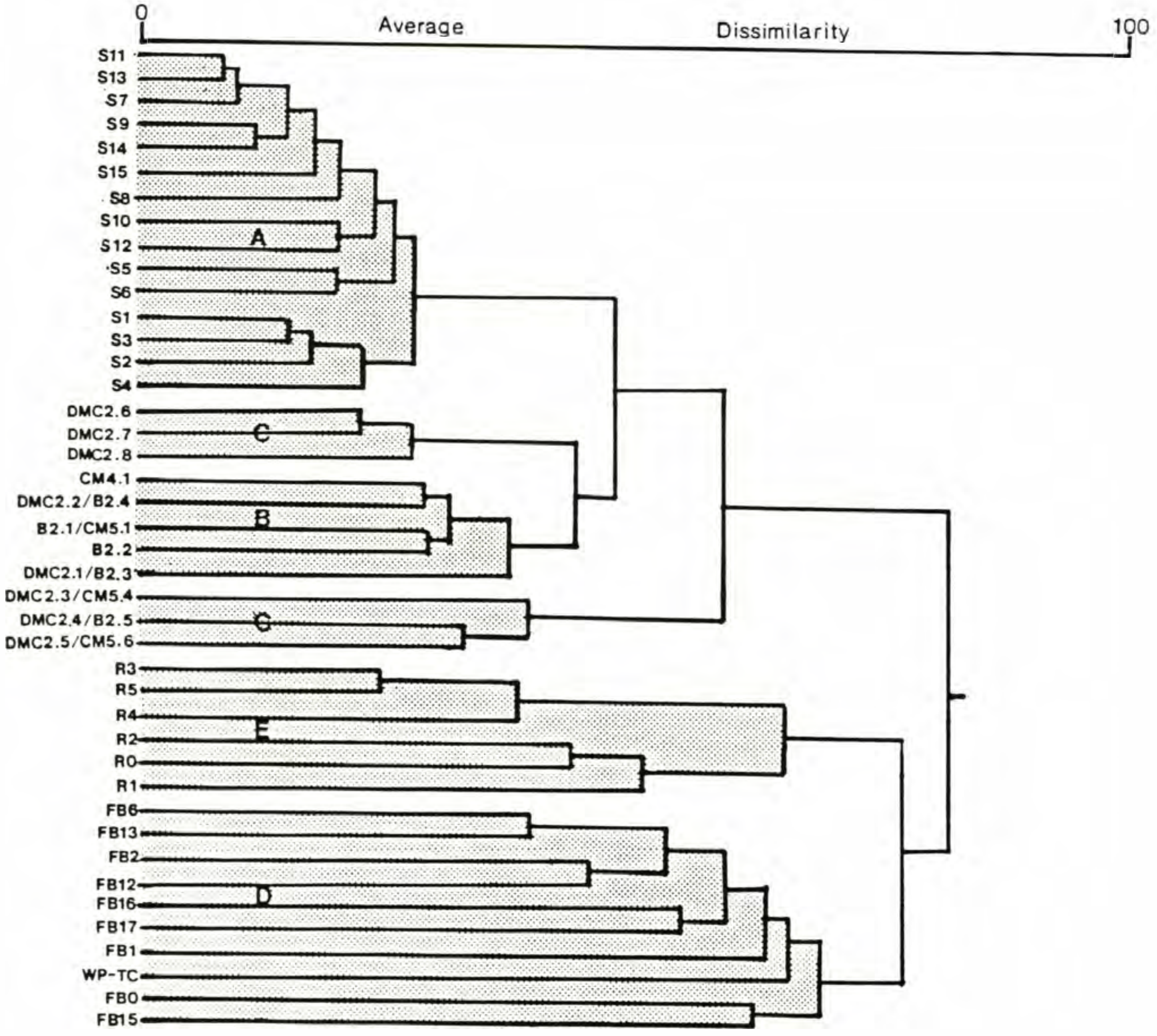


Figure 7. Clustering of sampled sites produced by the Canberra-Metric distance coefficient and the weighted pair-group method of cluster joining. Horizontal axis represents average dissimilarity, ranging from zero (complete similarity) to one hundred (complete dissimilarity).

portion of the Pisgah Member. This result is explained through consideration of the sizes of samples from the sites in question. Samples DMC2.6, DMC2.7, and DMC2.8 have among the lowest abundances of any of the collecting sites in the study (Appendix I). Samples characterized by low abundances will inherently contain relatively few species in common with samples having much higher abundances, since the number of species in a given assemblage is partially a function of sample size. When two such samples are compared using the Canberra Metric Distance Coefficient, they are shown to be dissimilar because of the disparity in sample size between the sites, not necessarily because of any inherent compositional difference in the assemblages. In the case of samples DMC2.6, DMC2.7, and DMC2.8, the samples clustered with the less diverse Assemblage B of the Littig Glauconite Member because of their low abundances. This interpretation is bourne out by results of clustering based on presence/absence data. The samples were further analyzed using Jaccard's dissimilarity coefficient and nearest-neighbor and furthest-neighbor complete-linkage methods of clustering (Clifford and Stephenson, 1975). Clusters produced using these methods were similar to those produced using the Canberra Metric distance coefficient; the only differences being that samples DMC2.6, DMC2.7, and DMC2.8, clustered with the other samples from the lowermost Pisgah Member, Assemblage C, and that the Ravine localities were not distinguished from the Frost Bluff samples. Based on the above analysis and inspection of the data, samples DMC2.6, DMC2.7, and DMC2.8, were grouped with the rest of Assemblage C.

Taxonomic Composition

Assemblage A

Assemblage A, the earliest Paleocene assemblage from the Brazos River localities is discussed in detail by Upshaw (1989). The most common species occurring in assemblage A are shown in Table 2. The assemblage is highly dominated by *Nuculana sp. B* (54.5%), Naticidae (12%), and *Litiopa sp. A* (9.5%). A bloom of *Litiopa sp. A* occurs immediately above the K-T boundary and coincides with peak abundances of local Cretaceous species, *Striarca webbervillensis* and *Vetercardiella webbervillensis* . The occurrences of these species are largely responsible for the smaller subcluster of samples S1-S4 in assemblage A (Figure 7). The means and ranges of the Shannon-Weaver Diversity index for each assemblage are shown in Figure 8. With a Shannon-Weaver index average of 1.33, assemblage A has far lower diversities than any of the other Paleocene molluscan assemblages.

Assemblage B

Table 3 shows the most common species present in the Littig Glauconite Member, assemblage B. As in assemblage A, *Nuculana sp. B* (17.3%) is the most common mollusk. Oysters,

Table 2. Major Faunal Constituents

Assemblage A

Taxa	**Mean Relative Abundance**	**Presence Percentage**	**PP x Relative Abundance**
Nuculana sp. B	54.5	100	5450
Naticidae	12.0	93.3	1119.6
Litiopa sp. A	9.5	53.3	506.4
Ostreidae	4.7	73.3	344.5
Nudiavagus sp. A	2.1	60	126
Corbula subengonata	1.9	60	114
Vetercardiella webbervillensis	2.2	40	88
Amuletum curvocostatum	1.0	60	60
Striarca webbervillensis	1.1	40	44

The data for Table 2 is from Upshaw (1989). Mean relative abundance is defined as the sum of the relative abundances for a given taxon divided by the number of sites which compose the assemblage. Presence percentage is the number of occurrences of a given taxon divided by the number of assemblage sites multiplied by one hundred. The fourth column is presence percentage multiplied by mean relative abundance. The method of ranking is from Walker (1974).

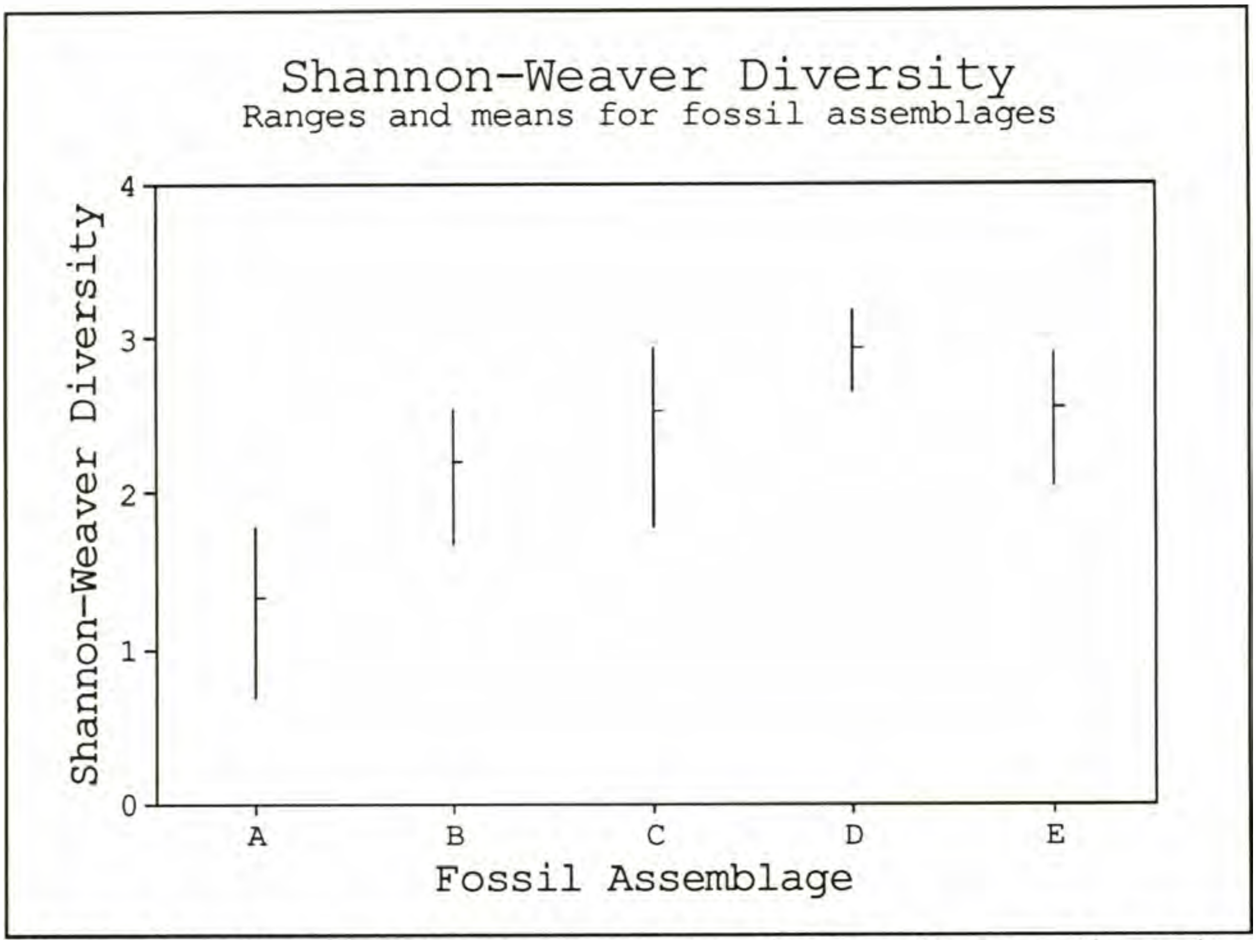


Figure 8. Means and ranges of the Shannon-Weaver diversity index for the studied assemblages.

most commonly *Ostrea pulaskensis*, are more common in assemblage B than in the other Paleocene assemblages. *Venericardia moa* (3.1%) is a fairly common mollusk which is restricted to the Littig Glauconite Member in the studied stratigraphic sections. Assemblage B is also characterized by a number of relatively uncommon species that have their main occurrences within the Littig Glauconite Member. These include: Cerithiidae sp. A (1 %), Aporrhaidae sp., *Calyptrophorus aldrichi*, and *Crassatella sp. A*, as well as a few unknown fasciolarids. Note the high incidence of unidentified taxa such as Nuculanidae (17.1%) and Naticidae

Table 3. Major Faunal Constituents

Assemblage B

Taxa	**Mean Relative Abundance**	**Presence Percentage**	**PP x Relative Abundance**
Nuculana sp. B	17.3	100	1730
Nuculanidae	17.1	80	1424
Ostrea pulaskensis	10.1	100	1010
Tornatellaea sp. indet.	7.8	100	780
Naticidae	7.2	100	720
Cucullaea sp. indet.	6.6	100	660
Crassatella sp. indet.	4.8	100	480
Amusium alabamense	3.9	80	312
Venericardia moa	3.1	100	310
Cerithidae sp. A	1.0	80	80
Retusa emoryi	1.0	80	80

(7.2%) within this assemblage. The presence of these unidentified taxa indicates the relatively poor preservation present within the Littig Glauconite Member. Despite the poor preservation, the mean Shannon-Weaver Diversity value of 2.34 is much higher than for assemblage A (Figure 8).

Assemblage C

The pectinid, *Amusium alabamense* (18%) dominates assemblage C (Table 4). The assemblage is also characterized by the peak abundances of *Cucullaea macrodonta* (6.7%), *Striarca (?) sp. A* (2.9%), and *Saccella sp.* Gardner, 1933 (1.9%). Less common species that are most abundant in the lowermost portion of the Pisgah member include: Cerithiidae sp. B, Fasciolariidae A, *Limopsis sp.*, and *Verticordia sp.* Harris, 1896. Assemblage C has the widest range of Shannon-Weaver Diversity values of any of the assemblages partly reflecting fluctuations in the abundance of the samples. The mean Shannon-Weaver diversity for Assemblage C is 2.53, higher than for assemblages A and B.

Assmblage D

The fauna of assemblage D most closely matches the typical Midway fauna described by Gardner (1933). Table 5 shows the dominant species found in the assemblage. The mean Shannon-Weaver diversity value of 2.93 is the highest for any of the assemblages (Figure 8). The ranges of the Shannon-Weaver diversity values are the smallest of any of the studied assemblages, indicating the high stability of

Table 4. Major Faunal Constituents

Assemblage C

Taxa	**Mean Relative Abundance**	**Presence Percentage**	**PP x Relative Abundance**
Amusium alabamense	18.0	100	1800
Naticidae	15.6	100	1560
Nuculanidae	8.4	100	840
Cucullaea macrodonta	6.7	83.3	558.1
Striarca (?) sp. A	2.9	83.3	241.6
Retusa emoryi	2.4	100	240
Turritellidae	2.4	100	240
Cucullaea sp. indet.	3.4	66.6	226.4
Venericardia sp. indet.	2.9	66.6	193.1
Jupiteria smirna	2.2	83.3	183.3
Saccella sp. Gardner	1.9	83.3	158.3

Table 5. Major Faunal Constituents

Assemblage D

Taxa	**Mean Relative Abundance**	**Presence Percentage**	**PP x Relative Abundance**
Jupiteria smirna	14.0	100	1400
Naticidae	11.0	100	1100
Cucullaea macrodonta	5.1	100	510
Venericardia eoa	4.0	100	400
Bittium estellense	4.2	90	378
Caryocorbula coloradoensis	4.5	80	360
Atys sp. Gardner	3.0	100	300
Nuculana saffordana?	2.8	100	280
Tornatellaea texana	3.1	90	279
Crassatella sp. indet.	2.3	100	230
Nucula mediavia	2.3	90	207
Volutocorbis texanus	1.7	80	136
Corbula milium	1.7	70	119

the fauna and the good preservation found in this portion of the stratigraphic section.

Assemblage E

Assemblage E (Table 6), which is found at the Ravine locality, is most similar to the coeval Frost Bluff fauna of Assemblage D (Figure 7). Of the 49 species which occur at the Ravine locality, 37 (76 %) also appear in coeval deposits at Frost Bluff. These two assemblages have fairly similar taxonomic compositions but differ significantly in terms of the relative proportions of the most commmon fauna. The most common fauna of assemblage E: *Venericardia eoa* (17.8%), *Crassatella sp. indet.*(11.3%), *"Turritella" premortoni* (10.7%), and *Caryocorbula coloradoensis* (8.5%), all occur in assemblage D. However, their relative abundances are much lower in assemblage D. Conversely, the most abundant fauna of assemblage D, *Jupiteria smirna* (14%) and *Cucullaea macrodonta* (5.1%) both occur in assemblage E but at much lower relative abundances. Assemblage E is also characterized by several species which are absent or are rare elsewhere in the studied Paleocene stratigraphic sections. These include: *Nuculana sp.* Gardner (4.3%), *Pitar sp.* (1.4%), *Brachidontes saffordi*, Epitoniidae sp.?, and *"Turritella" postmortoni?*. The average Shannon-Weaver diversity of assemblage E is 2.56, which lower than that of assemblage D and is probably related to the shallower water depositional environment at this locality (Figure 8).

Table 6. Major Faunal Constituents

Assemblage E

Taxa	**Mean Relative Abundance**	**Presence Percentage**	**PP x Relative Abundance**
Venericardia eoa	17.8	100	1780
Crassatella sp. indet.	11.3	100	1130
"Turritella" premortoni	10.7	100	1070
Caryocorbula coloradoensis	8.5	100	850
Turritellidae	5.9	83.3	491.6
Nuculana sp. Gardner	4.3	100	430
Corbulidae	4.7	83.3	391.6
Naticidae	3.7	83.3	308
Jupiteria smirna	2.9	83.3	241.6
Nuculana saffordana?	2.4	100	240
Cardiidae sp.	2.0	100	200
Nucula mediavia	3.1	66.6	186
Venericardia bulla	1.5	100	150
Pitar sp.	1.4	100	140

Taphonomy of the assemblages

The quality of fossil preservation is not even throughout the Paleocene stratigraphic sections. All of the assemblages have aragonitic shell material preserved, but in some of the samples dissolution is evident. The preservation is generally the best at Frost Bluff, with the exception of the topmost sample (FB17), and in the lower portion of the Ravine stratigraphic section. Partial replacement of shell material by secondary pyrite occurs uncommonly throughout the section.

In the Littig Glauconite Member, replacement of the original shell material by phosphate is common, making fossil identification difficult. Some of these phosphatized shell molds have been rounded, suggesting transportation by currents before final deposition. Phosphatized molds are particularly abundant in composite sample DMC2.2/B2.3; and the identifiable molluscan fossils in this sample are dominately oysters and pectins, which have calcitic rather than aragonitic shells. Because this sample shows such an extensive preservational bias, it was excluded from later analysis of diversity trends and trophic structure.

Fossils were commonly found in shell lenses and stringers at the Ravine locality. Care was taken to analyze samples without these stringers, since they represent local reworking of the deposits. The upper portion of the Ravine has poorer preservation than the lower portion. Sediments in the upper portion appear oxidized to a mustard-yellow color, and the sand-size fractions contain abundant secondary gypsum. Fossils from the uppermost two samples of the Ravine show partial dissolution of the shell material.

Sediment Grain-size Distribution

Figure 9 shows the percentage sand in different phi sizes for selected samples in the Latest Cretaceous and early Paleocene. Percentage sand ranges from less than 1 percent to a maximum of approximately 19 percent. In general, the vast majority of the sand is in the 3 to 4 phi (fine sand) size range. An exception to this trend may be seen in samples 5 and 6, which contain a large percentage of particles in the > 0 phi size range. These samples are both from the Littig Glauconite Member, zone P1b, and contain numerous phosphatized molluscan casts in the coarsest size-fraction.

Throughout most of the section, the majority of the sand-size particles are of biogenic origin and are predominately composed of the carbonate tests of planktonic foraminifera. Percentage sand showing the relative abundances of carbonate and non-carbonate components is shown in Figure 10. Molluscan shell debris is also a common constituent in many of the samples. Fish parts and unidentified spines round out the biogenic sand-size fraction.

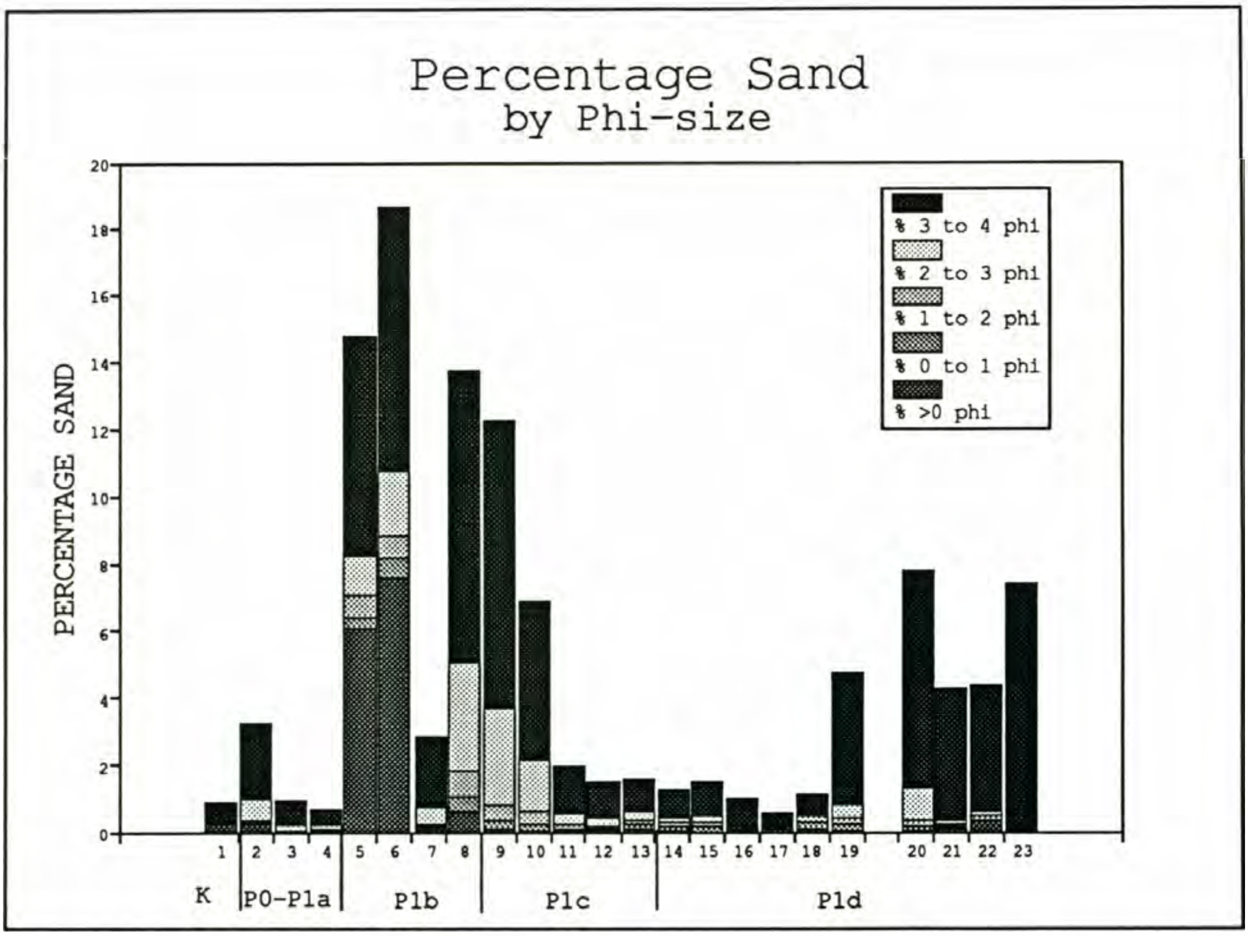


Figure 9. Percentage sand by phi-size for representative samples in each biozone. Sample 1 was collected from the top 15 cm. below the K-T boundary at B-2. Samples 2, 3, and 4 were located 0-5 cm., 100-110 cm., and 180-190 cm. above the K-T boundary at Brazos-1. Other samples are as follows: sample 5 = B2.1, sample 6 = CM4.1, sample 7 = DMC2.1, sample 8 = DMC2.2, sample 9 = DMC2.3, sample 10 = B2.5, sample 11 = DMC2.5, sample 12 = DMC2.6, sample 13 =DMC2.8, sample 14 = FB1, sample 15 = FB6, sample 16 = FB12, sample 17 = FB13, sample 18 = FB15, sample 19 = FB17, sample 20 = Wills Point Formation at Tehuacana Creek (WPTC), sample 21 = R0, sample 22 = R4, sample 23 = R5.

The coarsest sediments sampled in the studied sections are found in the Littig Glauconite Member, zone P1b, and the sand-size fraction of this sediment is overwhelmingly dominated by planktonic foraminifera.

Non-organic constituents of the sand include:

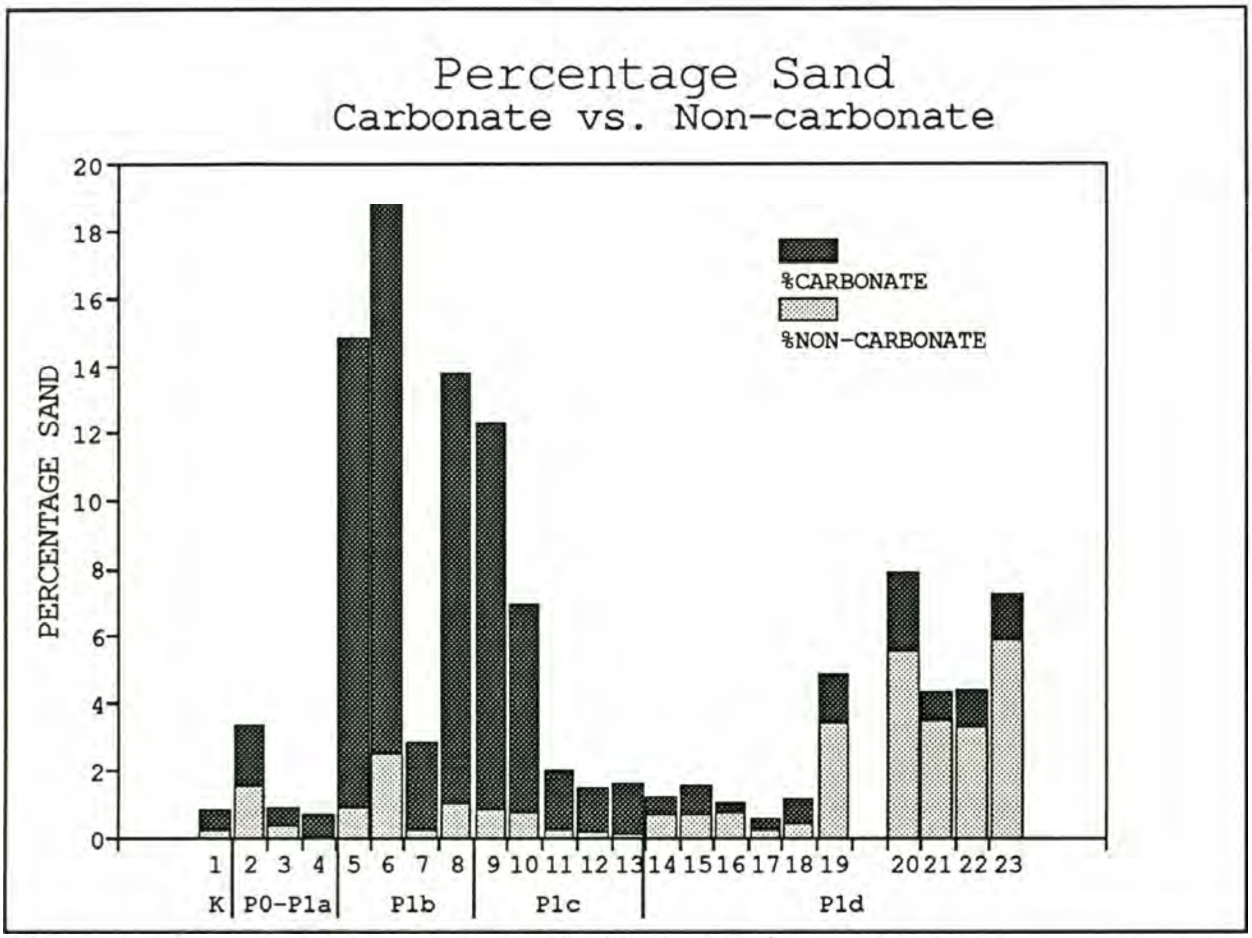


Figure 10. Percentage sand divided into carbonate and non-carbonate fractions for representative samples in each biozone. See Figure 9 for a list of the samples.

secondary pyrite and gypsum, glauconite, quartz, feldspar, muscovite, and biotite. Samples 2 and 19-23 are the only samples containing a significant component of detrital sand. Sample 2 was taken from immediately above the tsunami deposit, and the detrital component of the sand probably represents reworking of this coarse-grained unit. Samples 19-23 were all taken from near the top of the local Paleocene section and illustrate the greater influx of sand-size detrital sediments at the top of Frost Bluff, the single sample from Tehuacana Creek (WPTC), and the Ravine localities. As the name suggests, the Littig Glauconite Member contains common glauconite. Secondary pyrite and gypsum are relatively common throughout the studied stratigraphic sections.

Species Ranges

Brazos River Localities

Figure 11 shows total species ranges in order of first appearance for the Paleocene composite stratigraphic section of the Brazos River localities. Note the scale change in the stratigraphic column. The pattern of species first appearances is "stepped", with two of the major steps corresponding to an unconformity and a stratigraphic gap in the section, respectively. A major introduction of eight species corresponds to the unconformity at the base of the Littig Glauconite Member. A second apparent step or pulse of nine species first appearances occurs at the base of the Pisgah Member, and a third step of 18 species first appearances corresponds to the stratigraphic gap between the highest sample at Darting Minnow Creek (DMC2.8) and the lowest sample in Frost Bluff (FB0). As can be seen from the figure, only 12 of 25 molluscan species (48 %) found in the earliest Paleocene clays persist into foraminiferal biozone P1b, indicating a high degree of faunal turnover in the earliest Paleocene. The overall pattern of species first appearances is one of rapid species introductions in foraminifera zones P1b and P1c with increasing stability

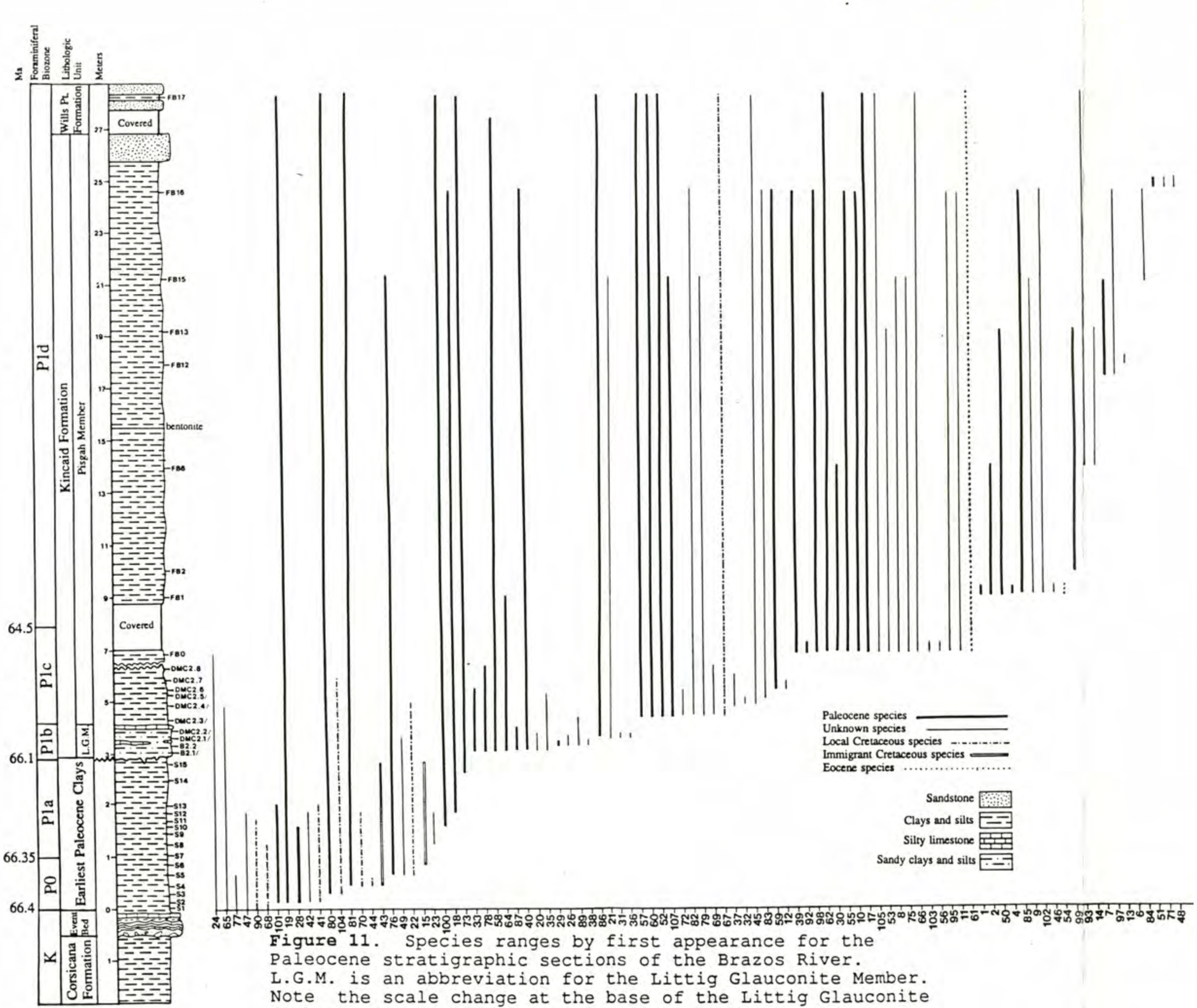


Figure 11. Species ranges by first appearance for the Paleocene stratigraphic sections of the Brazos River. L.G.M. is an abbreviation for the Littig Glauconite Member. Note the scale change at the base of the Littig Glauconite Member. Species numbers correspond to Table 1. Samples designated with a / are composite samples.

apparent in the assemblage as one moves upsection into Frost Bluff. Forty-eight species were introduced into the assemblage during the period of time encompassed by foraminiferal zones P1b and P1c, a duration of approximately 1.6 million years. Above the base of the Littig Glauconite Member, species introduced to the assemblage tend to persist upward through the stratigraphic section. Of the 28 species whose ranges include portions of the Littig Glauconite Member, zone P1b, the ranges of 20 (71%) extend upward into the next foraminiferal biozone, zone P1c. For species with ranges that include the lower part of the Pisgah Member, zone P1c, 37 of 53 (70%) continued into the next foraminiferal biozone, zone P1d. Sixteen species are restricted to the relatively coarser Littig Glauconite Member and the lowermost portion of the Pisgah Member, implying minor facies control over assemblages B and C.

The ranges of the species should be interpreted with caution because of the uneven preservation present in the Littig Glauconite Member. It is possible that species present higher in the section are represented only as unidentified taxa of the same family within the Littig Glauconite Member due to poor preservation. If one assumes that this is true, then four species ranges can be extended downward into the Littig Glauconite Member. These include: the downward extension of the ranges of *Nucula mediavia* and *Tornatellaea texana* to the base of the Littig Glauconite

Member, *Agaronia mediavia* down to B2.2, and *Polinices julianna* down to the base of the Paleocene section. This procedure is only possible for families with one identified species per family. For those families with more than one identified species per family, the potential role of preservational bias in the Littig Glauconite Member is not quantifiable.

Relatively poor preservation in the top sample of Frost Bluff (FB17) is doubtlessly a contributing factor to the termination of a number of species ranges at sample FB16. The single sample collected from the base of the Wills Point formation at Tehuacana Creek roughly correlates with topmost sample at Frost Bluff and 13 of the species whose ranges terminate below the top of Frost Bluff are found in the single sample from Tehuacana Creek. These include: *Caryophyllia mediavia, Dentalium sp. A, Dentalium sp. B, "Turritella" premortoni, Exilia cf. pergracilis, Volutocorbis texanus, Nucula mediavia, Pycnodonte sp., Ostrea pulaskensis,* Lucinidae sp. A, Semelidae sp. A, *Pitar sp.,* and *Cuspidaria sp. A.*

Ravine Locality

The total ranges of species by last appearance are shown for the Ravine locality in Figure 12. Species ranges are steadily lost as one moves upsection. This decrease in the number of species ranges is related to the poor preservation in the uppermost Ravine sample and to a

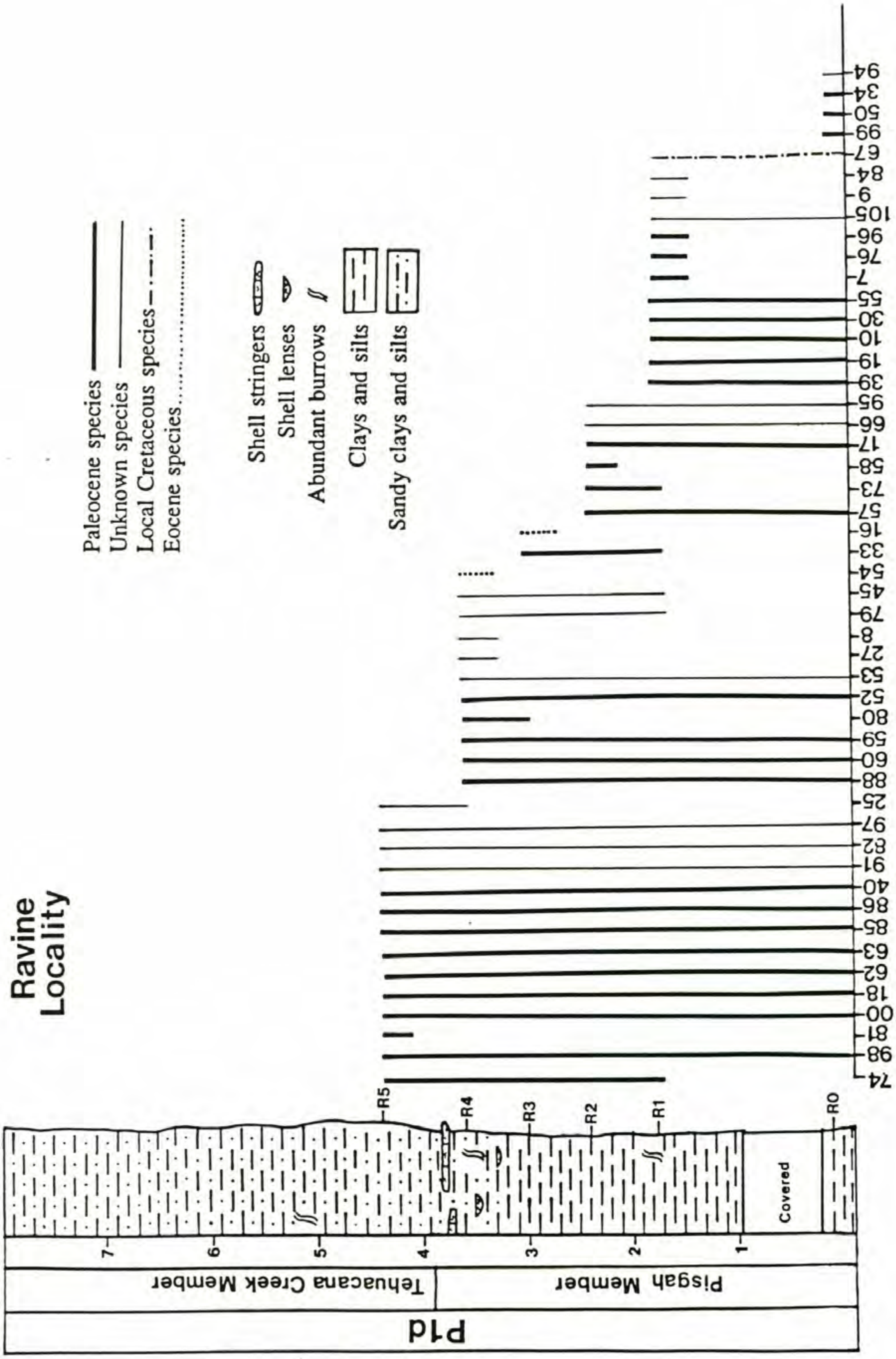


Figure 12. Species ranges by last appearance for the Ravine locality. Species numbers correspond to Table 1.

shallower-water depositional environment in the Tehucuana Creek Member.

Diversity

Species Richness

Species richness and species-range richness are illustrated for the studied Paleocene sections in Figure 13.

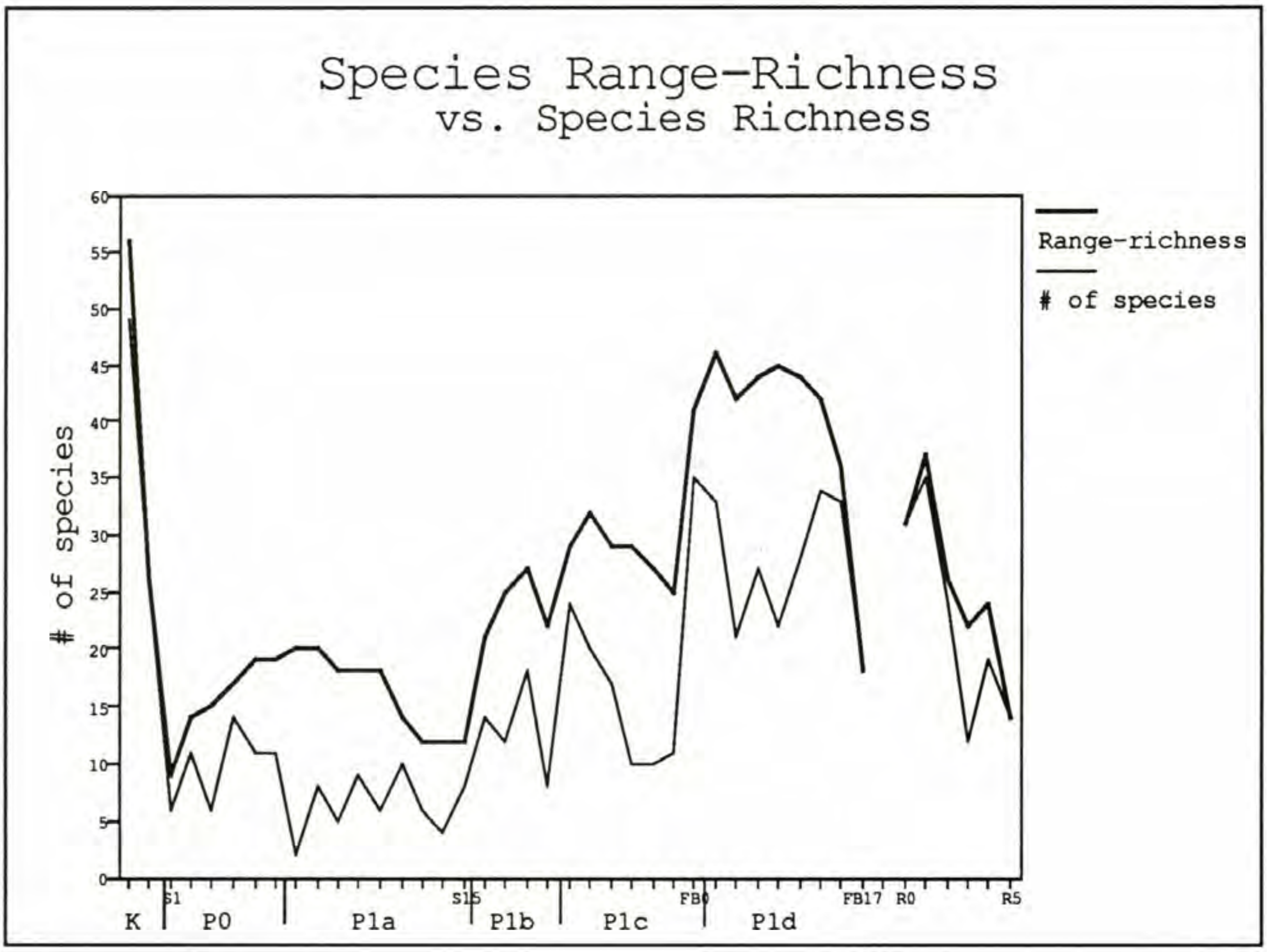


Figure 13. Species richness and species range-richness for the Latest Cretaceous and earliest Tertiary studied sections. The Cretaceous samples are from Kauffman's CM-1 data set. The first Cretaceous interval (LK-1) was collected from .65 -.8 meter below the event bed and the second interval represents the top 32 cm. of the Cretaceous strata. The samples are in the stratigraphic order shown in Figures 11 and 12. The break in biozone P1d corresponds to the samples from the Ravine locality that are coeval with deposits at

Frost Bluff and are therefore offset in this and subsequent figures.

Fluctuations in the species richness curve are stronger than in the species-range richness curve for the samples. Species richness is generally less than species-range richness, with changes in species richness being roughly mirrored by changes in the species-range richness. An exception to this trend is apparent at the top and bottom of the sections, where species richness and species-range richness are the same due to the artificial truncation of species ranges (Signor and Lipps, 1982). An overall pattern of an increase in the number of species and species ranges is observed as one moves upward through the Paleocene stratigraphic section to the top of Frost Bluff.

Species-Range Richness

Figure 14 shows trends in species-range richness for each origination category through the K-T transition at the studied localities, and Table 7 presents mean percentages of the various origination categories for each foraminiferal biozone. In the local Cretaceous section, species-range richness declines from 56 species, with the number of species ranges decreasing to 26 by 32 cm. below the base of the tsunami deposit. The species present are all local Cretaceous species by definition.

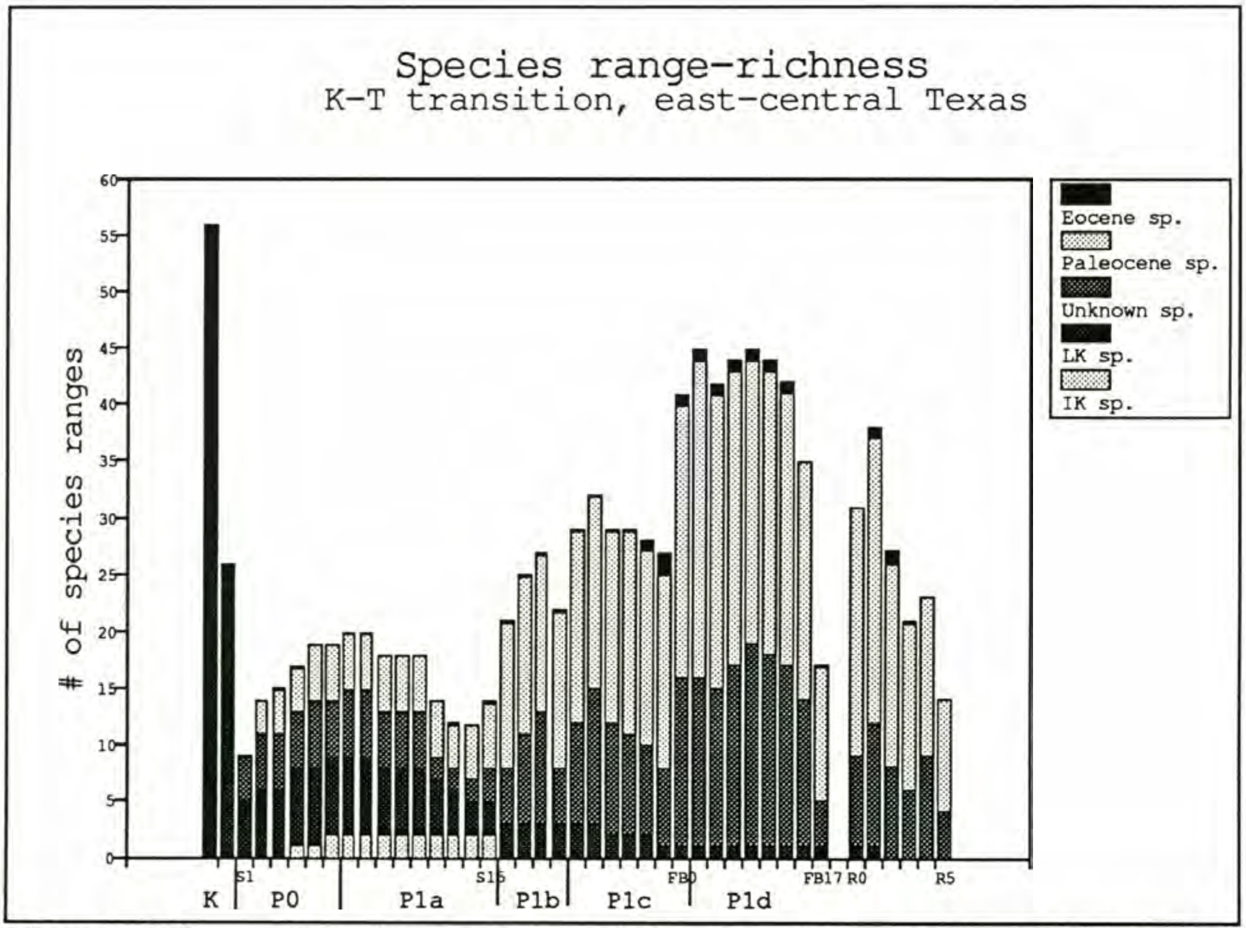


Figure 14. Species range-richness for each origination category across the K-T boundary, east-central Texas. LK sp. = Local Cretaceous species, IK sp. = Immigrant Cretaceous species.

Table 7. Mean relative abundances of origination categories and average number of species ranges for each biozone. See Table 1 for a key to the origination categories.

Foraminifera Biozone	**IK**	**LK**	**UnS**	**P**	**E**	**Ave. # of species ranges**
P0-P1a	9.3	36.2	27.8	27.9	0.0	15.8
P1b	0.0	12.8	28.9	58.4	0.0	23.8
P1c	0.0	6.8	32.6	60.3	0.4	30.3
P1d	0.0	2.8	34.7	59.6	3.0	39.6
P1d(Rav)	0.0	1.0	29.9	67.6	1.5	25.7

Immediately above the tsunami deposit, the number of species ranges decreases dramatically to nine. For the duration of the P0 and P1a zones, the number of species ranges varies between 9 and 20; and the fauna are relatively evenly divided between Cretaceous species (45.5 %), unknown species (27.8 %), and Paleocene species (27.9 %). The number of species ranges increases sharply to 21 at the unconformable base of the Littig Glauconite Member, zone P1b, and rises to a high of 27 species ranges near the top of this member. Paleocene species compose a much higher proportion of the species (58.4%) than in the earliest Paleocene, and the percentage of Cretaceous species (12.8. %) notably declines with the immigrant Cretaceous component of the fauna dropping completely out of the assemblages.

The number of species ranges for the Paleocene assemblages continues to increase through zone P1c, reaching a peak for this biozone of 41. Proportions of the origination categories are similar to those of zone P1b. The major increase in the number of species ranges to 41 occurs at the stratigraphic gap between the Darting Minnow Creek and Frost Bluff localities.

Forty-six species ranges, the maximum number of species ranges for the Paleocene stratigraphic sections, are found in sample FB1 at Frost Bluff, zone P1d. Small numbers (< 3 %) of previously described Eocene species appear in the assemblage at the base of Frost Bluff, and the proportions of the origination categories remain relatively constant through zone P1d. In coeval deposits at the Ravine, the number of species ranges is generally lower than at Frost Bluff and decreases as one moves upsection. The lone Cretaceous species present in zone P1d, *Solemya bilix*, is notable in that locally it drops out of the section below the K-T boundary and does not reappear in the Paleocene until the base of zone P1c. The period of absence for this mollusk in the local stratigraphic sections is probably well in excess of one million years.

The large percentage of unknown species (UnS) present throughout the local Paleocene stratigraphic sections is problematic, but understandable when one considers the small size of the fauna, the patchy preservation, and that the mollusks of these sections have not been previously examined in detail. It is probable that most of these unknown species originated in the Paleocene, since they are not found in the local Cretaceous sections.

Shannon-Weaver Diversity

Patterns of Shannon-Weaver diversity for the Brazos River localities are depicted in Figure 15. Species diversity drops from approximately 3.3 to 2.3 in the late Cretaceous. This drop in diversity is probably real because the numbers of individuals are similar for the samples being compared. In the earliest Paleocene, species diversity was quite low, averaging 1.34 for the duration of zones P0 and

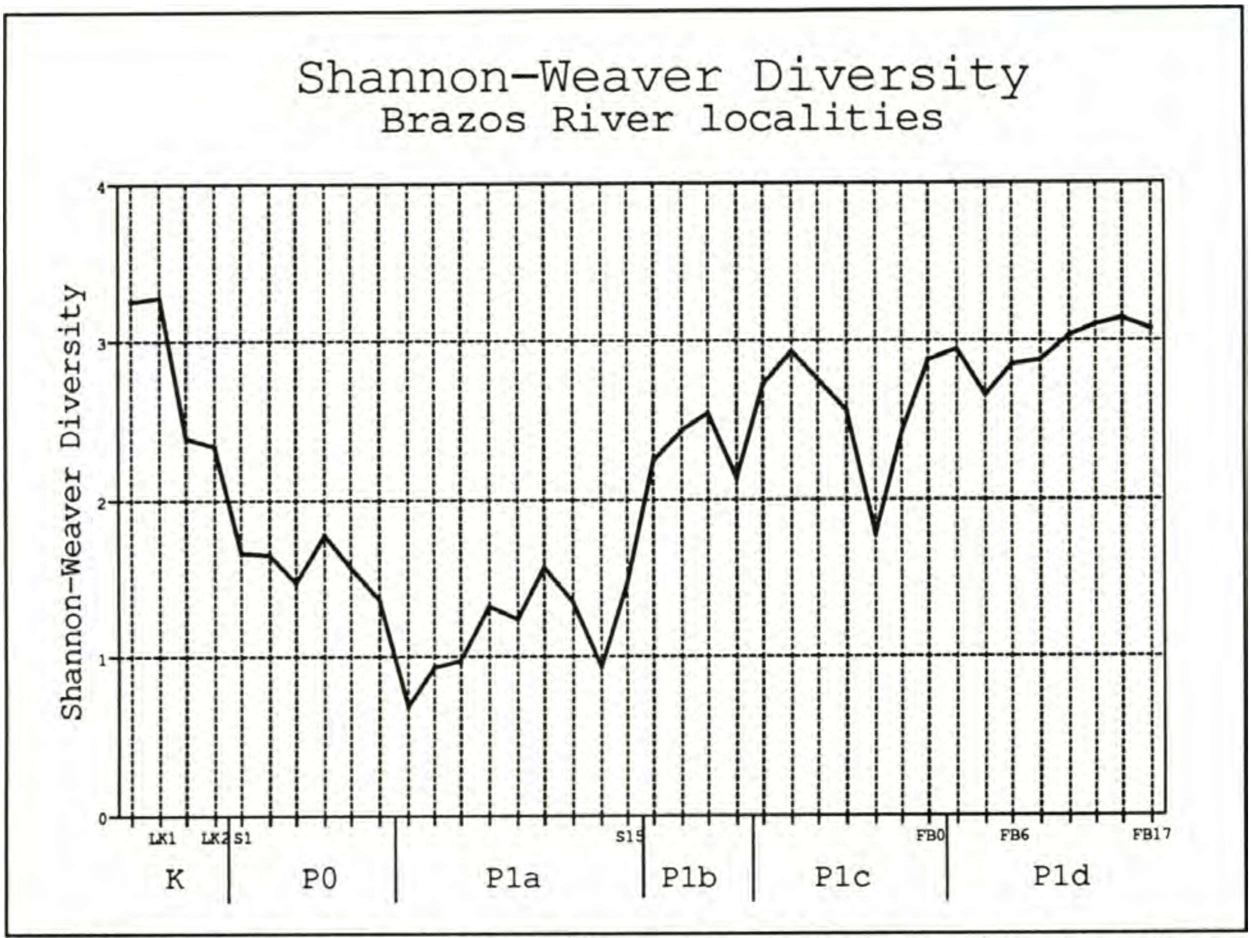


Figure 15. Shannon-Weaver diversity across the K-T boundary, Brazos River localities. Cretaceous intervals are .9-1.1 meters, .65-.8 meters, .32-.56 meters and 0.32-0 meters below the K-T boundary at the CM-1 locality.

P1a, a period of approximately 300,000 years. Species diversity jumps considerably to nearly Late Cretaceous levels at the unconformity at the base of the Littig Glauconite Member, zone P1b. Above the base of the Littig Glauconite Member, diversity increases fairly steadily to a peak of 3.1 in zone P1d. An exception to this trend is apparent in sample DMC2.7, which has much lower diversities than samples immediately above and below it. This sample has very low abundances and high proportions of pectinids which have calcitic shells, suggesting possible taphonomic

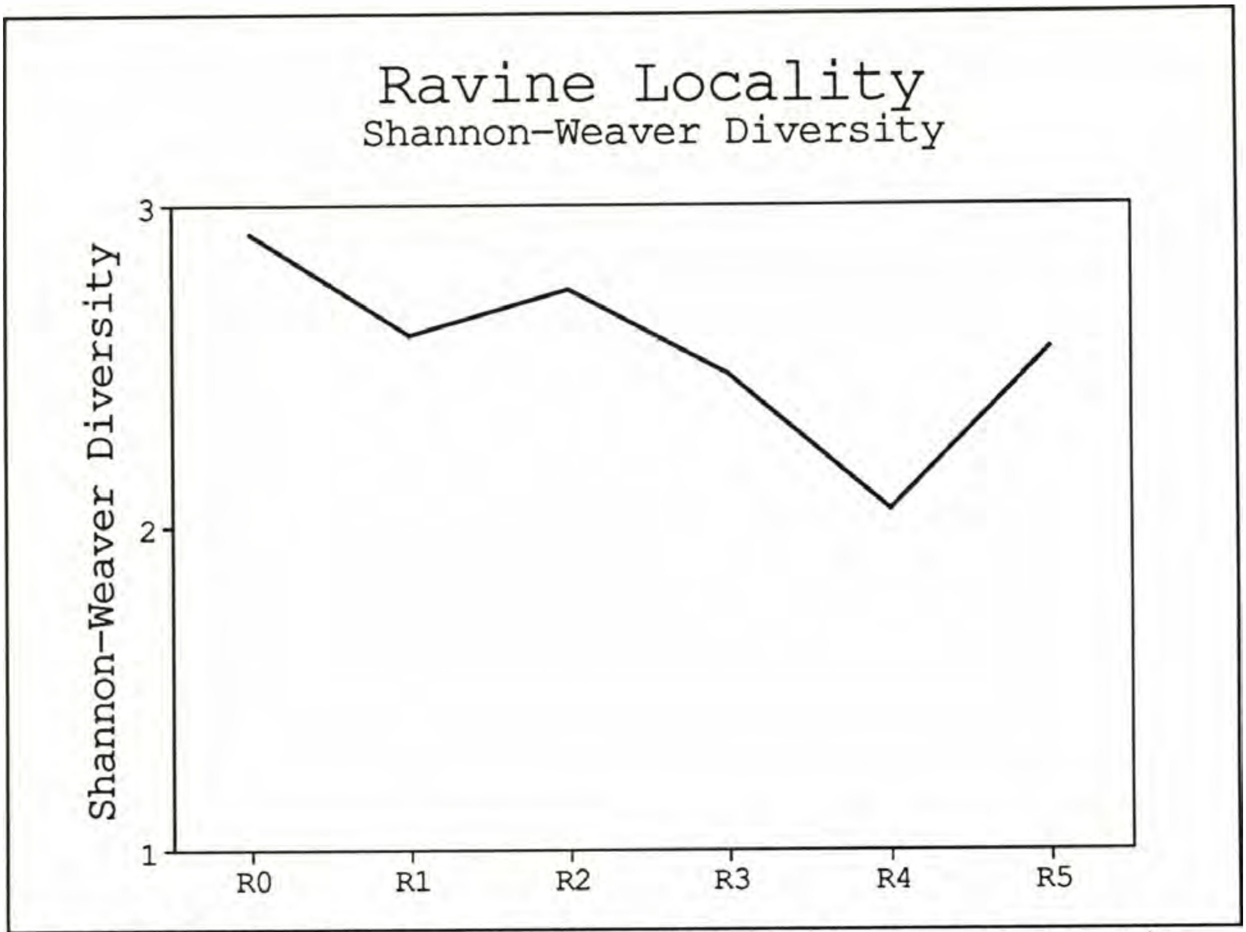


Figure 16. Shannon-Weaver diversity at the Ravine locality.

alteration of the assemblage. The pattern of species diversity at the Ravine, like the pattern of species richness and species range-richness for this locality, shows a sharp upsection decline (Figure 16).

Rarefaction Analysis

Representative rarefaction curves are shown for the studied sections in Figure 17. The curves show similar trends to the Shannon-Weaver index. The lower Cretaceous sample from CM-1 shows the highest diversity of any of the samples, and diversity drops notably in the latest Cretaceous. Samples from zones P0 and P1a are much less

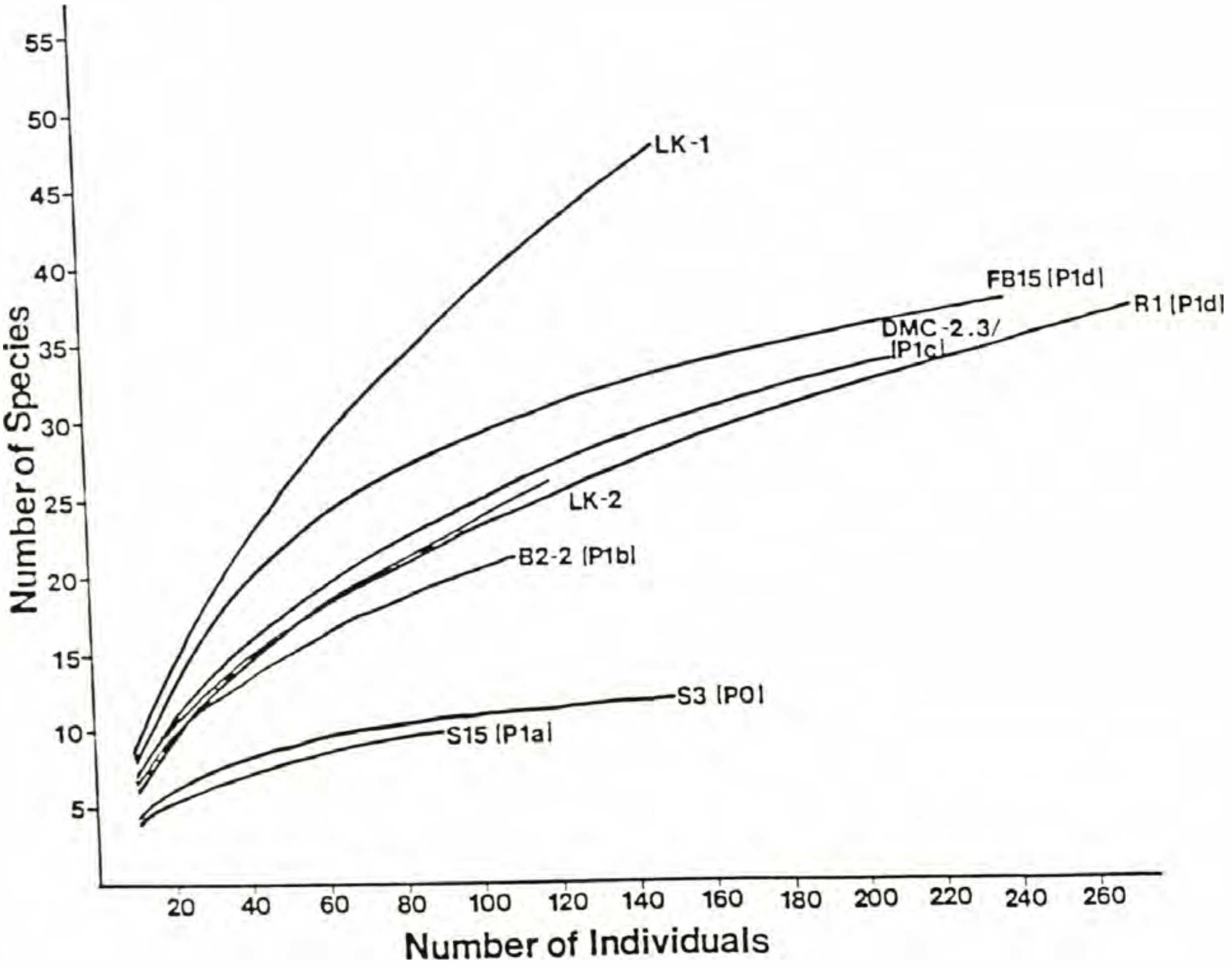


Figure 17. Representative rarefaction curves for the Late Cretaceous and early Paleocene. Samples LK1 and LK2 are from the Kauffman's CM-1 species list. See the caption of Figure 13 for the stratigraphic positions of these Cretaceous samples.

diverse than any of the other samples. Diversity is much higher in zone P1b than in the earliest Paleoceone samples and it steadily increases through zones P1c and P1d. The representative sample from the Ravine, R1, is an exception to this trend of increasing diversity upsection, since it is less diverse than the sample from P1c, and the sample from coeval deposits at Frost Bluff.

Life-habits of the fauna

A list of molluscan families found in this study and their life-habits is shown in Table 8. Relative abundances of the life-habit categories are shown in stratigraphic order for all of the studied samples in Appendix II. Several noteworthy trends are apparent across the Cretaceous-Tertiary boundary and in the Paleocene sections. Major molluscan life-habit trends across the K-T boundary are illustrated in Figure 18. A prominant feature of the earliest Paleocene, zone P0, is the bloom seen in the grazer trophic category (Upshaw, 1989). In zone P0, this category is represented by a single species of the gastropod family Litiopidae and reaches a maximum relative abundance of 40 percent. Modern species of the family Litiopidae are commonly found on floating sargussum weed and are thought to be herbivores (Abbott, 1974; Houbrick, 1987; Luque et al., 1988). The large bloom of *Litiopa sp. A* in the earliest Danian is included with the relative abundances of epifaunal grazers in Figure 18. Other local Paleocene epifaunal

Table 8. Life-habits of the fauna found in this study.

Name	**Life-habit**	**References**
Solitary Coral	CS-ES	Barnes, 1987
Bryzoa	SF-ES-Col	Barnes, 1987
Scaphopoda	CS-IB on foraminifera, small molluscs	Abbott, 1968; Stanton and Nelson, 1980
Gastropoda		
Vitrinellidae	DF-EM some also grazers, parasitic on annelids	Andrews, 1977 Stanton and Nelson, 1980
Turritellidae	SF-NSI some may graze and deposit-feed	Allmon, 1988
Cerithiidae	G-EM	Andrews, 1977
Litiopidae	G-P pelagic in floating sargassum weed	Abbott, 1974; Houbrick, 1987; Luque et al., 1988
Epitoniidae	CS-EM on anemones, worms, foraminifera	Abbott, 1968; Andrews, 1977
Aporrhaidae	DF-IG	Abbott, 1968
Strombidae	DF-IG	Abbott, 1968
Calyptraeidae	SF-EM	Andrews, 1977
Naticidae	CS-IB on bivalves, gastropods, scaphopods	Stanton and Nelson, 1980
Columbellidae	CS-EM on bivalves, crustaceans	Abbott, 1974; Andrews, 1977
Nassariidae	CS-IB largely scavengers	Abbott, 1968; Andrews, 1977
Fasciolariidae	CS-EM on bivalves, gastropods, polychaetes, barnacles	Andrews, 1977; Stanton and Nelson, 1980
Olividae	CS-IB on small molluscs, foraminifera	Andrews, 1977; Stanton and Nelson, 1980
Volutidae	CS-E(?)M	Stanton and Nelson, 1980
Turridae	CS-EM on annelids, nemerteans	Andrews, 1977; Stanton and Nelson, 1980
Pyramidellidae	PAR-G ectoparasite on polychaetes, cnidarians, molluscs, starfish	Stanton and Nelson, 1980
Acteonidae	CS-IB on annelids	Andrews, 1977
Ringiculidae	CS-I(?)B on polychaetes, foraminifera	Andrews, 1977
Atyidae	CS-IB	Andrews, 1977
Retusidae	CS-IB on other opistobranchs, foraminifera	Andrews, 1977; Stanton and Nelson, 1980
Bivalvia		
Nuculidae	DF-IB non-siphonate	Stanley, 1970
Nuculanidae	DF-IB siphonate	Stanley, 1970
Solemyidae	SF-SI deep burrower	Stanley, 1970
Arcidae	SF-NSI some are epifaunal	Stanley, 1970
Limopsidae	SF-NSI	
Cucullaeidae	SF-NSI	
Mytilidae	SF-NSI some are epifaunal, bysuss common	Stanley, 1970
Pectinidae	SF-EM some can swim and have eyes, bysuss common	Stanley, 1970
Ostreidae	SF-ES cementation common	Stanley, 1970; Andrews, 1977
Lucinidae	SF-SI	Stanley, 1970
Leptonidae/ Montacutidae	SF-ES some are commensal	Andrews, 1977
Sportellidae	unassigned	
Crassatellidae	SF-NSI	Andrews, 1977
Astartidae	SF-NSI	Stanley, 1970
Carditidae	SF-NSI	Stanley, 1970
Cardiidae	SF-SI with short siphons	Stanley, 1970
Tellinidae	DF-IB siphonate	Stanley, 1970
Semelidae	DF-IB siphonate, some suspension-feeders	Stanley, 1970; Andrews, 1977
Kelliellidae	unassigned	
Corbulidae	SF-SI	Stanley, 1970; Andrews, 1977
Veneridae	SF-SI	Stanley, 1970; Andrews, 1977
Hiatellidae	SF-SI	Andrews, 1977
Pholadiidae	SF-SI commonly borers	Andrews, 1977
Cuspidariidae	CS-IB on crustaceans, forams, siphonate	Morton, 1960; Levinton, 1982
Verticordiidae	CS-IB	Morton, 1960

Key to trophic categories

CS-N	Carnivore/scavenger, nektonic (ammonites)
CS-EM	Carnivore/scavenger, epifaunal-mobile
CS-ES	Carnivore/scavenger, epifaunal-sessile
CS-IB	Carnivore/scavenger, infaunal-burrower
DF-EM	Deposit-feeder, epifaunal-mobile
DF-IB	Deposit-feeder, infaunal-bivalve
DF-IG	Deposit-feeder, infaunal-gastropod
PAR-G	Parasite-gastropod
SF-COL	Suspension-feeder, colonial
SF-EM	Suspension-feeder, epifaunal-mobile
SF-NSI	Suspension-feeder, non-siphonate-infaunal
SF-SI	Suspension-feeder, siphonate-infaunal

grazers include 3 species of the gastropod family Cerithiidae and represent a fairly constant 5% of the fauna in the Paleocene. No molluscs of the grazing trophic group were found in the local Cretaceous sections.

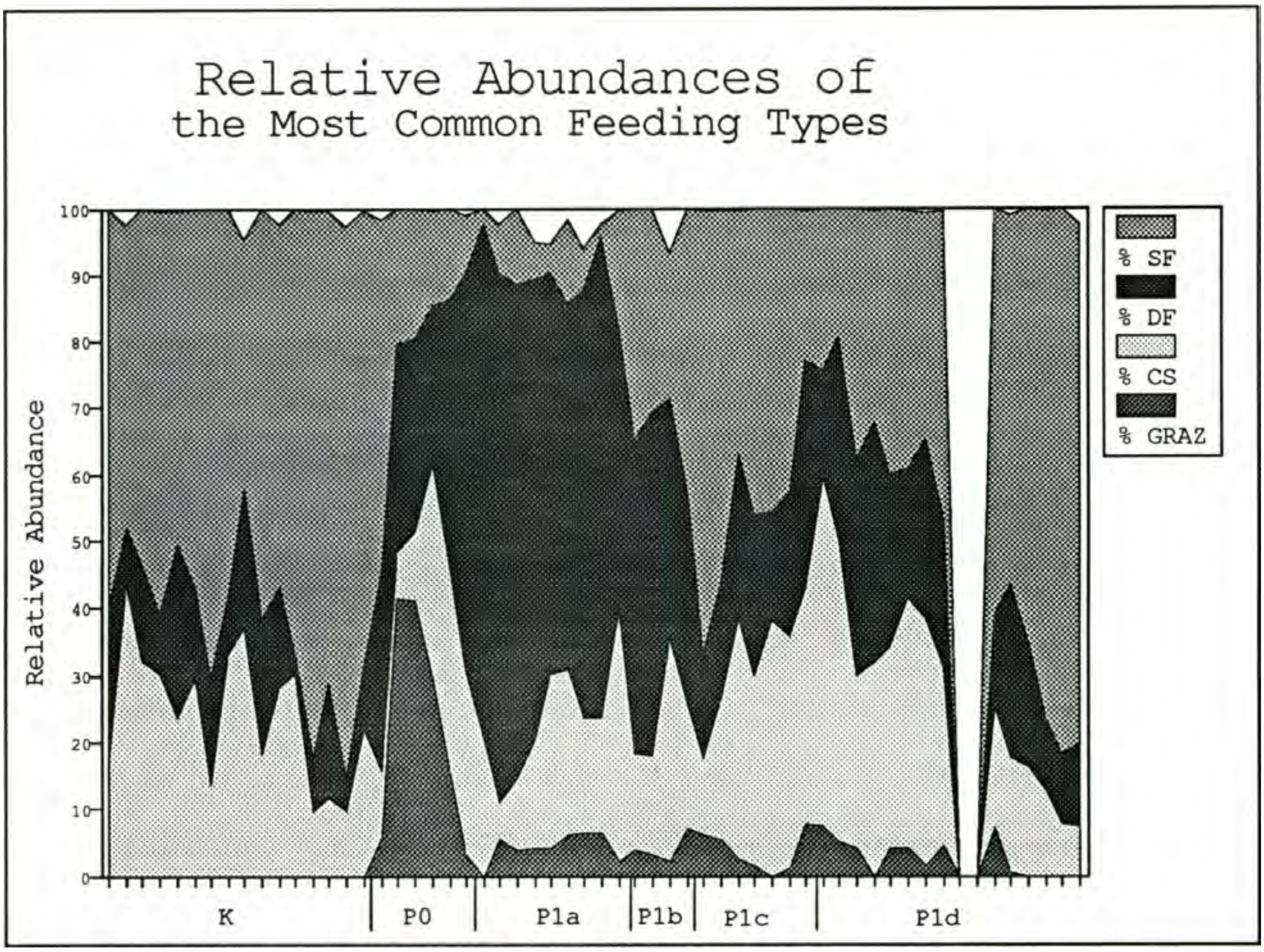


Figure 18. Relative abundance of the most common feeding types across the K-T boundary in east-central Texas. % SF = percentage of suspension-feeders, % DF = percentage of deposit-feeders, % CS = percentage of carnivore/scavengers, % GRAZ = percentage of grazers. See Appendix II for the stratigraphic order of the samples. The uncertainly correlated Sample WPTC was omitted from this and subsequent trophic figures, but is included in Appendix II. The gap within zone P1d offsets the Ravine fauna from the roughly coeval fauna of Frost Bluff.

As reported by Hansen et al. (1987) and Upshaw (1989), there is a large preponderance of deposit-feeders above the

Cretaceous-Tertiary boundary in zones P0 and P1a, reaching a maximum of 79 percent of the fauna in zone P1a (Figure 18). Deposit-feeders return to Cretaceous levels by the base of zone P1c. Concomitant with the increase in deposit-feeders immediately above the K-T boundary, is a large decrease in all of the various suspension-feeding categories (Hansen et al., 1987, Upshaw 1989) (Figures 18 and 19). In the Paleocene section, the proportion of suspension-feeders remains quite low through zones P0 and P1a and rebounds to near Cretaceous levels in zone P1b. Among the suspension feeders, oysters (SF-ES) were the dominant taxonomic group in the local Cretaceous, reaching a maximum relative abundance of approximately 65% in the studied sections (Figure 19). They are not particularly common in the Paleocene studied sections and never reach their former levels of abundance. A bloom of pectinids (SF-EM) occurs in zones P1b and P1c (Figure 19). Non-siphonate suspension feeders (SF-NSI) such as arcids and epifaunal sessile suspension-feeders (SF-ES) such as oysters are also particularly common in this interval. This increase in abundance of the Pectinidae and other suspensions-feeders correlates well with the peak abundances of sand-size sediment in the Littig Glauconite Member and lowermost portion of the Pisgah Member (Figures 9 and 10), implying some facies control over faunal distribution in this portion of the stratigraphic section. Very high relative abundances of non-siphonate infaunal and siphonate infaunal suspension-feeders occur in the Ravine, reflecting the high abundances of the families: Turritellidae, Carditidae, Crassatellidae, and Corbulidae at this locality.

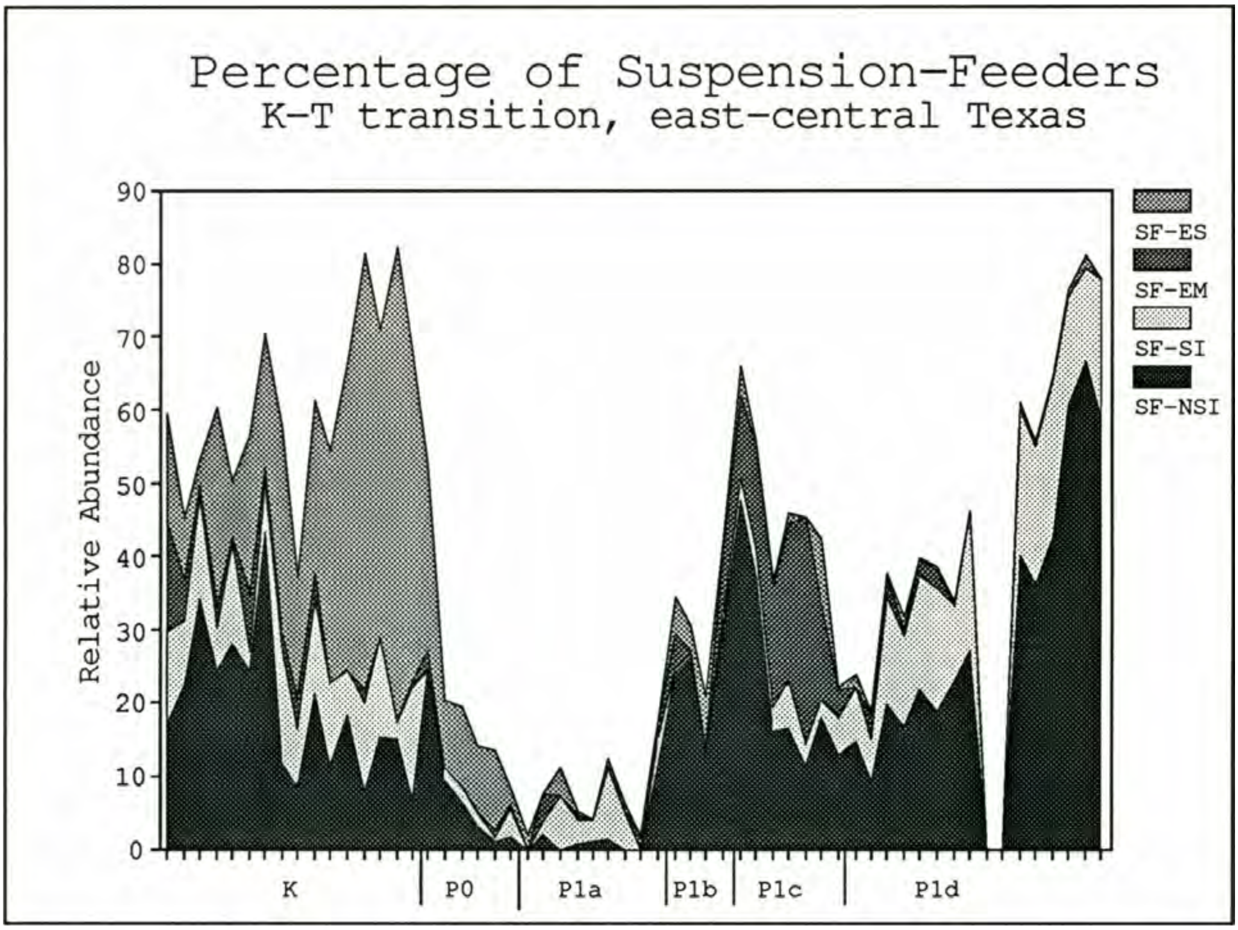


Figure 19. Relative abundance of suspension-feeders across the K-T boundary in east-central Texas. SF-ES = suspension-feeder, epifaunal-sessile (oysters), SF-EM = suspension-feeder, epifaunal-mobile (pectinids), SF-SI = suspension-feeder, siphonate-infaunal, SF-NSI = suspension-feeder, non-siphonate-infaunal.

Ammonites (CS-N) average between 10 and 20 percent of the fauna in the Cretaceous and show no decline below the Cretaceous-Tertiary boundary in the studied sections (Figure 20). They are present only as reworked fragments in zone P0 of the earliest Paleocene (Upshaw, 1989). Infaunal carnivore scavengers (CS-IB) in the gastropod families Naticidae, Acteonidae, Ringiculidae, and Retusidae, are much more abundant in the Paleocene than they were in the latest

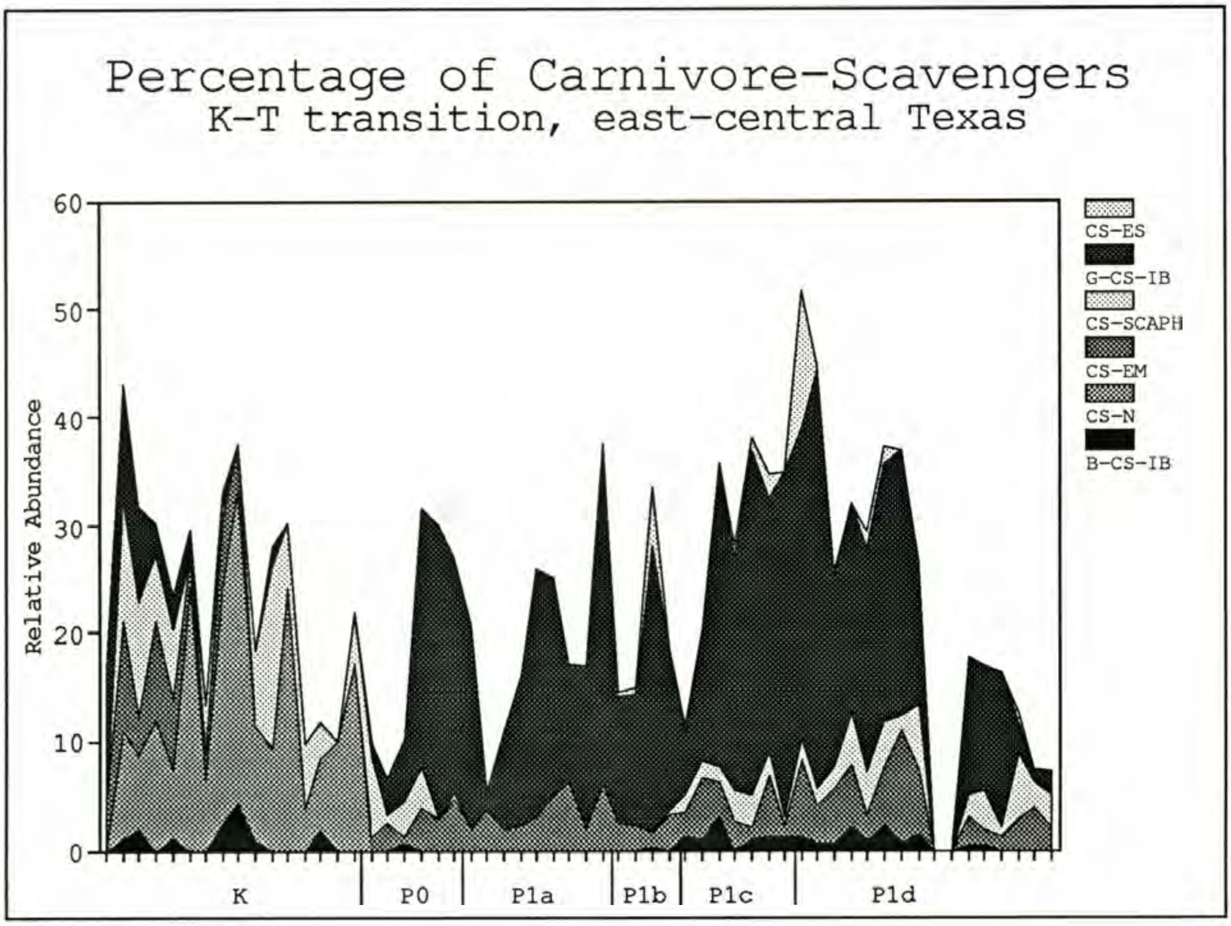


Figure 20. Relative abundance of carnivore/scavengers across the K-T boundary in east-central Texas. CS-ES = carnivore/scavenger, epifaunal-sessile (corals), G-CS-IB = gastropod, carnivore/scavenger, infaunal-burrower, CS-SCAPH = carnivore/scavenger, scaphopod, CS-EM = carnivore/scavenger, epifaunal-mobile, CS-N = carnivore/scavenger, nektonic (ammonites), B-CS-IB = bivalve, carnivore/scavenger, infaunal-burrower (Verticordiidae and Cuspidariidae).

Cretaceous (Figure 20). Other trends among carnivore-scavengers include a depression in the relative abundances of Scaphopoda and Cuspidariidae in zones P0 and P1a.

Epifaunal mobile carnivores remain fairly constant in their abundances throughout the Cretaceous and Danian sections. Solitary corals (CS-ES) are locally abundant in the Paleocene studied sections and are absent in Kauffman's Cretaceous data set. However, Farrand (1984) found solitary corals to be locally abundant in the Late Cretaceous Corsicana Formation of east-central Texas.

DISCUSSION

Depositional Environments and Paleoecology

An important question to be resolved is the extent to which changes in lithofacies influenced the pattern of molluscan faunal rebound seen at the studied stratigraphic sections. Changes in sedimentation rate and type can alter the composition of a marine benthic community. For example, when sedimentation rates for fine-grained detrital material are less than accumulation rates for shells, the substrate coarsens and becomes more stable, and epifaunal suspension-feeders such as oysters can colonize and dominate the now firmer substrate (Fursich, 1978). Conversely, an increase in the influx of fine-grained detrital sediment beyond the rate at which shells accumulate creates a finer-grained, soupier substrate better suited to the burrowing activities of deposit-feeding organisms (Fursich, 1978).

Analyses of benthic foraminifera suggest middle to outer shelf depths for the Cretaceous and earliest Danian stratigraphic sections of east-central Texas (Bourgeois et al., 1988). Excluding the tsunami deposit, there is no lithologic change crossing the K-T boundary (Bourgeois et al., 1988). The vast bulk of the sampled sediments are middle-shelf to outer-shelf clays and silts, ranging up to a maximum of 19 percent foraminiferal sand in the Littig Glauconite Member (Figures 9 and 10). Some relatively minor changes in the depositional environment are discernible within the Littig Glauconite Member and at the Ravine locality, and the molluscan fauna in part reflect these changes.

The presence of abundant glauconite and phosphatized molds, the high concentrations of planktonic foraminifera, and correspondingly coarser grain-size of the Littig Glauconite Member suggest that it represents a condensed zone of slow sedimentation. While studied sections of the Littig Glauconite Member lack the bored hardgrounds characteristic of many condensed sections, the thin, indurated silty-limestone units are probably local analogues, representing periods of lowest detrital influx and maximum foraminiferal accumulation.

The molluscan faunal composition of the Littig Glauconite Member (assemblage B) and the lowermost portion of the Pisgah Member (assemblage C) in part reflects the slowing of the detrital sedimentation rate and the resulting coarser grain-size of the sediment. Epifaunal suspension-feeders such as the oyster, *O. pulaskensis*, and the pectinid, *A. alabamense*, are more common in this portion of the stratigraphic section than elsewhere. Note the "bloom" in the SF-EM and SF-ES trophic categories, representing pectinids and oysters respectively, and their close correspondence to the peak in the sand-size particle distribution curve (Figures 10 and 19).

Sediments at the Ravine locality and the top of the Frost Bluff stratigraphic section are characterized by an increased abundance of detrital sand, averaging approximately five percent (Figure 10). Corresponding to this increase in detrital sand is a decrease in the abundance of planktonic foraminifera. The abundance of detrital sand and the paucity of planktonic foraminifera at these localities implies an increase in sedimentation rate (which would dilute the foraminifera), a shallowing of the depositional environment, or both. Calculations discussed earlier (see Sedimentation Rates) confirm an increase in the rate of sedimentation for this portion of the section. Linearly aligned *Turritella* spires and the occurrence of shells in lenses at the Ravine locality suggest sorting by currents and help support the interpretation of a shallower-water depositional environment at this locality.

The fauna of the Ravine, assemblage E, represents a shallower water middle-to-inner shelf assemblage. Characteristic of assemblage E is the increased abundance of molluscs in the families: Carditidae, Crassatellidae, Turritellidae, and Corbulidae. Scott (1974) described relatively shallow-water bay and shoreface benthic communities from the lower Cretaceous that were typified by many of the same molluscan families as in assemblage E. Of the few molluscan species restricted to assemblage E, bivalves of the genus *Brachidontes* are particularly common in modern shallow-water environments (Abbott, 1974).

The Effects of the K-T Extinctions

Local Extinction Rate

Upshaw (1989) evaluated the effects of the K-T extinction at the Brazos River localities and found that ninety-six percent of the local late Cretaceous molluscan fauna went extinct. Two local Cretaceous species were found above the base of the Littig Glauconite Member during the course of my study, and further analysis has reduced the Cretaceous data set slightly. The extinction rate is therefore lower than originally calculated. Of the 48 previously described Cretaceous species found in the Cretaceous stratigraphic sections of the Brazos River, five survived the extinction, yielding a local extinction rate of ninety percent. This severe level of extinction is higher than that observed for planktonic foraminifera (70 %) at the same localities (Keller, 1989), and is also considerably higher than the fifty percent extinction rate reported for marine macrofauna at the Braggs, Alabama, K-T stratigraphic section (Jones et al., 1987; Bryan and Jones, 1989).

Lazarus Species

Species which temporarily disappear from the rock record only to reappear unscathed in significantly younger sediments have been termed Lazarus Taxa (Jablonski, 1986b). This temporary disappearance of a taxon can be caused by facies changes, poor preservation, insufficient collection, and local extinctions. The proportion of Lazarus Taxa gives a rough indication of the completeness of the fossil record for a given stratigraphic interval, assuming these taxa were present locally for the interval in question (Jablonski, 1986b). The Lazarus effect for molluscs across the K-T boundary in the Brazos River region is small. Only one of the five previously described local Cretaceous survivors, *Solemya bilix*, disappears from the local stratigraphic section for any appreciable period of time. This species makes its first Paleocene appearance near the base of Zone P1c, well in excess of 300,000 years after the K-T extinctions. The rare occurrence of Lazarus Taxa fits in well with the relatively good preservation in and the complete nature of the Brazos River K-T stratigraphic sections.

Earliest Danian Effects

Life-habits, diversity, and the taxonomic composition of the molluscan fauna change dramatically across the K-T boundary. Diverse Late Maastrichtian molluscan faunas from the Brazos River locality are dominated by epifaunal suspension-feeders, particularly oysters. Immediately above the K-T extinction horizon, the depauperate earliest Paleocene molluscan assemblage is dominated by a bloom in the abundance of the pelagic herbivore, *Litiopa sp. A* (Upshaw, 1989). Levinton (1970) suggested that opportunistic species are most common in "young" environments of high physiological stress and may be recognized in the fossil record by their overwhelming dominance of an assemblage and rapid dissappearance. *Litiopa sp. A* is unknown from local Cretaceous deposits, dominant in zone P0, and becomes quite rare above zone P1a. The distribution pattern of *Litiopa sp. A* suggests that it may have been an opportunistic species exploiting ecospace in the physically unstable environment of the earliest Paleocene.

A dramatic increase in the relative abundance of deposit-feeders with a corresponding decrease in suspension-feeders across the K-T boundary has been noted at the Brazos River by several workers (Hansen et al., 1987; Upshaw, 1989; Hansen and Upshaw 1990). As discussed previously, this trophic change has been interpreted as being consistent with a bolide impact and a period of lowered marine productivity (Sheehan and Hansen, 1986; Arthur et al., 1987). This report confirms the above mentioned trophic trend across the K-T boundary at the Brazos River. The *Litiopa*-dominated assemblage of zone P0 rapidly shifted to a low diversity assemblage characterized by an undescribed deposit-feeding bivalve of the family Nuculanidae *(Nuculana sp. B)* within zone P1a (Upshaw, 1989; Hansen and Upshaw, 1990). This low diversity deposit-feeder-dominated assemblage persisted for approximately 300,000 years after the K-T extinctions. The relative abundances of deposit-feeders and suspension-feeders return to approximately Cretaceous levels within Zone P1b (Figures 18 and 19). Earliest Paleocene assemblages were characterized by a roughly even mixture of Cretaceous survivors, undescribed species, and newly evolved Paleocene species (Upshaw, 1989). By the beginning of zone P1b, most Cretaceous survivors had disappeared and the fauna was typified by an abundance of previously described Paleocene species. These changes in the trophic and taxonomic composition of the fauna coincide with a large increase in diversity at the P1a/P1b boundary (Figure 16), signifying a dramatic improvement in the marine environment approximately 300,000 years after the K-T extinctions.

Strangelove Ocean

A suppression of marine productivity immediately after the K-T extinctions has been noted at several localities based on geochemical data (Hsu, 1986; Arthur et al., 1987; Keller and Lindinger, 1989; Zachos et al., 1989). Biologically normal oceans are characterized by a decreasing gradient of the $^{13}C/^{12}C$ ratio from surface to deeper waters (Zachos et al., 1989). This vertical gradient is due to the activity of plankton, which incorporate carbon-12 into their cells in preference to carbon-13 (Hsu, 1986). The large biomass of plankton in the surface waters of the world's oceans results in a surface increase in the amount of carbon-13, thereby creating a depth gradient for this isotope. Variations in the amount of carbon-13 are expressed as delta ^{13}C per mil, referring to the difference between the number of carbon-13 atoms in a sample compared to that of a standard (Hsu, 1986). Theoretically, the tests of planktonic organisms in a particularly fertile ocean would contain a positive delta carbon-13 anomaly, while an ocean with suppressed productivity would yield a negative anomaly in delta carbon-13 for the tests of planktonic organisms. A negative delta carbon-13 anomaly has been termed a Strangelove perturbation (Hsu, 1986). The delta carbon-13 for benthic organisms should remain close to that of average seawater because isotope fractionation of bottom waters is insignificant due in part to the small biomass of benthic organisms (Hsu, 1986). Isotope analyses of benthic microfossils across the K-T boundary show little change in delta carbon-13, while delta carbon-13 crashes dramatically in planktonic microfossils (Hsu, 1986; Zachos et al., 1989). These results suggest a significant lowering of surface productivity in the world's oceans. Estimates for the duration of this period of lowered oceanic productivity vary from 10 thousand (Hsu, 1986) to .5 million (Zachos et al., 1989) to 1.5 million years (Arthur et al., 1987). Examination of the Paleocene molluscan fauna from the Brazos River localities supports this hypothesis of lowered productivity in the Danian marine environment. The low levels of diversity and abundance of the earliest Danian molluscan fauna, the presence of a possible opportunistic species immediately above the K-T extinction horizon, and the deposit-feeder dominance of these earliest Paleocene fauna, all support the hypothesis of a period of lowered marine productivity lasting approximately 300,000 years.

A strangelove perturbation in delta carbon-13 has been reported in samples from the Brazos River core (Keller, 1989). This negative incursion in delta carbon-13 begins at the K-T boundary as defined by Keller (1989) and peaks at the P0/P1a boundary. Earliest Danian planktonic foraminiferal assemblages from the Brazos River sections are characterized by small, morphologically simple forms interpreted as a stress-tolerant assemblage (Keller, 1989). Paleocene nannofossil assemblages from the Brazos River are dominated by *Thoracospharea sp.* and *Braadosphaera sp.* which have been interpreted as "disaster" fauna (Jiang and Gartner, 1986). These nannofossils persist locally for approximately one million years after the K-T extinctions, suggesting a prolonged disturbance in the marine environment at the Brazos River localities (Jiang and Gartner, 1986). A diversity study of Danian planktonic foraminifera from deep-sea cores also supports the idea of lowered marine productivity in the earliest Paleocene (Gerstel et al., 1987).

Long-term Changes

While the relative proportions of suspension-feeding and deposit-feeding molluscs returned to pre-extinction levels within zone P1b, some molluscan life-habits were more permanently affected. Oysters and other sessile epifaunal suspension-feeding molluscs were among the most diverse and abundant groups in the local Cretaceous stratigraphic section. These organisms became much less common in the Paleocene and never regained their former levels of abundance and diversity in the studied sections (Figure 20). A decline in soft-bottom epifaunal suspension-feeders at the end of the Cretaceous period has been noted as a general long-term evolutionary trend by Jablonski and Bottjer (1983). In their estimation, the K-T extinctions played only a partial role in the elimination of these Late Cretaceous continental shelf assemblages, since these communities persisted locally into the early Tertiary. These authors link the collapse of these soft-bottom suspension-feeding communities with a long-term increase in bioturbation and predation in the latest Mesozoic and early Cenozoic. They also suggest that early Tertiary sea-level regression played a major role by eliminating the epicontinental seas in which these communities thrived. The sudden decrease in the diversity and relative abundance of Ostreidae (SF-ES) at the K-T boundary at the Brazos River localities suggests that the K-T extinction event was a major factor in the demise of soft-bottom epifaunal suspension-feeding communities in east-central Texas.

The large increase in the infaunal carnivore-scavenger trophic category across the K-T boundary (Figure 21) is puzzling. This category is primarily composed of gastropods of family Naticidae and various opistobranchs. Vermeij (1977) documented a major marine community reorganization that took place during the late Mesozoic and into the early Tertiary, termed the Mesozoic marine revolution. This change in community structure was characterized by a radiation of predators and a corresponding increase in the proportion of taxa with adaptations against predation. The evolution of many predatory gastropods occurred in the Late Cretaceous as part of this community reorganization (Vermeij, 1977; Taylor et al., 1980). Increased infaunalization of bivalves and gastropods in the Late Cretaceous has also been posited as part of the Mesozoic marine revolution (Vermeij, 1977).

It is conceivable that the increase in the relative abundance of infaunal carnivorous gastropods in the earliest Paleocene is related to this large-scale change in faunal makeup. However, the Mesozoic marine revolution took place over several million years, and it seems unlikely that one would be able discern it in the short time-frame of approximately three million years represented by the studied K-T stratigraphic sections. Another problem with relating the increase in infaunal carnivorous gastropods with the Mesozoic marine revolution is that many of the species of infaunal carnivorous gastropods found in the Paleocene stratigraphic sections of the Brazos River are opistobranchs, a group of gastropods not previously associated with the Late Cretaceous radiation of carnivorous gastropods. The geologic history of most opistobranchs has been difficult to assess, because many either have no shells or possess very fragile shells and are therefore infrequently preserved (Taylor et al., 1980).

Molluscan Faunal Rebound

The Tertiary rebound of mollusks in the aftermath of the K-T extinction may have affected local assemblages for as much as 1.9 million years. Estimation of the duration of the rebound is based on the patterns of diversity and the first appearances of the fauna, which both stabilize at the base of zone P1d. The pattern of first appearances of the molluscan fauna (Figure 11) is difficult to interpret because of an unconformity and a stratigraphic gap in the local stratigraphic sections. Relatively poor preservation in the Littig Glauconite Member may also have distorted the pattern of molluscan first appearances, placing some first appearances artificially high in the section. It is possible that the apparent increase in numbers of species ranges and diversity above the base of the Littig Glauconite Member is partly attributable to these biasing factors, and that the bulk of the rebound occurred during the time of deposition of the Littig Glauconite Member, roughly 300,000 years after the K-T extinctions. The sharp change from a low diversity fauna composed of an even mixture of Cretaceous survivors, undescribed species, and Paleocene species to a much more diverse primarily Paleocene fauna across the P1a/P1b boundary implies a period of rapid faunal turnover and species proliferation corresponding to the basal Littig unconformity.

Increased faunal stability characterizes the molluscan assemblages above the base of the P1b biozone. In contrast to the earliest Danian molluscan assemblages of zones P0 and P1a, no "blooms" in the abundances of possible opportunistists were found above the base of zone P1b. Keeping in mind the preservational bias in the Littig Glauconite Member, diversity increased sharply to nearly Late Cretaceous levels at the P1a/P1b boundary and gradually stabilized through the rest of the studied sections, a period spanning at least 1.6 million years (Figure 16). Trophic proportions of the fauna also largely returned to pre-extinction levels within zone P1b (Figure 19) and remained relatively constant.

Local species longevity increased substantially above the base of zone P1b. Species longevity is difficult to evaluate because changes in sedimentation rate could not be precisely quantified (see Sedimentation Rates), and not all of the foraminiferal biozone boundaries have been dated. Baring huge changes in sedimentation rate (a relatively safe assumption since facies changes are minor), it appears that average species longevity increased dramatically above the base of the Littig Glauconite Member (Figure 12). Only forty-eight percent of the molluscan species present in the earliest Paleocene (zones P0 and P1a) continued into zone P1b. In contrast, the vast majority of the species present above the base zone P1b span at least one planktonic foraminiferal biozone boundary and the duration of these planktonic foraminiferal biozones is substantially greater than in the earliest Paleocene (P0 and P1a). The total duration of zones P0 and P1a is only 300,000 years. In contrast, the total duration of zones P1b and P1c is 1.6 million years and zone P1d spans approximately 1.5 million years (Berggren et al., 1985). The high degree of stability of the molluscan fauna above the base of zone P1b constrasts markedly with the large amount of faunal turnover apparent in the earliest Danian, and signifies a pronounced environmental improvement above the P1a/P1b boundary.

A problem with evaluating the model of molluscan faunal rebound proposed by Hansen (1988) is that his model dealt with broad-scale faunal changes across the entire Gulf of Mexico, while this study examines faunal changes at one particular locality in detail. An ecological recovery phase could not be resolved for the earliest Paleocene molluscan faunas of the Brazos River (Upshaw, 1989). Although the timing of the initial radiation phase as discussed by Hansen (1988) appears to be accurate, corresponding to zone P1b, none of the bloom families of the initial radiation phase (Cucullaeidae, Ostreidae, Carditidae, and Turritellidae) underwent extensive radiation in the studied stratigraphic sections. Instead, the increase in the number of species is broadly distributed among several families. Molluscs of the families Nuculanidae and Turridae appear to be the most speciose early Danian families with eight and five species respectively. The fact that none of the bloom families radiated within the studied local sections suggests that these families rebounded in geographic regions or depositional environments other than shelf-sediments of east-central Texas. In support of this hypothesis, Danian molluscs of the family Ostreidae were mainly restricted to the shallow-water Tehuacana Creek Member in east-central Texas (Gardner, 1933) and perusal of a compilation of Paleocene and Eocene molluscs by Palmer and Brann (1966) indicates that Paleocene Ostreidae were more common in nearshore shallow-water depostional environments than they were on the mid to outer continental shelf.

CONCLUSIONS

The virtually continuous Brazos River K-T stratigraphic sections record at least the first two million years of the Danian molluscan faunal rebound. Facies changes in these sediments are generally small, with the vast bulk of the sediments consisting of middle-shelf clays and silts. Minor variations in sediment type occur in the Littig Glauconite Member, a condensed zone, and at the Ravine locality, which represents a slightly shallower depositional environment than the rest of the studied sections.

Changes in the diversity, life-habits, and taxonomic compositon of the molluscan assemblages are striking across the K-T boundary. In the Late Cretaceous, local molluscan faunas were dominated by epifaunal suspension-feeders, dominately oysters, and were characterized by high levels of diversity. In contrast, earliest Paleocene faunas were characterized by low levels of abundance and diversity and an even mixture of Cretaceous survivors, undescribed species, and newly evolved Paleocene species (Upshaw, 1989; Hansen and Upshaw, 1990). A bloom in the abundance of an undescribed species of the pelagic herbivore family Litiopidae is restricted to the earliest Paleocene *G. cretacea* zone (PO) (Upshaw, 1989; Hansen and Upshaw, 1990). The distribution pattern of this mollusk suggests that it may be an opportunistic species that capitalized on the physically unstable environment of the earliest Paleocene.

Within the *G. eugubina* zone (P1a), the assemlages dominated by Litiopidae shifted to a low diversity assemblage characterized by an undescribed deposit-feeding bivalve of the family Nuculanidae (Upshaw, 1989; Hansen and Upshaw, 1990). This low diversity deposit-feeder assemblage persisted to the base of the *G. pseudobulloides* biozone (P1b), roughly 300,000 years after the K-T extinctions. The low levels of diversity and abundance, the deposit-feeder dominance, and the presence of a possible opportunistic species in the earliest Paleocene imply a period of lowered marine productivity lasting approximately 300,000 years. This interpretation is consistent with the hypothesized earliest Paleocene Strangelove Ocean inferred from carbon isotope ratios.

Some longer-term changes in the life-habits of the molluscan fauna are apparent across the K-T boundary in east-central Texas. Oyster-rich, epifaunal suspension-feeding molluscan assemblages that were locally dominant in the Late Cretaceous were disrupted across the K-T boundary and never regained their former levels of abundance or diversity. The collapse of soft-bottom epifanal suspension feeding communities at the end of the Cretaceous Period has been noted by Jablonski and Bottjer (1983), who linked it to late Mesozoic sea-level regression and increased predation and bioturbation. In contrast, this study suggests that the K-T extinction event had a large impact on these communities in east-central Texas. Infaunal carnivore-scavengers such as Naticidae and various opistobranchs become far more dominant in the Paleocene than they were in local Cretaceous sediments. This trend could be attributed to the Mesozoic marine revolution (Vermeij, 1977) or to local effects of the K-T mass extinctions.

Relative abundances of suspension-feeding and deposit-feeding mollusks returned to Cretaceous proportions, diversity dramatically increased to nearly pre-extinction levels, and the vast majority of the Cretaceous species disappeared near the base of the *G. pseudobulloides* biozone (Zone P1b). The large increase in diversity and the sudden change to a dominately Paleocene fauna across the unconformable base of the Littig Glauconite Member imply a particularly high rate of faunal turnover and immigration/speciation during this interval. Molluscan assemblages from above the base of the P1b zone are characterized by increased stability, with trophic structure and diversity leveling at near pre-extinction levels for at least 1.6 million years. Species longevity also increased dramatically during this interval. The molluscan faunal rebound appears to have occurred mainly in the *G. pseudobulloides* biozone (P1b), supporting observations of Hansen (1988), whose the initial radiation phase was hypothesized to occur in this same interval based on Danian molluscan occurrrences throughout the Gulf Coast. None of the "bloom" families of Hansen's (1988) initial radiation phase (Cucullaeidae, Ostreidae, Carditidae, or Turritellidae) were particularly speciose in the studied stratigraphic sections, suggesting the possibility that the radiation of these groups occurred in environments or geographic regions other than middle-shelf sediments of east-central Texas.

REFERENCES CITED

Abbott, R. T., 1968, Seashells of North America, a guide to field identification: New York, Golden Press, 280 p.

_____, R. T., 1974, American Seashells: New York, Van Nostrand Reinhold Co., 663 p.

Allmon, W. D., 1988, Ecology of recent Turritelline gastropods (Prosobranchia, Turritellidae): current knowledge and paleontological implications: Palaios, v. 3, p. 259-284.

Alt, D., Sears, J. M., and Hyndman, D. W., 1988, Terrestrial maria: the origins of large basalt plateaus, hotspot tracks and spreading ridges: Journal of Geology, v. 96, p. 647-622.

Alvarez, L. W., Alvarez, W., Asaro, F., and Michel, H. V., 1980, Extraterrestrial cause for the Cretaceous-Tertiary extinction: Science, v. 208, p. 1095-1108.

Andrews, J., 1977, Shells and shores of Texas (2nd ed.): Austin, University of Texas Press, 365 p.

Arthur, M. A., Zachos, J. C., and Jones, D. S., 1987, Primary productivity and the Cretaceous/Tertiary boundary event in the oceans: Cretaceous Research, v. 8, p. 43-54.

Barnes, R. D., 1987, Invertebrate Zoology (5th ed.): New York, Saunders College Publishing, 893 p.

Berggren, W. A., 1978, Recent advances in Cenozoic planktonic foraminiferal biostratigraphy, biochronology, and biogeography: Atlantic Ocean: Micropaleontology v. 24, p. 337-370.

Berggren, W. A., Dent, D. V., and Flynn, J. J., 1985, Jurassic to Paleogene: Part 2, Paleogene geochronology and chronostratigraphy, *in* Snelling, N. J., ed., The chronology of the geologic record: Geological Society of London Memoir 10, p. 141-195.

Bourgeois, J., Hansen, T. A., Weiberg, P. L., and Kauffman, E. G., 1988, A tsunami deposit at the Cretaceous-Tertiary Boundary: Science, v. 241, p. 567-570.

Bryan J. R., and Jones, D. S., 1989, Fabric of the Cretaceous-Tertiary Marine Macrofaunal Transition at Braggs, Alabama: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 69, p. 279-301.

Clifford, H. T, and Stephenson, W., 1975, An introduction to numerical classification: New York, Academic Press, 229 p.

Erickson, D. J. III, and Dickson, S. M., 1987, Global trace-element biogeochemistry at the K-T boundary: oceanic and biotic response to a hypothetical meteorite impact: Geology, v. 15, p. 1014-1017.

Everitt, B., 1974, Cluster Analysis: London, Heineman Educational Book Ltd., 122 p.

Farrand, R. B., 1984, Cretaceous macrofossil assemblages of the Corsicana Formation with implications on the Cretaceous-Tertiary boundary in east-central Texas (M. S. Thesis): University of Texas, Austin, 161 p.

Fursich, F. T., 1978, The influence of faunal condensation and mixing on the preservation of fossil benthic communities: Lethaia, v. 11, p. 243-250.

Gardner, J., 1933, The Midway Group of Texas: University of Texas Bulletin no. 3301, 401 p.

Gerstel, J., Thunnell, R., and Ehrlich, R., 1987, Danian faunal succession: planktonic foraminiferal response to a changing marine environment: Geology, v. 15, p. 665-668.

Gould, S. J., 1984, The cosmic dance of Siva: Natural History, v. 93, no. 8, p. 14-19.

Govoni, D. L., 1983, Gastropod molluscs from the Brightseat Formation (Paleocene: Danian) of Maryland (M. S. thesis): George Washington University, Washington D. C., 271 p.

Hallam, A., 1987, End-Cretaceous mass extinction event: Argument for terrestrial causation: Science, v. 238, p. 1237-1242.

Hansen, T. A., 1988, Early Tertiary radiation of marine molluscs and the long-term effects of the Cretaceous-Tertiary extinction: Paleobiology, v. 14, p. 37-51.

Hansen, T. A., Farrand, R. B., Montgomery, H. A., Bilman, H., and Blechschmidt, G., 1987, Sedimentology and extinction patterns across the Cretaceous-Tertiary boundary interval in east Texas: Cretaceous Research, v. 8, p. 229-252.

Hansen, T. A., and Upshaw, B., 1990, Aftermath of the K-T extinction: rate and nature of the early Paleocene molluscan rebound *in* Kauffman E. G., Walliser, O. H., eds., Extinction events in earth history, Lecture notes in the earth sciences, v. 30, Berlin, Springer-Verlag, p. 401-409.

Herm, D., Hillebrante, A. V., and Perch-Nielsen, K., 1981, Die Kreide/Tertiar-Grenze im Lattengebirge (Nordliche Kalkalpen) *in* mikropalaontologischer Sicht. Geol. Bav., vol 82, p. 319-344.

Houbrick, R. S., 1987, Anatomy of Alaba and Litiopa (Prosobranchia: Litiopidae): Systematic Implications: The Nautilus, v. 101 p. 9-18.

Hsu, K. J., 1986, Environmental changes in times of biotic crisis, *in* Raup, D. M., and Jablonski, D., eds., Patterns and processes in the history of life: Berlin, Springer-Verlag, p. 298-312.

Hurlbut, S. H., 1971, The nonconcept of species diversity: a critique of alternative parameters: Ecology, v. 52, p. 577-586.

Jablonski, D., 1986a, Background and mass extinctions: the alternation of macroevolutionary regimes: Science, v. 239, p. 129-133.

Jablonski, D., 1986b, Evolutionary consequences of mass extinctions, *in* Raup, D. M., and Jablonski, D., eds., Patterns and processes in the history of life: Berlin, Springer-Verlag, p. 313-329.

Jablonski, D., 1986c, Causes and consequences of mass extinction: a comparative approach, *in* Elliott, D. K., ed., Dynamics of extinction: New York, John Wiley and Sons, p. 183-228.

Jablonski D., and Bottjer, D. J., 1983, Soft-bottom epifaunal suspension-feeding assemblages in the Late Cretaceous: implications for the evolution of benthic paleocommunities, *in* Tevesz, M. J. S. and McCall, P. L., eds., Biotic interactions in recent and fossil benthic communities, New York, Plenum Press, p. 747-812.

Jiang, M.J., 1980, Calcareous nannofossils from the uppermost Cretaceous and lowermost Tertiary of central Texas (M. S. Thesis): Texas A & M University, College Station, Texas, 160 p.

Jiang, M. J., and Gartner, S., 1986, Calcareous nannofossil succesion acrosss the Cretaceous/Tertiary boundary in east-central Texas: Micropaleontology, v. 32, p. 232-255.

Jones, D. S., Mueller, P. A. , Bryan, J. R., Dobson, J. P., Channell, J. E. T., Zachos, J. G., and Arthur, M. A., 1987, Biotic, geochemical, and paleomagnetic changes across the Cretaceous boundary at Braggs, Alabama: Geology, v. 15, p. 311-315.

Keller, G., 1988, Extinction, survivorship and evolution of planktonic foraminifera across the Cretaceous/Tertiary Boundary at El Kef, Tunisia: Marine Micropaleontology, v. 13, p. 239-263.

_____, 1989, Extended Cretaceous/Tertiary boundary extinctions and delayed population change in planktonic foraminifera from the Brazos River, Texas: Paleoceanography, v. 4, p. 287-332.

Keller, G., and Lindinger M., 1989, Stable isotope, TOC and $CaC0_3$ record across the Cretaceous/Tertiary boundary at El Kef, Tunisia: Palaeogeography, palaeoclimatology, palaeoecology, v. 73, p. 243-265.

Kellough, G. R., 1959, Biostratigraphic and paleoecologic study of Midway foraminifera along Tehuacana Creek, Limestone County, Texas: Transactions of the Gulf Coast Association of Geological Societies, v. 9, p. 147-160.

Kellough, G. R., 1965, Paleoecology of the foraminiferida of the Wills Point Formation (Midway Group) in northeast Texas: Transactions of the Gulf Coast Association of Geological Societies, v. 15, p. 73-153.

Kitchell J. A., Clark, D. L., and Gombos, A. M. Jr., 1986, Biologic selectivity of extinction: a link between background and mass extinction: Palaios, v. 1, p. 504-511.

Kocurek, G., and Hansen, T. A., 1982, Sedimentological nature of the Cretaceous-Tertiary contact in south-central Texas, *in* Maddocks, R. F., Texas ostracoda, guidebook of excursions and related papers for the Eighth International Symposium on Ostracoda: Houston, University of Houston, p. 231-237.

Levinton, J. S., 1970, The paleoecological significance of opportunistic species: Lethaia, v. 3, p. 69-78.

Levinton, J. S., 1982, Marine Ecology, Englewood Cliffs, New Jersey, Prentice-Hall Inc., 526 p.

Lewis, J. S., Watkins, G. H., Hartman, H. and Prinn, R. G., 1982, Chemical consequences of major impact events on Earth *in* Silver L. T., and Schultz P. H., eds., Geological Implications of impacts of large asteroids and comets on the Earth: Geological Society of America Special Paper 190, p. 215-221.

Luque, A. A., Templado, J., and Burnay, L. P., 1988, On the systematic poistion of the genera *Litiopa* Rang, 1829 and *Alaba* H. and A. Adams, 1853: *in* Ponder W. F., Eernisse, D. J., and Waterhouse, J. H., eds., Prosobranch Phylogeny, Proceedings of a syposium held at the 9th International Malacological Congress, Malacological Review Supplement 4, Edinburgh, p. 180-193.

McGowen, M. K., and Lopez, C. M., 1983, Depositional systems in the Nacatoch Formation (Upper Cretaceous), northeast Texas and southwest Arkansas: Austin, State Bureau of Economic Geology, 59 p.

Morton J. E., 1960, Molluscs: an introduction to their form and functions: New York, Harper and Brothers, 232 p.

Officer, C. B, and Drake, C. L., 1985, Terminal Cretaceous environmental events: Science, v. 227, p. 1161-1167.

Palmer K. V. W., and Brann, D., 1965, Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States, Bulletins of American Paleontology, v. 48, no. 218, Part I, Ithaca, Paleontological Research Institution. p. 1-470.

______, 1966, Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States, Part II, Bulletins of American Paleontology, v. 48, no. 218, Ithaca, Paleontological Research Institution, p. 471-1057.

Peet, R. K., 1974, The measurement of species diversity: Annual Review of Ecological Systems, v. 5, p. 285-307.

Pielou, E. C., 1984, The interpretation of ecological data: a primer on classification and ordination: New York, Wiley Inc., 263 p.

Premoli Silva, I. and Bolli, H. M., 1973, Late Cretaceous to Eocene planktonic foraminifera and stratigraphy of Leg 15 sites in the Carribbean Sea, *in* Initial reports of the Deep Sea Drilling Project, 15, Washington D. C., U. S. Government Printing Office, p. 499-547.

Prinn, R. G., and Fegley, B. Jr., 1987, Bolide impacts, acid rain, and biospheric traumas at the Cretaceous-Tertiary boundary: Earth and Planetary Science Letters, v. 83, p. 1-15.

Rampino, M. R., and Strothers, R. B., 1988, Flood basalt volcanism during the last 250 million years: Science, v. 241, p. 663-668.

Sanders, H. L., 1968, Marine benthic diversity: a comparative study: American Naturalist, v. 102, p. 243-282.

Scott, R. W., 1974, Bay and shoreface benthic communities in the lower Cretaceous: Lethaia, v. 30, p. 315-330.

Sepkoski, J. J., 1986, Phanerozoic overview of mass extinction *in* Raup D. M., and Jablonski, D. eds., Patterns and Processes in the History of Life, Berlin, Springer-Verlag, p. 277-295.

Sheehan P. M., and Hansen, T. A., 1986, Detritus-feeding as a buffer to extinction at the end of the Cretaceous: Geology, v. 14, p. 868-870.

Signor, P. W., III, and Lipps, J. H., 1982, Sampling bias, gradual extinction patterns and catastrophes in the fossil record: *in* Silver, L. T., and Schultz P. H., eds., Geological implication of large asteroids and comets on the earth: Geological Society of America special paper 190, p. 291-296.

Simpson, G. G., 1953, The major features of evolution: New York, Columbia University Press, 434 p.

Smit J., 1982, Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous-Tertiary boundary, *in* Silver, L. T., and Schultz, P. H., eds., Geological implications of impacts of large asteroids and comets on the earth: Geological Society of America special paper 190, p. 329-362.

Sneath, P. H., and Sokal, R. R., 1973, Numerical taxonomy: the principals and practice of numerical classification: San Francisco, W. H. Freeman, 573 p.

Stanley, S. M., 1970, Shell form and function in the Bivalvia (Mollusca): Geological Society of America, Memoir 125, 296 p.

Stanton, R. J., 1982, Cenezoic Stratigraphy of Texas, *in* Maddocks R. F., ed., Texas ostracoda: guidebook of excursions and related papers for the eighth international symposium on ostracoda: Houston, University of Houston, p. 242-252.

Stanton R. J., and Nelson, P. C., 1980, Reconstruction of the trophic web in paleontology: community structure in the Stone City Formation (middle Eocene, Texas): Journal of Paleontology, v. 54, p. 118-135.

Taylor, J. D., Morris, N. J., and Taylor C. N., 1980, Food specialization and the evolution of predatory prosobranch gastropods: Palaeontology, v. 23, part 2, p. 375-409.

Tipper, J. C., 1979, Rarefaction and Rarefiction: the use and abuse of a method in paleoecology: Paleobiology, v. 5, p. 423-434.

Toon , O. B., Pollack J. B., Ackerman T. P., Turco, R. P., Mckay, C. P., and Liu, M. S., 1982, Evolution of an imapact-generated dust cloud and its effects on the atmosphere *in* Silver, L. T., and Schultz, P. H., eds., Geological implications of impacts of large asteroids and comets on the earth: Geological Society of America, Special Paper 190, p. 187-200.

Upshaw, B. III, 1989, The early Danian (Paleocene) molluscan faunal rebound from the terminal Cretaceous mass extinction: Brazos River, east-central Texas (M. S. thesis): Western Washington University, Bellingham, Washington, 139 p.

Valentine, J. W., 1973, Evolutionary paleoecology of the marine biosphere: Englewood Cliffs, New Jersey, Prentice Hall Inc., 511 p.

Vermeij, G. R., 1977, The Mesozoic marine revolution: evidence from snails, predators and grazers: Paleobiology, v. 3. p. 245-258.

Walker, K. R., 1974, Mud substrate *in* Ziegler, A. M., Walker, K. R., Anderson, E. J., Kauffman, E. G., Ginsburg, R. N., and James, N. P., eds. Principles of benthic community analysis: University of Miami, Miami, Florida, p. 5.1-5.11.

Weise, B. R., 1979, Wave dominated deltaic systems of the Upper Cretaceous San Miguel Formation, Maverick Basin, south Texas: Transactions of the Gulf Coast Association of Geological Societies, v. 29, p. 202-214.

Wilkinson, L., 1989, SYSTAT: the system for statistics: Evanston, SYSTAT Inc., 822 p.

Winker, C. D., 1984, Clastic shelf margins of the post-Comanchean Gulf of Mexico: Implications for deep-water sedimentation, *in* Characteristics of Gulf basin deep-water sediments and their exploration potential, Fifth Annual Research Conference, Austin Texas: Gulf Coast Section, Society of Economic Paleontologists and Mineralogists Foundation, p. 109-120.

Wolbach, W. S., Lewis, R. S., and Anders, E., 1985, Cretaceous extinctions: evidence for wildfires and the search for meteoritic material: Science, v. 225, p. 1030-1032.

Zachos, J. C., Arthur, M. A., and Dean, W.E., 1989, Geochemical evidence for suppression of pelagic marine productivity at the Cretaceous-Tertiary boundary: Nature, v. 337, p. 61-64.

APPENDIX I

Species lists for the Danian molluscan assemblages collected in this study.

See Upshaw (1989) for the faunal list of the earliest Paleocene. Further study has modified Upshaw's data slightly. *Turritella houstoni* was examined by Dr.Warren Allmon and was identified as *"Turritella" premortoni* (Govonni) (Allmon, personal communication, 1990). *Cuspidaria grandis* was found above the base of the Littig Glauconite member in this study and was therefore considered to be a local Cretaceous species rather than a reworked taxon. Two of Upshaw's previously unidentified bivalves were identified as *Lucina cf. ulheri* (sample 4) and *Corbula milium* (sample 11) respectively, thereby adding two Paleocene species to his earliest Paleocene assemblages. Pteriidae, Cadulus, and Ostreidae collected by Upshaw (1989) from the earliest Paleocene clays were not considered to be reworked taxa for the purposes of trophic analysis in this study.

	CM4.1	B2.1	B2.2	B2.3	B2.4	B2.5	CM5.1	CM5.4	CM5.6	DMC2.1	DMC2.2	DMC2.3	DMC2.4
Bryzoan	3												
Serpulid													
Arthropod pincer													
Corals													
Caryophyllia dumblei?													
Caryophyllia mediavia?													
Caryophyllia sp?													
Platytrochus primaevus													
Flabellum conoideum?													
Balanophyllia ponderosa?													
Solitary corals indet.	21	1	1					1				1	1
Scaphopoda													
Dentalium mediaviense													
Dentalium sp. A													
Dentalium sp. B													
Dentalium sp. indet.						1		1		1		1	
Cadulus phoenicia?													
Cadulus sp. indet.												1	
Scaphopoda indet.								1	1				2
Gastropoda													
Solariorbis proius													
Solariorbis sp. A													
Solariorbis (?) sp. B													
Solariorbis sp. C													
Vitrinellidae sp. A													
Vitrinellidae						4			4				
"Turritella" premortoni	3	1				1				1			
"Turritella" prehumerosa													
"Turritella" postmortoni?													
Turritellidae	4	2	9	1		2	1	2	5	3		1	1
Bittium estellense				8		3	1	1			1		
Nudiavagus sp. A		2										1	1
Nudiavagus sp. indet.			1										
Cerithiidae sp. A	7	1	4							1			
Cerithiidae sp. B						5		2		1			1
Cerithiidae							2	9	1	7		1	
Litiopa sp. A									1				
Epitoniidae (?) sp.													
Aporrhaidae sp.			1	1						1			
Calyptraea sp.													
Calyptrophorus popenoe			5										
Calyptrophorus sp. indet.	4									1			
Polinices julianna													
Naticidae	60	1	10	7	2	4	6	4	22	6	2	2	8
Columbellidae sp.										1			
Nassariidae sp.						1							
Exilia cf. pergracilis							1			1			
Falsifusus harrisi?													
Fasciolariidae sp. A			1				1		1			1	1
Fasciolariidae sp. B										1			
Fasciolariidae sp. C													1
Fasciolariidae (?) sp. D			1										
Fasciolariidae sp. indet.						2							
Agaronia mediavia													
Olividae	2												
Volutocorbis texanus		2		3									

	CM4.1	B2.1	B2.2	B2.3	B2.4	B2.5	CM5.1	CM5.4	CM5.6	DMC2.1	DMC2.2	DMC2.3	DMC2.4
Volutidae	2		1			3		2	1				
Turridae sp. A						1							
Turridae sp. B													
Turridae sp. D													
Turridae sp. R										1			
Turridae	3		1			1		1		1		1	1
Creonella obscurplica													
Acteonidae sp. A													
Tornatellaea quercollis?													
Tornatellaea texana								3					
Tornatellaea sp. indet.	29	2	10	3	2		7			17	1		1
Ringicula butleriana?													
Ringicula dubia													
Ringicula sp. A													
Ringiculidae													
Atys sp. Gardner						4		1	1				
Retusa emoryi	6		1				3	3	9	3			4
Gastropod A	2												
Gastropod B	10												
Gastropod C	6												
Gastropod D	1												
Gastropod E	3												
Gastropod F	1												
Gastropod G													
Gastropod H												1	
Bivalvia													
Nucula mediavia													
Nuculidae		2				2		2	4				2
Jupiteria smirna								2	7				
Nuculana cf. corpulentoides													
Nuculana saffordana?													
Nuculana sp. (Gardner)													
Nuculana sp. B	2	21	32	35	3	8	22	12		39	7	13	
Nuculana sp. C													
Saccella sp. Gardner		1			1	3		2	3			4	2
Nuculanidae	127	18	51		3		12		7			1	9
Solemya bilix								1	1				1
Striarca (?) sp. A						7		9	1			3	5
Arcidae sp. B													
Limopsis sp.						3		8	3			1	
Cucullaea macrodonta								26		7	1	15	9
Cucullaea sp. indet	28	7	16	6	5	15	7		5				
Brachidontes saffordi													
Mytilidae sp.													
Amusium alabamense	3			9		12	7	19	19	13	5	7	14
Pectinidae		1	1		5								
Ostrea pulaskensis	26	3	2		32					1	6		
Pycnodonte sp.												1	
Ostreidae		4	4	2			1	5			2	4	1
Phacoides julianne													
Lucina cf. ulheri			1	1			1	1	1	1		1	
Lucinidae sp. A								2	1				2
Lucinidae						2				1	1		
Leptonidae/Montacutidae sp.													
Sportellidae													
Venericardia bulla													
Venericardia eoa				1		2		25				14	6

	CM4.1	**B2.1**	**B2.2**	**B2.3**	**B2.4**	**B2.5**	**CM5.1**	**CM5.4**	**CM5.6**	**DMC2.1**	**DMC2.2**	**DMC2.3**	**DMC2.4**
Venericardia moa	9	5	13	1	1						1		
Carditidae				15	7	13	8		2	14	1		
Crassatella gabbi	1												
Crassatella sp. A			2		1			1					
Crassatella sp. indet	3	3	5	12	3	2	5	3	2	13	2	2	1
Cardiidae sp.													
Tellina cf. quihi													
Tellina sp. A													
Tellina sp. B													
Tellinidae													1
Semelidae sp.													
Kelliella (?) evansi													
Kelliellidae													
Pitar sp.													
Caryocorbula coloradoensis													
Caryocorbula kennedyi													
Corbula milium	1							2		1			
Corbulidae						1			1	1			
Panopea sp.													
Martesia sp.?													
Cuspidaria grandis	1							1					
Cuspidaria sp. A													
Cuspidaria sp. B													
Cuspidariidae									1				
Verticordia sp. Harris						1		2	4				1
Bivalve E													
Totals	368	77	173	105	65	103	85	154	108	138	30	77	76
Shannon-Weaver Diversity	2.54	2.13	2.44	2.02	1.53	2.81	2.18	2.72	2.66	2.28	1.99	2.46	2.68

	DMC2.5	DMC2.6	DMC2.7	DMC2.8	FB0	FB1	FB2	FB6	FB12	FB13	FB15	FB16	FB17	WP/TC
Bryzoan														
Serpulid					x									
Arthropod pincer	x													
Corals														
Caryophyllia dumblei?						6		1						
Caryophyllia mediavia?						10								17
Caryophyllia sp?										2	3			
Platytrochus primaevus														1
Flabellum conoideum?						2								
Balanophyllia ponderosa?														1
Solitary corals indet.	1	1	1	2		14	1				1			14
Scaphopoda														
Dentalium mediaviense									1		1			
Dentalium sp. A					1	1		1	1	2	4			3
Dentalium sp. B						2	1		1		2			5
Dentalium sp. indet.	1		1		1	2	1	2	1	2	3	2	1	3
Cadulus phoenicia?											1			
Cadulus sp. indet.	1						1		1	1				6
Scaphopoda indet.		2	2	2									3	
Gastropoda														
Solariorbis proius					1	9	2	4	1	3	2	1		
Solariorbis sp. A					2							1		
Solariorbis (?) sp. B		1												
Solariorbis sp. C										1				
Vitrinellidae sp. A								1		1				
Vitrinellidae				1	3		2							
"Turritella" premortoni					5	2					7	4		1
"Turritella" prehumerosa					1	3				3			1	7
"Turritella" postmortoni?														
Turritellidae		2	5	1			1	1				1	3	
Bittium estellense					18	19	9	6		4	9	2	3	9
Nudiavagus sp. A														
Nudiavagus sp. indet.														
Cerithiidae sp. A														
Cerithiidae sp. B	3	1			1						1			
Cerithiidae				1							1			
Litiopa sp. A					1									
Epitoniidae (?) sp.														
Aporrhaidae sp.														
Calyptraea sp.														
Calyptrophorus popenoe														
Calyptrophorus sp. indet.														
Polinices julianna					2			1						
Naticidae	13	12	30	17	51	53	42	9	8	12	35	17	3	5
Columbellidae sp.														
Nassariidae sp.														
Exilia cf. pergracilis		1												1
Falsifusus harrisi?														
Fasciolariidae sp. A														
Fasciolariidae sp. B														
Fasciolariidae sp. C	1		1											
Fasciolariidae (?) sp. D														
Fasciolariidae sp. indet.														
Agaronia mediavia					4	2	4	1		1	2	3		
Olividae	1	1		1									1	
Volutocorbis texanus	3			5	2	10	2	4		1	8	6		1

	DMC2.5	DMC2.6	DMC2.7	DMC2.8	FB0	FB1	FB2	FB6	FB12	FB13	FB15	FB16	FB17	WP/TC
Volutidae		1							3					
Turridae sp. A					1	1	2	2	1			4	3	
Turridae sp. B						3								
Turridae sp. D												1		
Turridae sp. R														
Turridae						4	2	1	2	2	7	5	1	
Creonella obscurplica						1				1				
Acteonidae sp. A							2	1	1	1				
Tornatellaea quercollis?												1		
Tornatellaea texana					2	4	16	5	5		11	2	3	2
Tornatellaea sp. indet.	1									3				24
Ringicula butleriana?						2								
Ringicula dubia					8					5	6	6		
Ringicula sp. A					1									
Ringiculidae						3			1					
Atys sp. Gardner	7			2	8	9	3	8	4	4	5	7	1	2
Retusa emoryi		3	1	1	6	1			1		6	2	1	5
Gastropod A														
Gastropod B														
Gastropod C														
Gastropod D														
Gastropod E														
Gastropod F														
Gastropod G														
Gastropod H														
Bivalvia														
Nucula mediavia		5	3	3	6	5	14	7	3	2	4	4		5
Nuculidae	4												2	
Jupiteria smirna	6	1	3	1	54	16	27	27	26	19	36	21	5	5
Nuculana cf. corpulentoides					5	2		1		1	2	3	2	
Nuculana saffordana?					12	5	2	3	3	4	5	7	2	3
Nuculana sp. (Gardner)														
Nuculana sp. B														
Nuculana sp. C					3		5				2	1	1	
Saccella sp. Gardner	2	2	1			1								
Nuculanidae	11	8	9	14		4	1	1						
Solemya bilix	1	2	1		2	1	3	3	1	1	5	4	3	2
Striarca (?) sp. A	3		2	1										
Arcidae sp. B												1		
Limopsis sp.														
Cucullaea macrodonta	6		1	12	18	18	8	12	2	6	13	5	3	3
Cucullaea sp. indet		5	3								5		2	
Brachidontes saffordi														1
Mytilidae sp.					1						1			
Amusium alabamense	13	16	30	12	10		6	4	1	3	6			
Pectinidae														1
Ostrea pulaskensis				1										1
Pycnodonte sp.											1			1
Ostreidae	1	1		7			1							
Phacoides julianne									1				2	
Lucina cf. ulheri	1					2						1	2	2
Lucinidae sp. A	1	3		1	1					1		1		1
Lucinidae			2		1			1		1	1		2	1
Leptonidae/Montacutidae sp.	1				1	5		1	2	2	1	1		
Sportellidae											1	1		
Venericardia bulla						1	1	1	4	2	8	11		
Venericardia eoa					5	3	4	10	3	13	7	10	2	3

	DMC2.5	DMC2.6	DMC2.7	DMC2.8	FB0	FB1	FB2	FB6	FB12	FB13	FB15	FB16	FB17	WP/TC
Venericardia moa														
Carditidae	3	4		2	1				1	2	8		5	
Crassatella gabbi														
Crassatella sp. A														
Crassatella sp. indet	1	1			2	10	2	4	7	1	1	3	2	2
Cardiidae sp.														
Tellina cf. quihi					1									
Tellina sp. A								1		1		1	1	
Tellina sp. B														
Tellinidae		1			1				2				2	
Semelidae sp.					1			1	2	1	1	2		4
Kelliella (?) evansi														
Kelliellidae					1									
Pitar sp.									1			1		5
Caryocorbula coloradoensis					3	8	6	15	7	11	23	4		
Caryocorbula kennedyi											1			
Corbula milium					3	7		2			12	1	1	8
Corbulidae				1	1		1		3	3	4	3	3	2
Panopea sp.						1				1		1		
Martesia sp.?					1									
Cuspidaria grandis			1											
Cuspidaria sp. A					3	3		1		1	4		1	3
Cuspidaria sp. B														1
Cuspidariidae									2			1		
Verticordia sp. Harris	1			1			1				2			
Bivalve E														
Totals	87	74	97	89	256	255	173	143	103	125	269	153	67	161
Shannon-Weaver Diversity	2.67	2.55	1.78	2.41	2.87	2.94	2.65	2.84	2.87	3.03	3.1	3.13	3.07	3.18

	R0	R1	R2	R3	R4	R5	B2.1/ CM5.1	DMC2.1/ B2.3	DMC2.2/ B2.4	DMC2.3/ CM5.4	DMC2.4/ B2.5	DMC2.5/ CM5.6
Bryzoan												
Serpulid												
Arthropod pincer												
Corals												
Caryophyllia dumblei?												
Caryophyllia mediavia?												
Caryophyllia sp?				1								
Platytrochus primaevus												
Flabellum conoideum?												
Balanophyllia ponderosa?												
Solitary corals indet.							1			2	1	1
Scaphopoda												
Dentalium mediaviense		4										
Dentalium sp. A					1							
Dentalium sp. B		3										
Dentalium sp. indet.	5	6	2	2	2	2		1		2	1	1
Cadulus phoenicia?												
Cadulus sp. indet.										1		1
Scaphopoda indet.	1			4	1	1				1	2	1
Gastropoda												
Solariorbis proius	1	2										
Solariorbis sp. A												
Solariorbis (?) sp. B												
Solariorbis sp. C												
Vitrinellidae sp. A												
Vitrinellidae											4	4
"Turritella" premortoni	9	7	18	14	55	2	1	1			1	
"Turritella" prehumerosa	4		2									
"Turritella" postmortoni?				1								
Turritellidae	1	1		9	4	22	3	4		3	3	5
Bittium estellense	20	1					1	8	1	1	3	
Nudiavagus sp. A							2			1	1	
Nudiavagus sp. indet.												
Cerithiidae sp. A							1	1				
Cerithiidae sp. B								1		2	6	3
Cerithiidae							2	7		10		1
Litiopa sp. A												1
Epitoniidae (?) sp.					1	1						
Aporrhaidae sp.								2				
Calyptraea sp.					1							
Calyptrophorus popenoe												
Calyptrophorus sp. indet.		1	1	1	2			1				
Polinices julianna	1	1										
Naticidae	16	16	16	3		2	7	13	4	6	12	35
Columbellidae sp.								1				
Nassariidae sp.											1	
Exilia cf. pergracilis		1		1			1	1				
Falsifusus harrisi?	1											
Fasciolariidae sp. A							1			1	1	1
Fasciolariidae sp. B								1				
Fasciolariidae sp. C											1	1
Fasciolariidae (?) sp. D												
Fasciolariidae sp. indet.											2	
Agaronia mediavia	2	1										
Olividae												1
Volutocorbis texanus	4					1	2	3				3

	R0	R1	R2	R3	R4	R5	B2.1/ CM5.1	DMC2.1/ B2.3	DMC2.2/ B2.4	DMC2.3/ CM5.4	DMC2.4/ B2.5	DMC2.5/ CM5.6
Volutidae		1			2					2	3	1
Turridae sp. A		1	3		1						1	
Turridae sp. B												
Turridae sp. D												
Turridae sp. R								1				
Turridae	3	2		2	2			1		2	2	
Creonella obscurplica	1											
Acteonidae sp. A	3	2	2									
Tornatellaea quercollis?												
Tornatellaea texana		10	10		1					3		
Tornatellaea sp. indet.	9	1					9	20	3		1	1
Ringicula butleriana?					1							
Ringicula dubia	1	4										
Ringicula sp. A												
Ringiculidae												
Atys sp. Gardner	4	8	4							1	4	8
Retusa emoryi			1				3	3		3	4	9
Gastropod A												
Gastropod B												
Gastropod C												
Gastropod D												
Gastropod E												
Gastropod F												
Gastropod G						1						
Gastropod H										1		
Bivalvia												
Nucula mediavia	11	28	18		3							
Nuculidae				2		2	2			2	4	8
Jupiteria smirna	9	21	7	5	1					2		13
Nuculana cf. corpulentoides												
Nuculana saffordana?	8	18	4	1	3	2						
Nuculana sp. (Gardner)	8	23	8	2	6	7						
Nuculana sp. B							43	74	10	25	8	
Nuculana sp. C	1	1	1									
Saccella sp. Gardner							1		1	6	5	5
Nuculanidae					1		30		3	1	9	18
Solemya bilix	1	1								1	1	2
Striarca (?) sp. A										12	12	4
Arcidae sp. B												
Limopsis sp.										9	3	3
Cucullaea macrodonta		1	3					7	1	41	9	6
Cucullaea sp. indet	3	3		1	1	1	14	6	5		15	5
Brachidontes saffordi		2	3	2		1						
Mytilidae sp.												
Amusium alabamense		1					7	22	5	26	26	32
Pectinidae							1		5			
Ostrea pulaskensis							3	1	38			
Pycnodonte sp.		1			1					1		
Ostreidae	3	1	1	1	1		5	2	2	9	1	1
Phacoides julianne			1		1							
Lucina cf. ulheri						1	1	2		2		2
Lucinidae sp. A	1	1	1			2				2	2	2
Lucinidae								1	1		2	
Leptonidae/Montacutidae sp.												1
Sportellidae		2										
Venericardia bulla	1	4	4	2	4	1						
Venericardia eoa	51	86	47	16	25	13		1		39	8	

	R0	R1	R2	R3	R4	R5	B2.1/ CM5.1	DMC2.1/ B2.3	DMC2.2/ B2.4	DMC2.3/ CM5.4	DMC2.4/ B2.5	DMC2.5/ CM5.6
Venericardia moa							5	1	2			
Carditidae						6	8	29	8		13	5
Crassatella gabbi	1	2	1		1							
Crassatella sp. A									1	1		
Crassatella sp. indet	45	26	20	17	14	10	8	25	5	5	3	3
Cardiidae sp.	7	5	5	2	1	3						
Tellina cf. quihi												
Tellina sp. A												
Tellina sp. B	1											
Tellinidae			2		1	1					1	
Semelidae sp.	1	1	2									
Kelliella (?) evansi		1										
Kelliellidae												
Pitar sp.	4	2	4	2	2	1						
Caryocorbula coloradoensis	25	33	25	7	8	10						
Caryocorbula kennedyi	1											
Corbula milium	2	1	2			1		1		2		
Corbulidae	16	26	12	4	8			1			1	1
Panopea sp.												
Martesia sp.?												
Cuspidaria grandis										1		
Cuspidaria sp. A	1	2										
Cuspidaria sp. B												
Cuspidariidae												1
Verticordia sp. Harris										2	2	5
Bivalve E						1						
Totals	287	366	230	102	156	95	162	243	95	231	179	195
Shannon-Weaver Diversity	2.91	2.6	2.74	2.48	2.05	2.56	2.24	2.13	1.67	2.72	2.93	2.75

APPENDIX II

Relative abundances of trophic categories across the K-T boundary, east-central Texas.

The samples are listed in stratigraphic order. Samples labelled RB are those Cretaceous samples collected by Farrand (1984) from the riverbed at the Brazos-1 locality of Hansen et al. (1987). Numbers corresponding to these clay-rich samples refer to meters below the tsunami deposit at this locality.

Samples labelled CM refer to samples collected from Cretaceous clays of the Cottonmouth-1 locality by Kauffman. Sample intervals are given in meters below the tsunami deposit.

CM1 = 1.0 - 1.1 meters
CM2 = .9 - 1.0 meters
CM3 = .73 - .81 meters
CM4 = .65 - .73 meters
CM5 = .56 - .65 meters
CM6 = .46 - .56 meters
CM7 = .32 - .46 meters
CM8 = .16 - .32 meters
CM9 = .12 - 0 meters

Trophic designations are as follows:

SF-NSI = suspension-feeder, non-siphonate-infaunal
SF-SI = suspension-feeder, siphonate-infaunal
SF-COL = suspension-feeder, colonial (bryzoan)
SF-EM = suspension-feeder, epifaunal-mobile (pectinids)
SF-ES = suspension-feeder, epifaunal-sessile (oysters)
DF-IB = deposit-feeder, infaunal-bivalve
DF-IG = deposit-feeder, infaunal-gastropod
DF-EM = deposit-feeder, epifaunal-mobile
B-CS-IB = bivalve, carnivore-scavenger, infaunal-burrower (Cuspidariidae and Verticordiidae)
PAR-G = parasite, gastropod
CS-N = carnivore/scavenger, nektonic (ammonites)
CS-EM = carnivore-scavenger, epifaunal-mobile
CS-SCAPH = carnivore/scavenger, scaphopod
G-CS-IB = gastropod, carnivore/scavenger, infaunal-burrower
CS-ES = carnivore/scavenger, epifaunal-sessile, (corals)
G-EM = grazer, epifaunal-mobile
G-P = grazer, pelagic
UNASSIG = unassigned
% SF = Total percentage of suspension-feeders
% DF = Total percentage of deposit-feeders
% CS = Total percentage of carnivore/scavengers
% GRAZ = Total percentage of grazers.

Appendix Two (cont.). Relative abundances of trophic categories across the K-T boundary, east-central Texas.

	RB11.5	**RB6.5**	**RB4.5**	**RB4.0**	**RB2.75**	**RB1.75**
SF-NSI	17.0	22.2	33.9	24.2	28.0	24.3
SF-SI	12.8	8.9	14.3	6.1	14.0	2.7
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	14.9	5.6	1.8	3.0	1.1	8.1
SF-ES	14.9	8.9	3.6	27.3	7.5	21.6
DF-IB	23.4	8.9	14.3	9.1	25.8	13.5
DF-IG	0.0	0.0	0.0	0.0	0.0	0.0
DF-EM	0.0	0.0	0.0	0.0	0.0	0.0
B-CS-IB	0.0	1.1	1.8	0.0	1.1	0.0
PAR-G	0.0	0.0	0.0	0.0	0.0	0.0
CS-N	0.0	10.0	7.1	12.1	6.5	24.3
CS-EM	4.3	10.0	3.6	9.1	6.5	2.7
CS-SCAPH	0.0	11.1	10.7	6.1	6.5	0.0
G-CS-IB	12.8	11.1	8.9	3.0	3.2	2.7
CS-ES	0.0	0.0	0.0	0.0	0.0	0.0
G-EM	0.0	0.0	0.0	0.0	0.0	0.0
G-P	0.0	0.0	0.0	0.0	0.0	0.0
UNASSIG	0.0	2.2	0.0	0.0	0.0	0.0
%SF	59.6	45.6	53.6	60.6	50.5	56.8
%DF	23.4	8.9	14.3	9.1	25.8	13.5
%CS	17.0	43.3	32.1	30.3	23.7	29.7
%GRAZ	0.0	0.0	0.0	0.0	0.0	0.0

	RB0.75	**CM1**	**CM2**	**CM3**	**CM4**	**CM5**
SF-NSI	43.2	11.5	8.3	21.1	11.3	18.2
SF-SI	6.8	15.4	8.3	13.2	11.3	6.1
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	2.3	2.6	4.2	3.5	0.0	0.0
SF-ES	18.2	28.2	16.7	23.7	32.1	42.4
DF-IB	15.9	9.0	20.8	20.2	15.1	3.0
DF-IG	0.0	0.0	0.0	0.0	0.0	0.0
DF-EM	0.0	0.0	0.0	0.0	0.0	0.0
B-CS-IB	0.0	2.6	4.2	0.9	0.0	0.0
PAR-G	0.0	0.0	0.0	0.0	0.0	0.0
CS-N	6.8	21.8	29.2	10.5	9.4	24.2
CS-EM	2.3	6.4	4.2	0.0	0.0	0.0
CS-SCAPH	4.5	1.3	0.0	7.0	17.0	6.1
G-CS-IB	0.0	1.3	0.0	0.0	1.9	0.0
CS-ES	0.0	0.0	0.0	0.0	0.0	0.0
G-EM	0.0	0.0	0.0	0.0	0.0	0.0
G-P	0.0	0.0	0.0	0.0	0.0	0.0
UNASSIG	0.0	0.0	4.2	0.0	1.9	0.0
%SF	70.5	57.7	37.5	61.4	54.7	66.7
%DF	15.9	9.0	20.8	20.2	15.1	3.0
%CS	13.6	33.3	37.5	18.4	28.3	30.3
%GRAZ	0.0	0.0	0.0	0.0	0.0	0.0

	CM6	**CM7**	**CM8**	**CM9**	**S1**	**S2**
SF-NSI	8.0	15.3	15.0	6.7	24.3	9.3
SF-SI	12.0	13.6	2.5	15.4	0.0	1.7
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	2.0	0.0	0.0	1.0	2.9	0.0
SF-ES	60.0	42.4	65.0	45.2	25.7	9.3
DF-IB	8.0	16.9	5.0	9.6	30.0	30.5
DF-IG	0.0	0.0	0.0	0.0	0.0	0.8
DF-EM	0.0	0.0	0.0	0.0	0.0	0.0
B-CS-IB	0.0	1.7	0.0	0.0	0.0	0.0
PAR-G	0.0	0.0	0.0	0.0	0.0	0.0
CS-N	4.0	6.8	10.0	17.3	0.0	0.0
CS-EM	0.0	0.0	0.0	0.0	1.4	2.5
CS-SCAPH	6.0	3.4	0.0	4.8	7.1	0.8
G-CS-IB	0.0	0.0	0.0	0.0	1.4	3.4
CS-ES	0.0	0.0	0.0	0.0	0.0	0.0
G-EM	0.0	0.0	0.0	0.0	0.0	1.7
G-P	0.0	0.0	0.0	0.0	5.7	39.8
UNASSIG	0.0	0.0	2.5	0.0	1.4	0.0
%SF	82.0	71.2	82.5	68.3	52.9	20.3
%DF	8.0	16.9	5.0	9.6	30.0	31.4
%CS	10.0	11.9	10.0	22.1	10.0	6.8
%GRAZ	0.0	0.0	0.0	0.0	5.7	41.5

	S3	**S4**	**S5**	**S6**	**S7**	**S8**
SF-NSI	6.5	3.1	1.1	1.6	0.0	1.9
SF-SI	1.9	1.9	0.6	3.9	0.0	1.9
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	0.0	0.4	1.1	0.8	0.0	3.7
SF-ES	11.0	8.8	10.8	2.3	2.1	0.0
DF-IB	29.2	23.8	40.9	60.2	77.1	79.6
DF-IG	0.0	0.0	0.0	0.0	0.0	0.0
DF-EM	0.0	0.0	0.0	0.0	0.0	0.0
B-CS-IB	0.6	0.0	0.0	0.0	0.0	0.0
PAR-G	0.0	0.0	0.0	0.0	0.0	0.0
CS-N	0.0	0.0	0.0	0.0	0.0	0.0
CS-EM	0.6	3.8	2.8	4.7	2.1	3.7
CS-SCAPH	3.2	3.8	0.0	0.8	0.0	0.0
G-CS-IB	5.8	24.1	27.3	21.9	18.8	1.9
CS-ES	0.0	0.0	0.0	0.0	0.0	0.0
G-EM	0.0	1.5	2.3	0.8	0.0	1.9
G-P	40.9	28.4	13.1	2.3	0.0	3.7
UNASSIG	0.0	0.4	0.0	0.8	0.0	1.9
%SF	19.5	14.2	13.6	8.6	2.1	7.4
%DF	29.2	23.8	40.9	60.2	77.1	79.6
%CS	10.4	31.8	30.1	27.3	20.8	5.6
%GRAZ	40.9	29.9	15.3	3.1	0.0	5.6

	S9	**S10**	**S11**	**S12**	**S13**	**S14**
SF-NSI	0.0	0.8	1.0	1.5	0.0	0.0
SF-SI	7.4	3.3	3.1	9.6	4.9	0.0
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	0.0	0.8	0.0	0.0	0.0	2.1
SF-ES	3.7	0.8	0.0	1.5	1.2	0.0
DF-IB	74.1	68.3	60.4	54.8	64.2	72.3
DF-IG	0.0	0.8	0.0	0.0	0.0	0.0
DF-EM	0.0	0.0	0.0	0.0	0.0	0.0
B-CS-IB	0.0	0.0	0.0	0.0	0.0	0.0
PAR-G	0.0	0.0	0.0	0.0	0.0	0.0
CS-N	0.0	0.0	0.0	0.0	0.0	0.0
CS-EM	1.9	2.4	3.1	5.2	6.2	2.1
CS-SCAPH	0.0	0.0	0.0	0.0	0.0	0.0
G-CS-IB	9.3	13.8	22.9	20.0	11.1	14.9
CS-ES	0.0	0.0	0.0	0.0	0.0	0.0
G-EM	1.9	4.1	4.2	5.9	6.2	6.4
G-P	1.9	0.0	0.0	0.0	0.0	0.0
UNASSIG	0.0	4.9	5.2	1.5	6.2	2.1
%SF	11.1	5.7	4.2	12.6	6.2	2.1
%DF	74.1	69.1	60.4	54.8	64.2	72.3
%CS	11.1	16.3	26.0	25.2	17.3	17.0
%GRAZ	3.7	4.1	4.2	5.9	6.2	6.4

	S15	**B2.1/ CM5.1**	**B2.2**	**CM4.1**	**DMC2.1/ B2.3**	**DMC2.3/ CM5.4**
SF-NSI	11.2	24.1	26.0	13.0	30.5	47.6
SF-SI	4.1	0.6	0.6	0.3	2.1	3.0
SF-COL	0.0	0.0	0.0	0.8	0.0	0.0
SF-EM	2.0	4.9	0.6	0.8	9.1	11.3
SF-ES	0.0	4.9	3.5	7.1	1.2	4.3
DF-IB	42.9	46.9	48.0	35.1	30.5	15.6
DF-IG	0.0	0.0	3.5	1.1	1.2	0.0
DF-EM	0.0	0.0	0.0	0.0	0.0	0.0
B-CS-IB	0.0	0.0	0.0	0.3	0.0	1.3
PAR-G	0.0	0.0	0.0	0.0	0.0	0.0
CS-N	0.0	0.0	0.0	0.0	0.0	0.0
CS-EM	6.1	2.5	2.3	1.4	3.3	2.2
CS-SCAPH	0.0	0.0	0.0	0.0	0.4	1.7
G-CS-IB	31.6	11.7	12.1	26.4	14.8	5.6
CS-ES	0.0	0.6	0.6	5.7	0.0	0.9
G-EM	2.0	3.7	2.9	1.9	7.0	6.1
G-P	0.0	0.0	0.0	0.0	0.0	0.0
UNASSIG	0.0	0.0	0.0	6.3	0.0	0.4
%SF	17.3	34.6	30.6	22.0	42.8	66.2
%DF	42.9	46.9	51.4	36.1	31.7	15.6
%CS	37.8	14.8	15.0	33.7	18.5	11.7
%GRAZ	2.0	3.7	2.9	1.9	7.0	6.1

	DMC2.4/ B2.5	**DMC2.5/ CM5.6**	**DMC2.6**	**DMC2.7**	**DMC2.8**	**FB0**
SF-NSI	37.4	15.9	16.2	11.3	18.0	12.9
SF-SI	3.4	3.6	6.8	3.1	2.2	5.1
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	14.5	16.4	21.6	30.9	13.5	3.9
SF-ES	0.6	1.0	1.4	0.0	9.0	0.4
DF-IB	15.1	22.6	23.0	16.5	20.2	32.0
DF-IG	0.6	0.0	0.0	0.0	0.0	0.0
DF-EM	2.2	2.1	1.4	0.0	1.1	2.3
B-CS-IB	1.1	3.1	0.0	1.0	1.1	1.2
PAR-G	0.0	0.0	0.0	0.0	0.0	0.0
CS-N	0.0	0.0	0.0	0.0	0.0	0.0
CS-EM	5.6	3.1	2.7	1.0	5.6	1.2
CS-SCAPH	1.7	1.5	2.7	3.1	2.2	0.8
G-CS-IB	11.7	27.7	21.6	32.0	23.6	32.0
CS-ES	0.6	0.5	1.4	1.0	2.2	0.0
G-EM	5.6	2.1	1.4	0.0	1.1	7.4
G-P	0.0	0.5	0.0	0.0	0.0	0.4
UNASSIG	0.0	0.0	0.0	0.0	0.0	0.4
%SF	55.9	36.9	45.9	45.4	42.7	22.3
%DF	17.9	24.6	24.3	16.5	21.3	34.4
%CS	20.7	35.9	28.4	38.1	34.8	35.2
%GRAZ	5.6	2.6	1.4	0.0	1.1	7.8

	FB1	**FB2**	**FB6**	**FB12**	**FB13**	**FB15**
SF-NSI	14.5	9.2	19.6	16.5	21.6	18.6
SF-SI	7.5	5.8	14.7	12.6	16.0	17.1
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	0.0	3.5	2.8	1.0	2.4	2.2
SF-ES	2.0	0.6	0.7	1.9	0.0	0.7
DF-IB	12.9	28.3	28.7	35.0	22.4	18.6
DF-IG	0.0	0.0	0.0	0.0	0.0	0.0
DF-EM	3.5	2.3	3.5	1.0	3.2	0.7
B-CS-IB	1.2	0.6	0.7	1.9	0.8	2.2
PAR-G	0.4	0.0	0.0	0.0	0.8	0.0
CS-N	0.0	0.0	0.0	0.0	0.0	0.0
CS-EM	7.1	3.5	4.9	5.8	2.4	5.6
CS-SCAPH	2.0	1.7	2.1	4.9	4.0	4.1
G-CS-IB	29.0	38.7	17.5	19.4	20.8	24.2
CS-ES	12.5	0.6	0.7	0.0	1.6	1.5
G-EM	7.5	5.2	4.2	0.0	4.0	4.1
G-P	0.0	0.0	0.0	0.0	0.0	0.0
UNASSIG	0.0	0.0	0.0	0.0	0.0	0.4
%SF	23.9	19.1	37.8	32.0	40.0	38.7
%DF	16.5	30.6	32.2	35.9	25.6	19.3
%CS	52.2	45.1	25.9	32.0	30.4	37.5
%GRAZ	7.5	5.2	4.2	0.0	4.0	4.1

	FB16	**FB17**	**WP/TC**	**R0**	**R1**	**R2**
SF-NSI	22.9	26.9	10.6	40.1	36.1	42.6
SF-SI	10.5	19.4	13.0	19.9	18.9	21.7
SF-COL	0.0	0.0	0.0	0.0	0.0	0.0
SF-EM	0.0	0.0	0.6	0.0	0.3	0.0
SF-ES	0.7	0.0	1.2	1.0	0.5	0.4
DF-IB	25.5	22.4	10.6	13.6	25.1	18.3
DF-IG	0.0	0.0	0.0	0.0	0.3	0.4
DF-EM	1.3	0.0	0.0	0.3	0.5	0.0
B-CS-IB	0.7	1.5	2.5	0.3	0.5	0.0
PAR-G	0.0	0.0	0.0	0.3	0.0	0.0
CS-N	0.0	0.0	0.0	0.0	0.0	0.0
CS-EM	10.5	6.0	1.2	2.8	1.4	1.3
CS-SCAPH	1.3	6.0	10.6	2.1	3.6	0.9
G-CS-IB	24.8	13.4	23.6	12.5	11.7	14.3
CS-ES	0.0	0.0	20.5	0.0	0.0	0.0
G-EM	1.3	4.5	5.6	7.0	0.3	0.0
G-P	0.0	0.0	0.0	0.0	0.0	0.0
UNASSIG	0.7	0.0	0.0	0.0	0.8	0.0
%SF	34.0	46.3	25.5	61.0	55.7	64.8
%DF	26.8	22.4	10.6	13.9	26.0	18.7
%CS	37.3	26.9	58.4	18.1	17.2	16.5
%GRAZ	1.3	4.5	5.6	7.0	0.3	0.0

	R3	**R4**	**R5**
SF-NSI	60.8	66.7	58.9
SF-SI	14.7	12.8	18.9
SF-COL	0.0	0.0	0.0
SF-EM	0.0	0.0	0.0
SF-ES	1.0	1.9	0.0
DF-IB	9.8	9.6	12.6
DF-IG	1.0	1.3	0.0
DF-EM	0.0	0.0	0.0
B-CS-IB	0.0	0.0	0.0
PAR-G	0.0	0.0	0.0
CS-N	0.0	0.0	0.0
CS-EM	2.9	3.8	2.1
CS-SCAPH	5.9	2.6	3.2
G-CS-IB	2.9	1.3	2.1
CS-ES	1.0	0.0	0.0
G-EM	0.0	0.0	0.0
G-P	0.0	0.0	0.0
UNASSIG	0.0	0.0	2.1
%SF	76.5	81.4	77.9
%DF	10.8	10.9	12.6
%CS	12.7	7.7	7.4
%GRAZ	0.0	0.0	0.0