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ORIGIN OF THE GRAYSON MICROMORPH FAUNA (UPPER CRETACEOUS) OF NORTH-CENTRAL TEXAS

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ABSTRACT—The macrofauna of the Grayson Formation (Upper Cretaceous) of Texas has been described as a micromorph fauna. Sedimentologic and paleontologic studies of the Grayson claystone in north-central Texas show that it contains a micromorph fauna. The small shell size of some of the Grayson oysters and ammonoids is probably an adaptive strategy evolved by these organisms for survival in a soft substrate environment. The small shell size of the oyster specimens *Ilymatogyra arietina* (Roemer) may be a consequence of progenesis, which is one mechanism whereby organisms can adapt to a soft substrate. Grayson pyritized specimens are probably a result of microreducing environments that developed within individual shells in the soft mud.

INTRODUCTION

THE Upper Cretaceous macrofauna of Texas has been described by Hill (1901), Adkins (1920, 1928), Cooke (1946, 1955), Perkins (1960) and Clark (1965). This fauna is characterized by abundant oysters, pectinids and small ammonoids which are preserved as pyritized internal molds. The fauna has been categorized as micromorph by Scott (1924) and Kummel (1948) because of the presence of small ammonoids.

Several explanations for the Grayson micromorph assemblage have been offered. Scott (1924) suggested that the micromorph ammonoids are stunted individuals because they lived in anaerobic waters. Later he (1940) stated that they are either small species or preserved inner whorls of larger specimens. Kummel (1948) concluded that the ammonoids are stunted individuals because the water in which they lived contained excessive iron. According to Britton & Stanton (1973), the micromorphs are juveniles killed by seasonal fluctuations in the environment.

Paedomorphosis and transportation in addition to stunting and juvenility have been identified by Mancini (1978) as major factors contributing to micromorph faunas. Two processes that produce paedomorphic organisms are progenesis and neoteny (Gould, 1977). Progenesis involves precocious sexual maturation of an organism in a morphologically juvenile stage. Neoteny is retardation of somatic development. Progenesis is the process advocated in this paper as the mechanism leading to micromorph faunas.

Progenesis is one mechanism by which organisms can adapt to fluctuating environmental conditions or to an unstable fluid substrate. Animals living in an unstable fluctuating environment must tolerate conditions that are marginal for their survival and must propagate during periods that are conducive to growth and reproduction. Early sexual maturation would be advantageous for these organisms, allowing them to reproduce during the short periods conducive to growth and reproduction.

Progenic organisms can evolve on a soft substrate, which typically consists predominantly of clay-size particles and has a high water content. Such a substrate generally has a low bearing strength and, therefore, would offer little support to epifaunal organisms. Animals which become sexually mature in the juvenile stage would be selectively favored because they would be able to reproduce before succumbing to the hazards inherent in a soft substrate environment. The hazards for these animals include sinking into the soft mud as they increase in size, having their respiratory and feeding mechanisms fouled by sediment particles that have been agitated into suspension from turbulence or biogenic activity, and/or being overturned by vagrant animals and sinking into the mud (Surlyk, 1972; Richards & Bambach, 1975).

The small body size of the progenic organisms is advantageous for survival in a soft substrate environment. Such a body plan maximizes support from the substrate by keeping the surface-to-volume ratio large, thereby reducing the force per unit area applied by the animal on the substrate (Stanley, 1970). The

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water above the sediment-water interface tends to have low concentrations of dissolved oxygen (Thayer, 1975). A small body size is beneficial for respiration under these lowered oxygen tensions, because it reduces the amount of oxygen consuming biomass and produces a higher surface-to-volume ratio for oxygen diffusion (Alexander, 1975; Thayer, 1975).

A transported micromorph fauna is formed when the smaller individuals of an assemblage are winnowed out and concentrated separately. The size uniformity within the fauna is the result of sorting by sedimentary processes.

A fauna comprised chiefly of juveniles is a consequence of a catastrophic kill-off in an immature ecosystem. The kill-off is usually precipitated by an environmental change. The organisms may thrive during normal conditions but then are killed before they reach maturity. The catastrophic event may be seasonal or at indefinite intervals of time, but the kill-off must affect each generation to result in a micromorph fauna recognizable in the fossil record.

Stunting is a nongenetic condition which results from some physical or chemical abnormality in the environment. The stunted condition can be corrected during the lifetime of the individual through elimination of the abnormality causing the stunting. Stunting implies a reduction in the rate of growth during a particular season but not a reduction in the duration of life span.

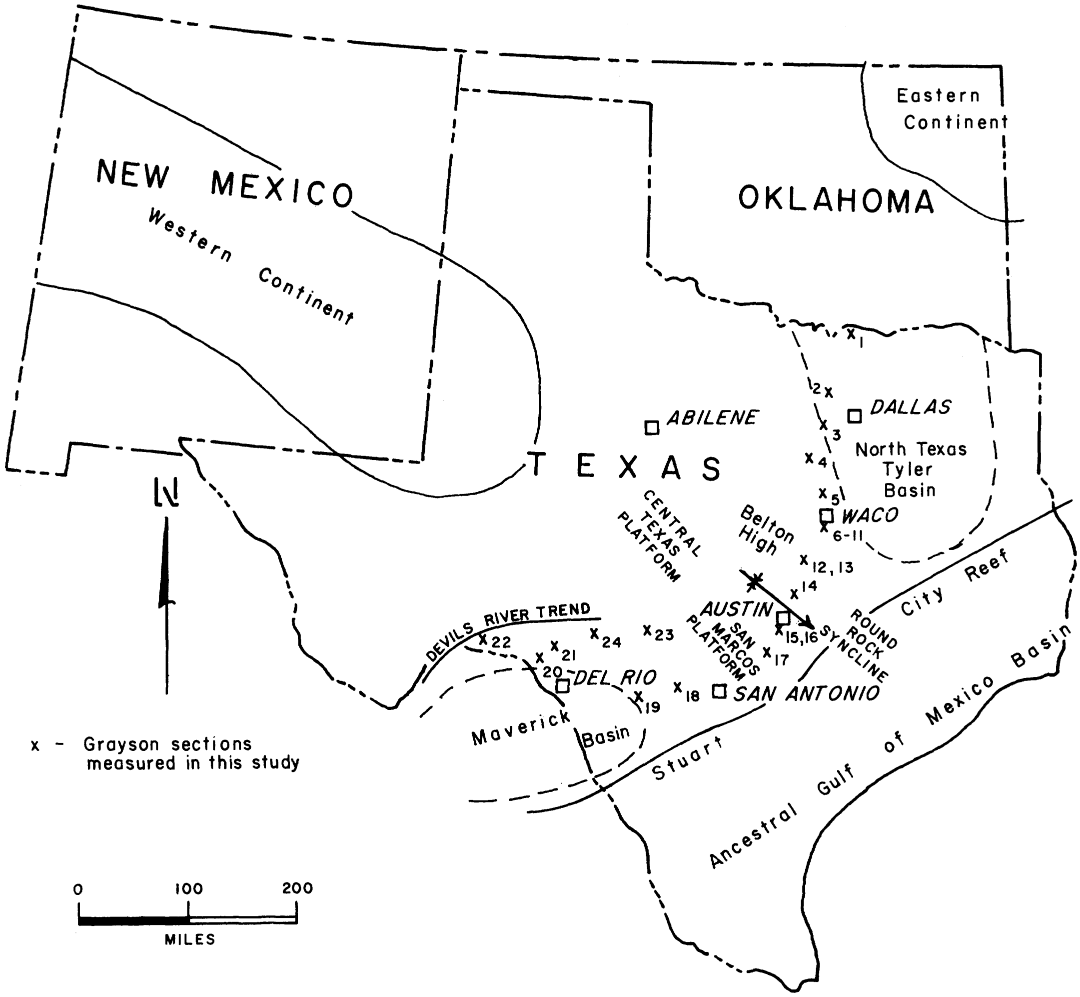
Certain characteristics of micromorph faunas and the associated sedimentary rocks are useful in recognizing the various micromorph faunas. A listing of those parameters which can be utilized in recognizing the respective micromorph faunas is presented below. See Mancini (1978) for a complete discussion of the characteristics which are potentially diagnostic in distinguishing the various origins of micromorphs.

Populations comprised of stunted organisms are characterized by a normal age distribution, a moderately positively skewed size-frequency distribution and a sigmoidal survivorship curve. Growth is typically slow and, therefore, individuals of a smaller body size than normal exhibit ornamentation characteristic of sexually mature organisms. Faunal diversity is usually low because marginal living conditions are present. Other lines of evidence, such as trophic structure, trace fossils, microfaunal composition and sediment geochemistry, are useful in recognizing stunted micromorphs.

The shells of micromorphs resulting from sorting by sedimentary processes usually are more broken, abraded and altered than the shells of micromorphs originating by the other mechanisms. These populations typically have a narrow and symmetric size-frequency distribution which reflects size sorting. Some evidence of the sedimentary process, such as stratification, may be evident in the associated sedimentary rocks. Elongate fossils present may show some preferred orientation as a result of current or wave activity.

Juvenile populations are characterized by a highly positively skewed size-frequency distribution and a rapidly decreasing survivorship curve. Growth is terminated in the juvenile stage; therefore, individuals exhibit immature ornamentation. Faunal diversity is low because these micromorphs are part of an immature ecosystem which never attains a high level of stability. Without stability, diversity does not increase through niche subdivision and specialization (Hutchinson, 1959). Because these faunas are most likely replenished from adjacent areas after a kill-off, geographic isolation probably did not occur.

Populations comprised predominantly of progenic organisms are characterized by a moderately to highly positively skewed size-frequency distribution and a decreasing, then linear or linear survivorship curve. Growth is rapid and early sexual maturation of the organism still in a morphologically juvenile stage occurs. As a consequence, normal adult and gerontic animals are rare. Faunal diversity is low to moderate depending on the instability of the environment. The trophic structure of a community associated with a soft substrate is generally dominated by filter-feeding organisms having morphologic adaptations for survival on a fluid substrate (Carter, 1972). Geographic isolation is necessary for these populations to be maintained. Without geographic isolation the progenic effect would be diluted by the accumulation of juveniles that could not adapt to the unstable conditions of a soft substrate or fluctuating environment. The progenic individuals present in these predominantly juvenile populations would be difficult to recognize in the geologic record. Other lines of evidence include trace fossils, micro-



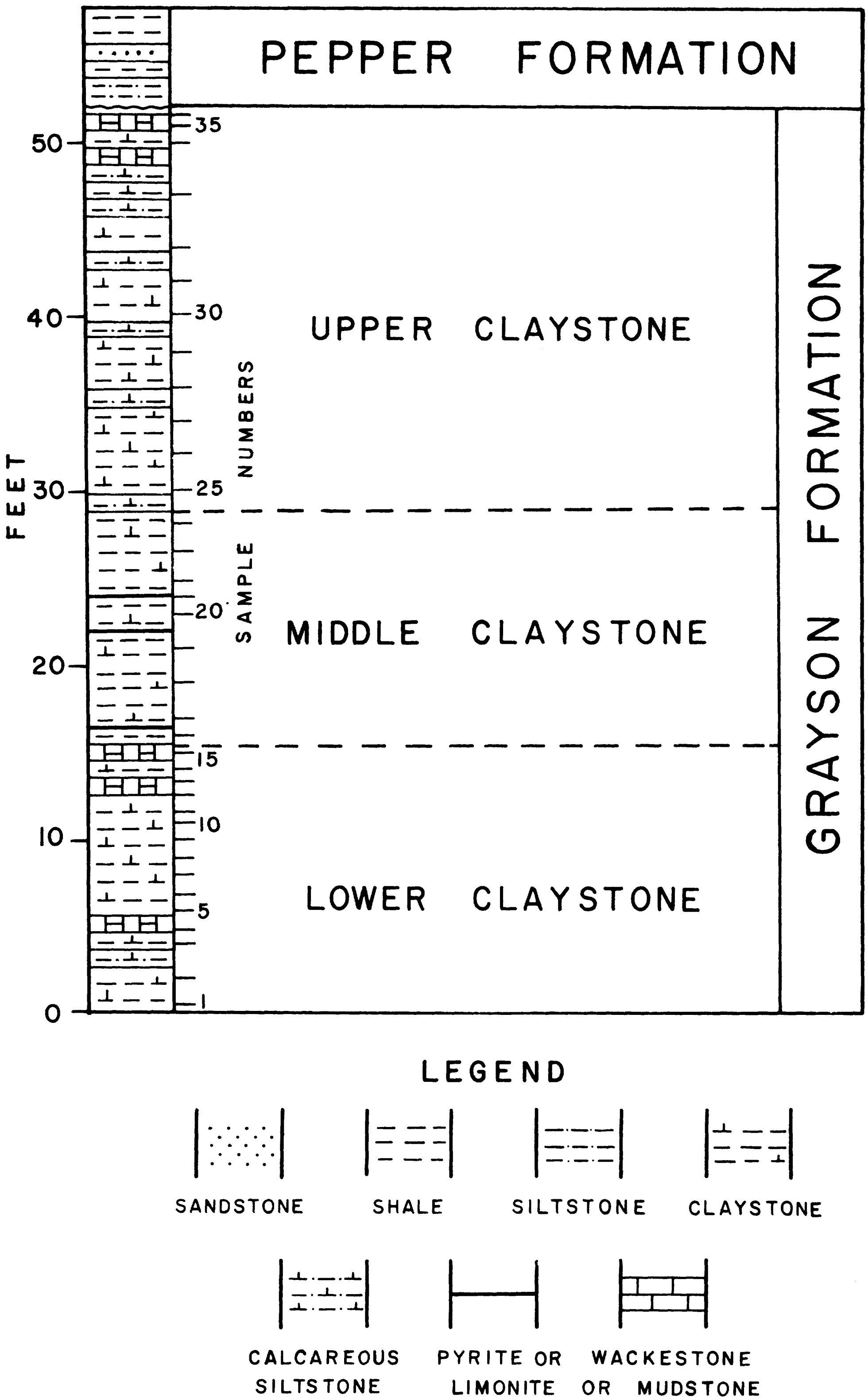
TEXT-FIG. *1*—Major structural features controlling the deposition of Late Washita sediments, and Grayson sections measured in this study (modified from Tucker, 1962; Smith, 1970; Rose, 1972).

faunal composition and sediment texture and geochemistry.

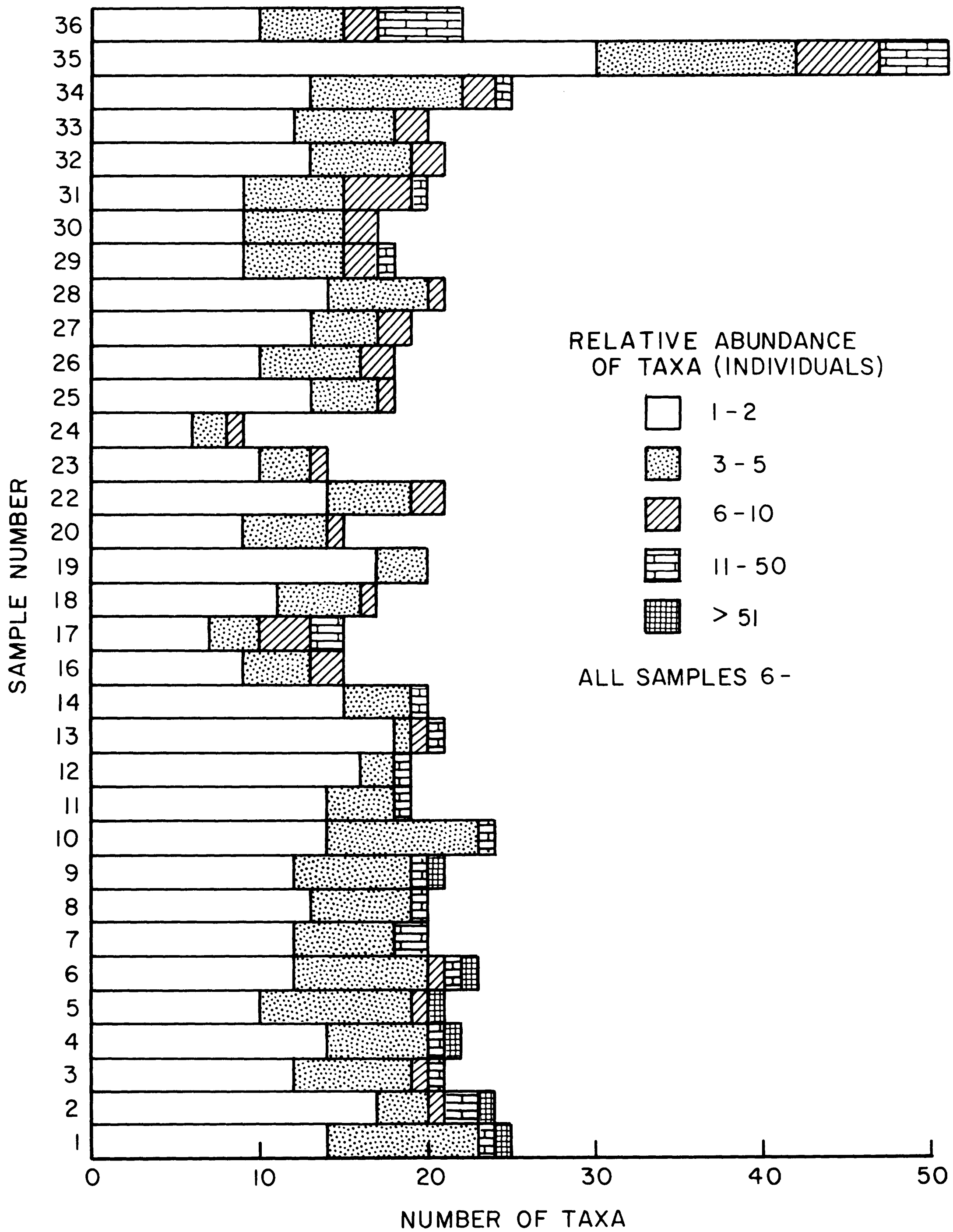
The objective of this paper is to determine whether the Grayson micromorphs are a consequence of stunting, juvenility, transportation or progenesis. The Grayson Formation and fauna have been studied from the Rio Grande to the Red River. The primary source of faunal and sedimentologic data is from the Waco Spillway (measured section 6) because the micromorphs are most abundant in this area (Text-fig. 1). The measured sections located in Text-fig. 1 are described in detail by Mancini (1977).

GRAYSON SEDIMENT AND FAUNAL CHARACTERISTICS

General statement.—The Grayson Formation in the area between the Central Texas Platform and the Stuart City Reef Trend (Text-fig. 1) is characterized by sediments and fauna indicative of normal marine inner to middle neritic depositional conditions (Mancini, 1977). The major structural features controlling deposition were the San Marcos and Central Texas Platforms and the North Texas Tyler and Maverick Basins (Winter, 1962; Rose, 1972). The formation is remarkably uniform in thickness, 24–30 m (80–100 ft), in out-



TEXT-FIG. 2—Waco Dam Spillway measured section, Waco, McLennan County, Texas.



TEXT-FIG. *3*—Macrofaunal richness (number of taxa) and equitability (relative abundance of taxa) at the Waco Spillway section, McLennan County, Texas. Each bar of the histogram represents the total number of taxa, and the subdivisions in a bar depict the number of taxa that represent 1–2, 3–5, 6–10, 11–50, or more than 51 individuals in the assemblage. See Text-fig. 2 for sample number elevation.

crop, and it consists of a gray or brown calcareous claystone interbedded with white nodular wackestone, brown, thin-bedded calcareous siltstone and/or brown or red weathering laminated or massive mudstone (Mancini, 1977). The thickness of the Grayson Formation in the area of the Waco Spillway is 24.4 m (80 ft) (Adkins, 1924, 1933).

Although predominantly normal marine conditions prevailed throughout Grayson deposition, there were variations in the physical environment as evidenced by the vertical sediment and faunal changes in the Waco Spillway section. At this locality the Grayson Formation can be divided into a lower calcareous claystone interbedded with mudstone, a middle claystone interlaminated with pyritic or limonitic seams and an upper calcareous claystone interbedded with siltstone and nodular wackestone (Text-fig. 2).

Macrofaunal composition.—The Grayson fauna is of moderate diversity and consists of numerous stenohaline benthic invertebrates, including some infaunal organisms. The fauna consists of sponges, corals, bryozoans, bivalves, gastropods, nautiloids, ammonoids, belemnoids, asteroids, regular and irregular echinoids, crinoids, annelids, elasmobranchs, holosts and teleosts. For a complete listing of the Grayson macrofossils identified in this study see Mancini (1977, table 2).

At the Waco Spillway section the composition and diversity, including richness and equitability, change vertically in the section. Richness is measured as the total number of taxa present, and equitability is measured as the number of individuals present per taxon. Richness is high and equitability is low in the lower claystone (Text-fig. 3). This claystone is characterized by numerous specimens of the oyster *Ilymatogyra arietina* (Roemer) and the heteromorph ammonoids *Mariella (Plesioturrilites) bosquensis* (Adkins) and *Scaphites subevolutus* Bose. Richness is low and equitability is high in the middle claystone. This claystone is typified by the oyster *Texigryphaea roemeri* (Marcou) and pyritized bivalves, gastropods and cephalopods. The upper claystone has moderate richness and equitability and is characterized by *T. roemeri* and pectinids. The nodular wackestone associated with the upper claystone has the highest richness and equitability. Ammonoids are the predominant invertebrates here.

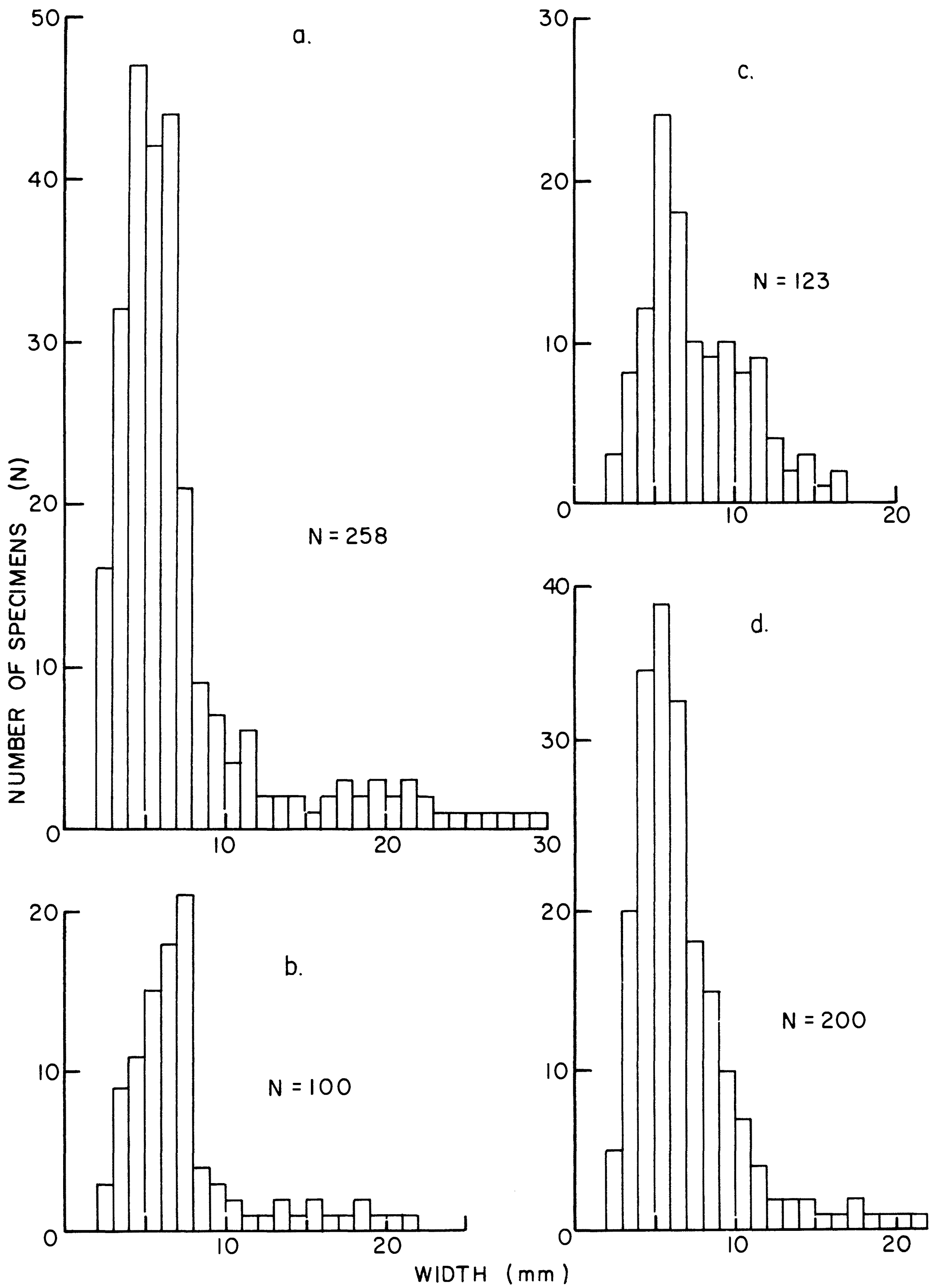
The moderate diversity of the fauna suggests that neither abnormal salinity nor low oxygen conditions prevailed during Grayson deposition. Low faunal diversity is common in present-day hyposaline (Segerstrale, 1957) and low oxygen (Caspers, 1957) seas and may be characteristic of ancient hypersaline environments (Hallam, 1965). The presence of stenohaline animals also indicates that normal salinities persisted during Grayson deposition. Low salinity environments conspicuously lack normal marine stenohaline animals such as corals, bryozoans, echinoderms and cephalopods (Segerstrale, 1957; Vogel, 1959b). The abundance of benthic organisms, including some infaunal animals, implies that bottom conditions were not toxic.

The moderate Grayson faunal diversity indicates that this environment was moderately stable, for high diversity is associated with high environmental stability (Sanders, 1968; Valentine, 1971). The Grayson environment, therefore, was not subjected to large scale fluctuations in environmental conditions nor was it part of an immature ecosystem. Low diversity is associated with fluctuating unstable environments (Valentine, 1971) and with immature ecosystems (Hutchinson, 1959; Gouldren, 1969). A soft substrate may have been present in the Grayson environment for such environments commonly have moderate diversity (Mancini, 1978).

The Grayson macrofaunal trophic structure is dominated by epifaunal filter-feeding organisms (Mancini, 1977). The upper claystone and lowermost part of the middle claystone support the highest percentage of detritus-feeding animals at the Waco Spillway section. Infaunal organisms are abundant in the middle claystone and are least common in the lower claystone in this section. See Mancini (1977, table 2) for a listing of feeding types for specific genera.

A trophic structure dominated by epifaunal filter-feeding organisms may be typical of a fluid substrate. The bivalve fauna of the Upper Cretaceous Chalk Formation of England is also dominated by epifaunal filter-feeding organisms (Carter, 1972).

The British bivalves adapted to life on a soft substrate with the life habits of swimming, byssal attachment, cementation and secretion of a gryphaeate lower valve (Carter, 1972). The Grayson bivalves associated with the

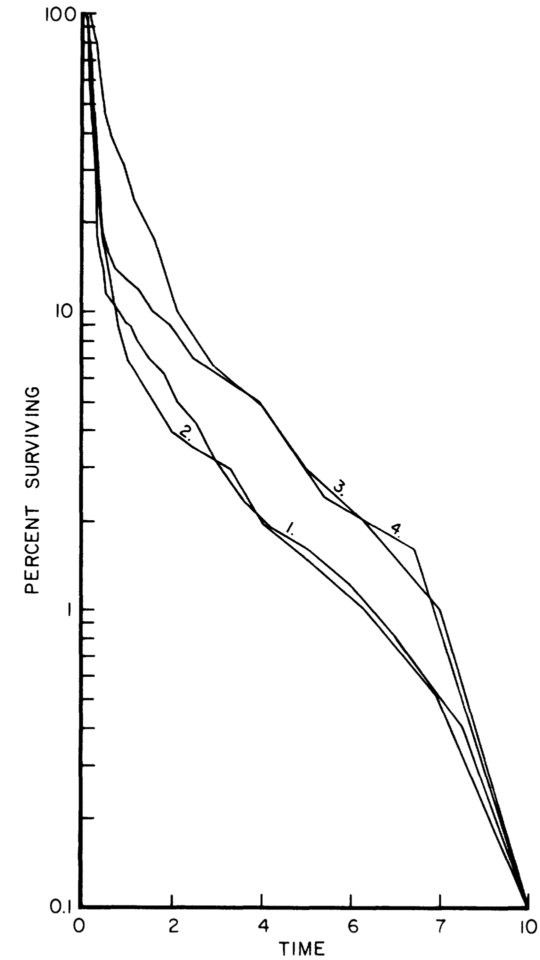


TEXT-FIG. 4—Size-frequency histograms for populations of the oyster *Ilymatogyra arietina* from *a,* the basal beds from north-central Texas; *b,* south-central Texas; *c*, the Waco Spillway section, McLennan County, Texas; and *d*, southwest Texas.

claystone developed similar morphologies. They adapted to the Grayson fluid substrate by being cemented, attached by a byssus, anchored by supporting structures or by secretion of a gryphaeate lower valve. The oysters *Ostrea perversa* Cragin, *Pycnodonte* sp. and *Anomia* sp. were cemented to local hard substrates comprised primarily of shell material. The bivalves *Striarca washitensis* (Adkins) and *Phelopteria* sp. were attached by a byssus to local hard substrates, such as shells. The pectinid *Plicatula incongrua* Conrad was anchored to the substrate by supporting structures. The oyster *Texigryphaea roemeri* and the pectinids *Neithea subalpinus* (Bose) and *N. texanus* (Roemer) secreted a gryphaeate lower valve.

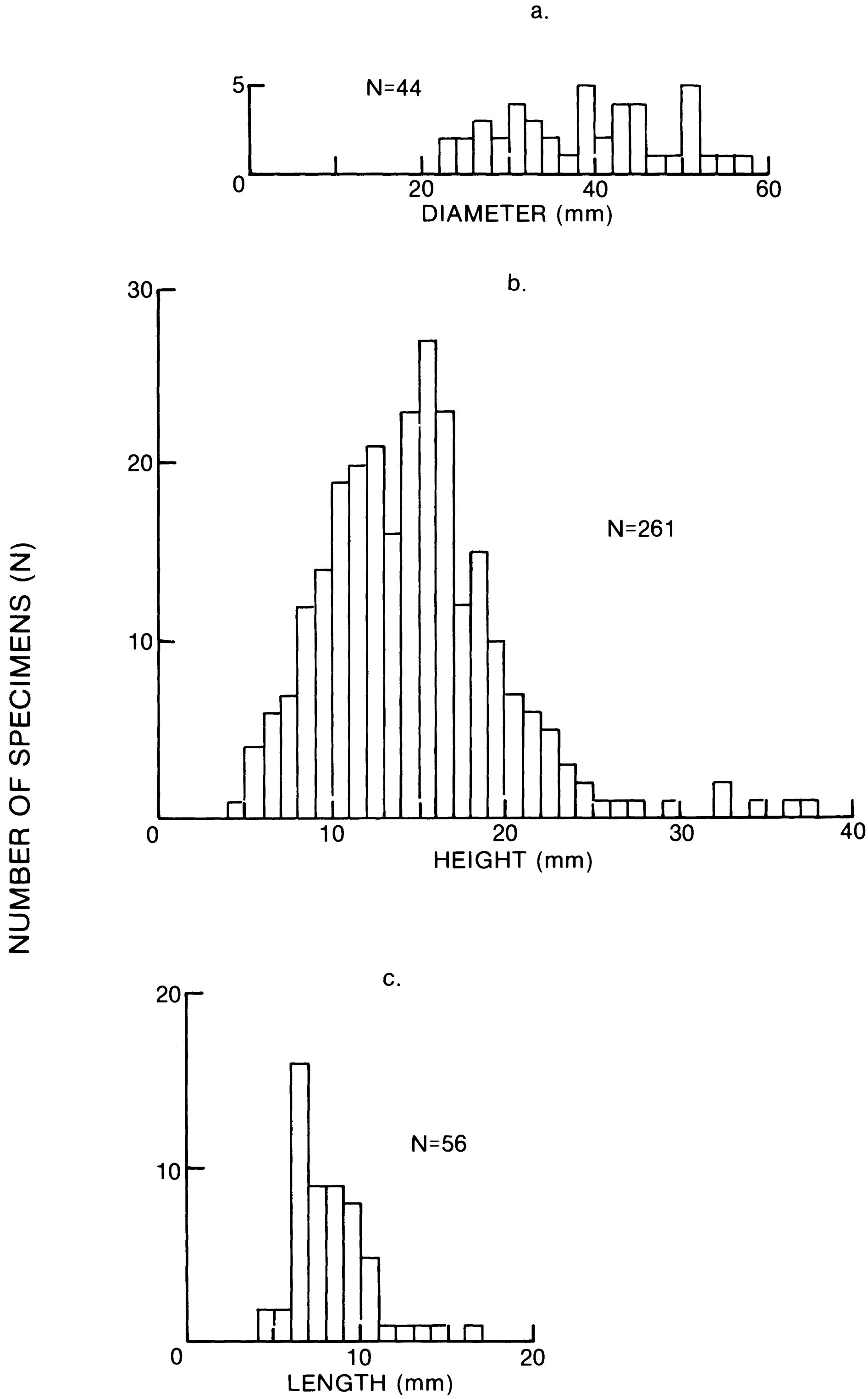
Population dynamics.—Most of the specimens contained in the lower and middle claystone are small in body size. Only a few small specimens occur in the upper claystone and none in the wackestone. Echinoids, gastropods and most of the bivalves are of normal shell size throughout the section. Their shell sizes fall into the range of natural variability reported by Stanton (1947), Stephenson (1952, 1953), Perkins (1960) and Scott (1970) for Comanchean molluscs and by Cooke (1946, 1955) for Comanchean echinoids. The cephalopods and corals of the claystone are of a smaller shell size than normal. These specimens are small in shell size compared to the dimensions reported for Comanchean nautiloids by Miller & Harris (1945), ammonoids by Hyatt (1903) and Collignon (1964), and corals by Wells (1933).

The morphology of the oyster *Ilymatogyra arietina* differs from north-central to southwest Texas; therefore, its population dynamics were studied at a number of Grayson localities. The size-frequency histograms (Text-fig. 4) and survivorship curves (Text-fig. 5) suggest that throughout Texas these oyster populations consist of a large number of juveniles and a few adult and gerontic animals. Such population dynamics are typical of the majority of Grayson invertebrate populations. Size-frequency histograms and survivorship curves representative of the Grayson populations are illustrated in Text-figs. 6 and 7 and Text-figs. 8 and 9, respectively. The size-frequency histograms and survivorship curves for the remainder of the Grayson populations are illustrated in Mancini (1974, Ph.D. dissertation, Texas A&M).

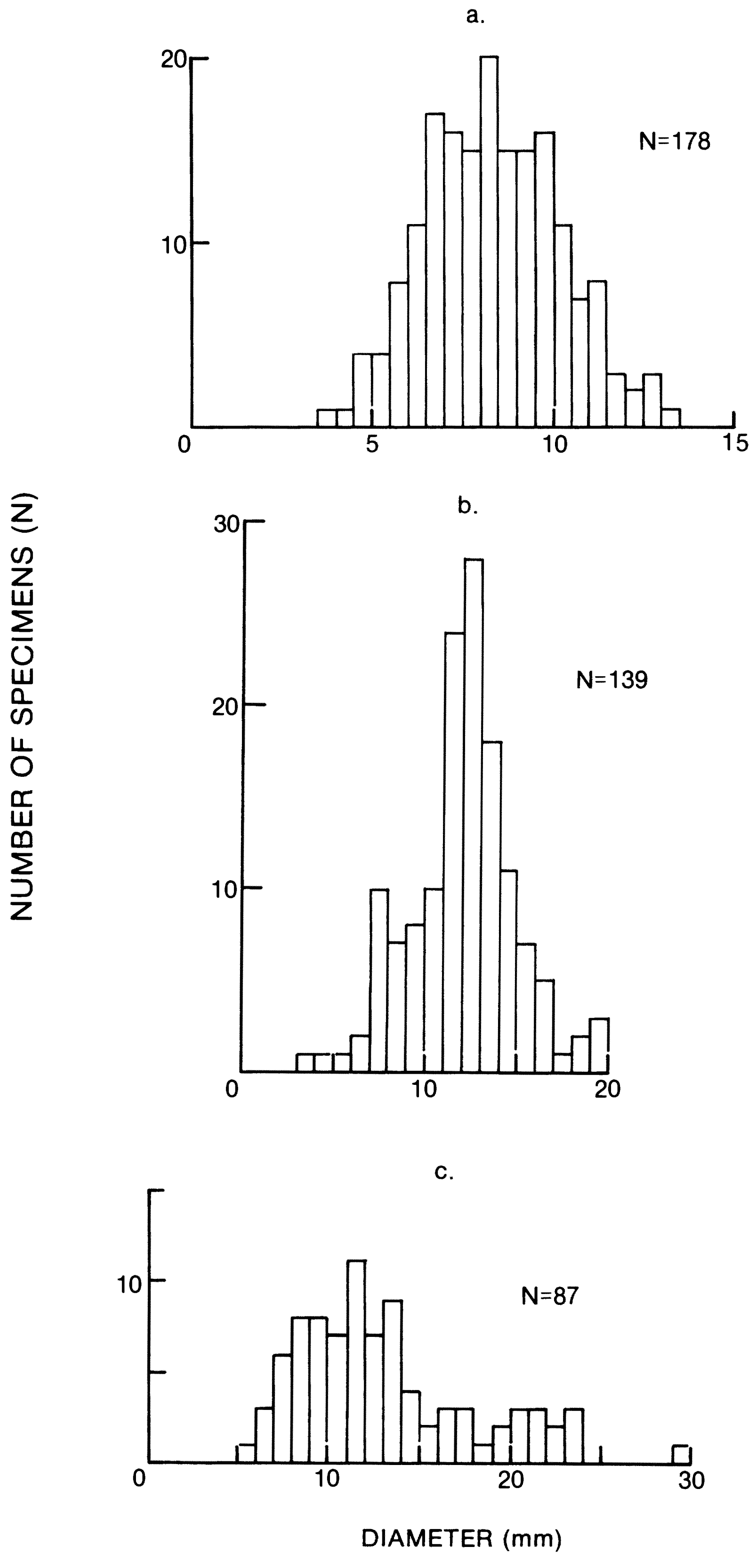


TEXT-FIG. 5—Survivorship curves for populations of the oyster *Ilymatogyra arietina* from *1*, the basal beds from north-central Texas; *2*, south-central Texas; *3*, the Waco Spillway section, McLennan County, Texas; and *4*, southwest Texas.

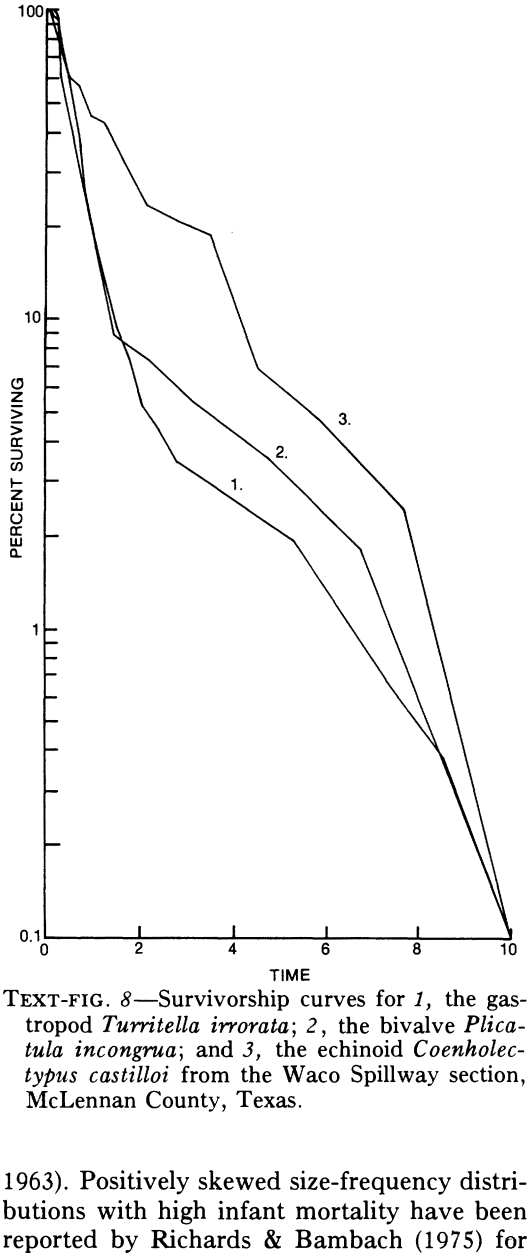
Most of the Grayson populations are characterized by symmetric or positively skewed size-frequency histograms (Text-figs. 4, 6, 7; Mancini, 1974, text-figs. 16–19, Ph.D. dissertation, Texas A&M). Although a narrow and symmetric size-frequency distribution can be representative of a transported assemblage (Fagerstrom, 1964; Mancini, 1978), such a distribution can also be characteristic of living bivalve populations that have not been sorted by sedimentary processes (Craig & Hallam,



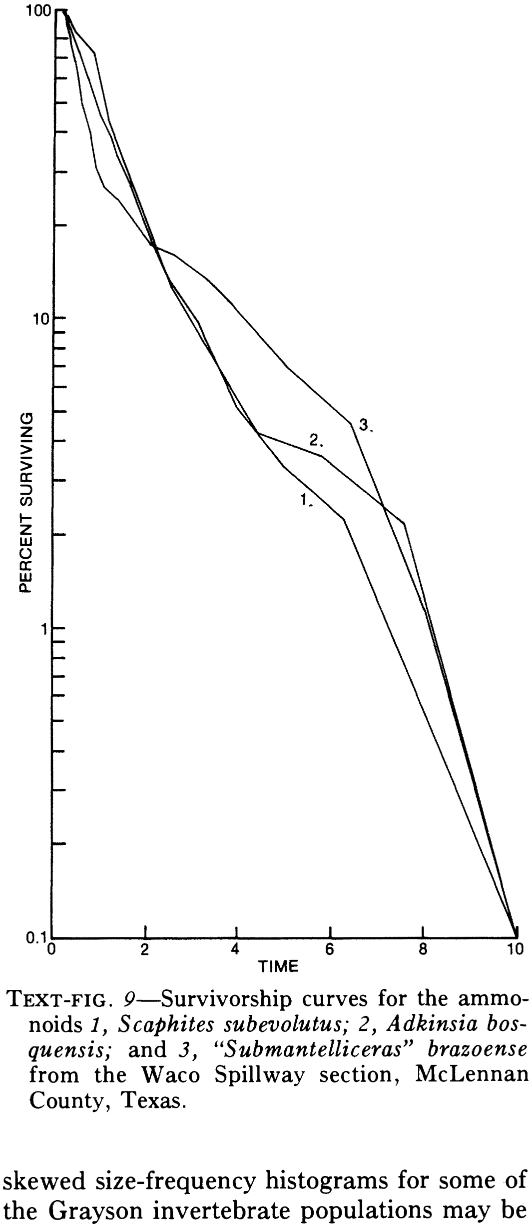
TEXT-FIG. 6—Size-frequency histograms for populations of *a,* the echinoid *Coenholectypus castilloi; b,* the gastropod *Turritella irrorata*; and *c*, the bivalve *Plicatula incongrua* from the Waco Spillway section, McLennan County, Texas.



TEXT-FIG. 7—Size-frequency histograms for populations of the ammonoids *a*, *Scaphites subevolutus; b*, *Adkinsia bosquensis;* and *c*, *"Submantelliceras" brazoense* from the Waco Spillway section, McLennan County, Texas.



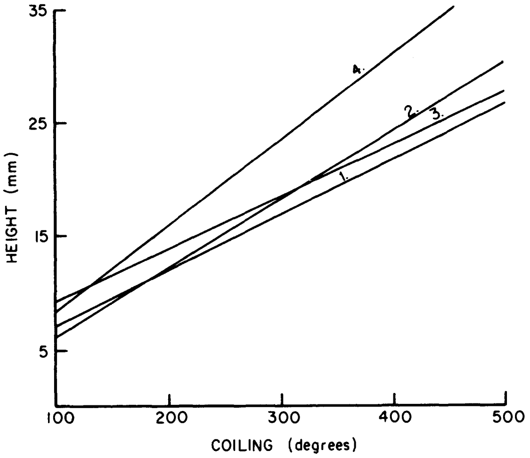
TEXT-FIG. *8*—Survivorship curves for *1,* the gastropod *Turritella irrorata*; *2,* the bivalve *Plicatula incongrua*; and *3,* the echinoid *Coenholectypus castilloi* from the Waco Spillway section, McLennan County, Texas.



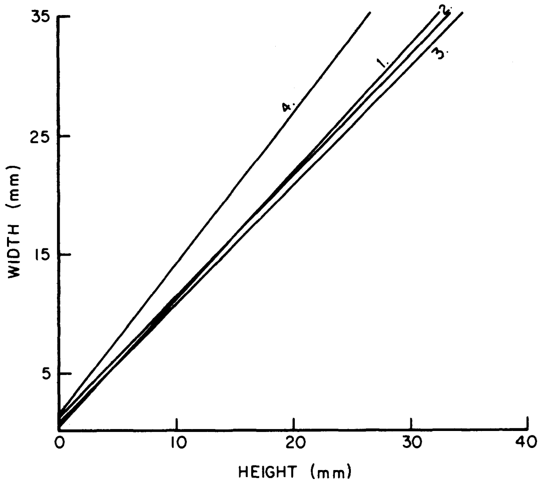
TEXT-FIG. *9*—Survivorship curves for the ammonoids *1, Scaphites subevolutus; 2, Adkinsia bosquensis;* and *3, "Submantelliceras" brazoense* from the Waco Spillway section, McLennan County, Texas.

1963). Positively skewed size-frequency distributions with high infant mortality have been reported by Richards & Bambach (1975) for Ordovician brachiopod populations which inhabited muddy bottoms where suitable attachment surfaces were rare. Moderately positively skewed size-frequency distributions can be representative of populations comprised of stunted individuals or progenic organisms inhabiting an unstable environment (Mancini, 1978). Highly positively skewed size-frequency distributions can be representative of populations composed of juveniles or progenic animals living on a soft substrate. The positively skewed size-frequency histograms for some of the Grayson invertebrate populations may be a consequence of their living in a soft substrate environment.

The survivorship curves for the Ordovician brachiopods revealed a high rate of infant mortality followed by a lower mortality rate for older ages (Richards & Bambach, 1975). Such a survivorship curve has been described by Mancini (1978) as decreasing, then linear. The survivorship curves for most of the Grayson invertebrate populations are sigmoidal (Text-figs. 5, 8, 9; Mancini, 1974, text-figs. 21–24, Ph.D. dissertation, Texas A&M).



TEXT-FIG. *10*—Shell morphological change (height versus degree of coiling) in the oyster *Ilymatogyra arietina* from different Texas localities: *1*, southwest Texas; *2*, south-central Texas; *3*, basal beds from north-central Texas; and *4*, Waco Spillway section, McLennan County, Texas.

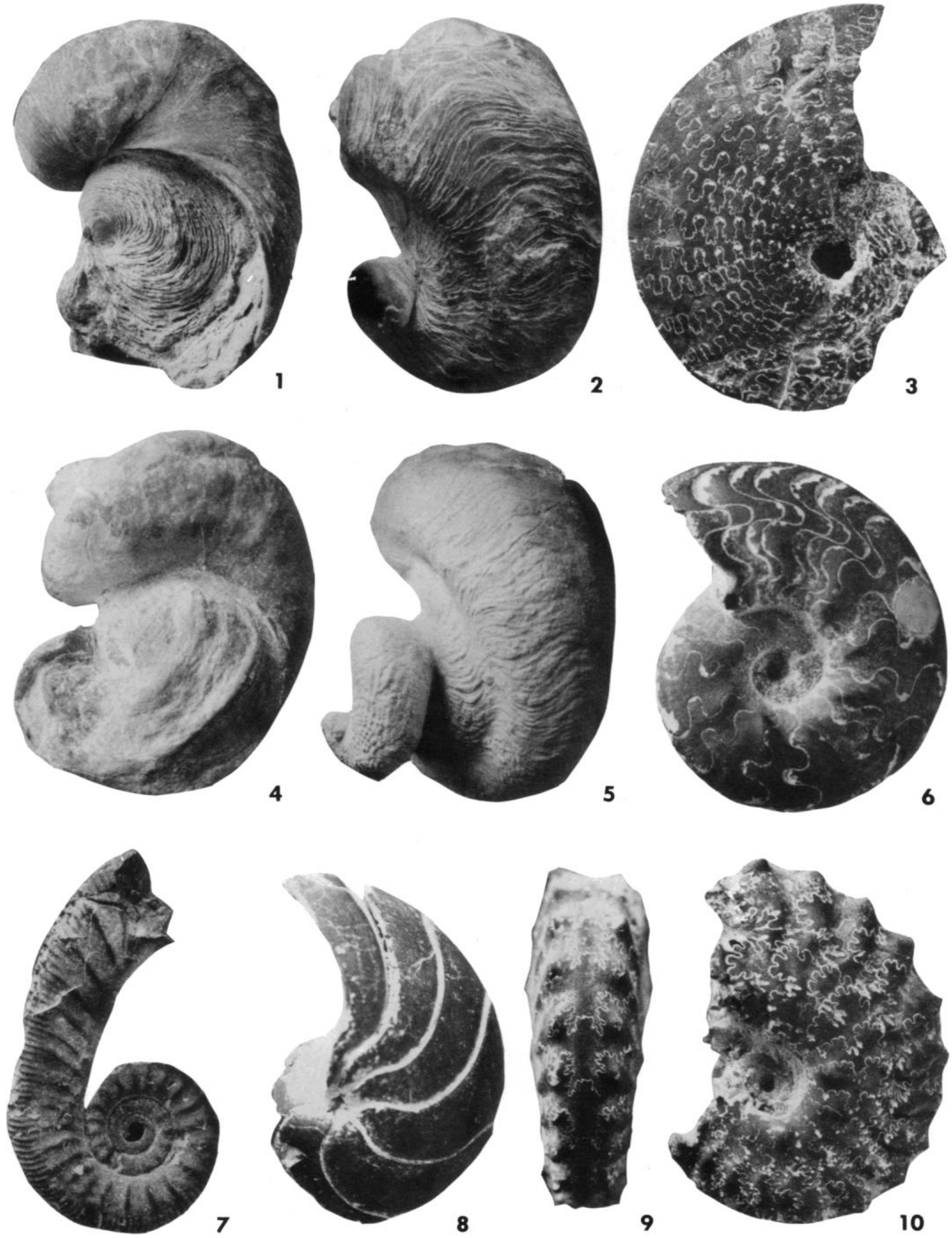


TEXT-FIG. *11*—Shell morphological change (width versus height) in the oyster *Ilymatogyra arietina* from different Texas localities: *1*, southwest Texas; *2*, south-central Texas; *3*, basal beds from north-central Texas; and *4*, Waco Spillway section, McLennan County, Texas.

Probably the major reason that the Grayson invertebrate populations do not have survivorship curves similar to those for the Ordovician brachiopods (Richards & Bambach, 1975, text-fig. 14b) is that Grayson animals were free-living. The life habits of the Grayson epifaunal bivalves have been identified, and a discussion of the life habits of some of the oysters and ammonoids will follow. Free-living animals inhabiting a soft bottom environment do not have to contend with the same hazards as attached invertebrates and, therefore, mortality rates for these animals may be reduced. Free-living organisms do not have to compete for available attachment space. Mobile benthic gastropods and heteromorph ammonoids are less likely to sink into the mud with increasing size or as a result of being overturned. Nektonic cephalopods searching for prey in the water column are not as likely to have their respiratory mechanisms fouled by sediment particles suspended above the sediment-water interface. They do not have to contend with the lowered oxygen tensions that are common in the water above the sediment-water interface.

The oyster specimens of *Ilymatogyra arietina* from southwest (Val Verde and Terrell Counties), and south-central (Bell through Hays, Medina and Uvalde Counties) Texas and from the basal Grayson beds of north-central (McLennan through Denton Counties) Texas probably lived on a firm substrate in a nearshore environment with a moderate sedimentation rate (Mancini, 1977). The highly coiled lower valve of these oysters may have been an adaptation to elevate these suspension-feeding organisms off the bottom and provide better access to the plankton present in the water column. The oyster populations from the lower Grayson beds in north-central Texas have individuals with lower valves which are not as coiled (Pl. 1, figs. 1, 2, 4, 5; Text-fig. 10). These oysters also have a higher width-to-height ratio (Text-fig. 11) than the lower valves of the typically coiled oysters. In addition, the oysters from the Waco Spillway section do not exhibit the typical ornamentation as described by Bose (1919). Instead, the majority of the oysters from the Waco Spillway section develop smooth ornamentation at a smaller body size than normal resulting in an abbreviated ribbed stage. The smooth ornamentation is characteristic of sexually mature individuals (Bose, 1919).

The lower valve morphology of the oysters from the Waco Spillway section is broad and flat, approximating a gryphaeate lower valve. A gryphaeate shape increases support for organisms living on soft muds by permitting only partial submergence of the animal. This lim-



EXPLANATION OF PLATE 1

FIGS. *1,2*—*Ilymatogyra arietina* (Roemer). Progenic adult with a broad and flat lower valve from the Waco Spillway section, TAMU 102, ×1.9. Figured specimens are assigned Texas A&M University (TAMU) repository numbers and are stored in the Geology Department Repository, Texas A&M University, College Station, Texas.

3—*Engonoceras bravoense* Bose. Lateral view of TAMU 113, ×2.4.

4,5—*Ilymatogyra arietina* (Roemer). Normal adult with a coiled lower valve from southwest Texas, TAMU 101, ×2.

ited sinking provides a broader bearing surface, enhances buoyancy and allows contact with the underlying sediment which may be firm and sufficient to support the organism (Thayer, 1975). With such an adaptation, the commissure can be maintained above the sediment-water interface in a near horizontal position (Carter, 1972). This commissure orientation would provide more surface area for feeding, cleansing and respiration. The hazards of living in a soft substrate environment include lowered oxygen tensions and the presence of clastic particles suspended in the water above the sediment-water interface (Alexander, 1975; Thayer, 1975). The availability of additional surface area for cleansing, feeding and respiration would be an asset, therefore, to suspension-feeding organisms living on a fluid substrate. Precocious sexual maturation is another means by which these animals adapted to their environment. The progenic oysters would have the opportunity to reproduce and perpetuate their species before sinking into the soft mud because they increased in size or because they were overturned by vagrant animals.

The small cephalopods are small adult animals, juveniles or the preserved inner whorls of larger individuals. The preservation of part of the living chamber and the more closely spaced last few sutures of *Scaphites subevolutus* (Pl.1, fig. 7; Text-fig. 12) suggest that this ammonoid was of small body size as an adult. Adult ammonoids are characterized by the last few sutures being more closely spaced. With the attainment of sexual maturity, growth probably slowed down in these animals resulting in the septa or suture lines becoming more closely spaced (Callomon, 1963). The plots of suture spacings versus whorl width plus height are drawn after the method employed by Vogel (1959a) for recognizing stunted ammonoids. Although the last few sutures are more closely spaced on *Adkinsia bosquensis* (Adkins), there is an overall irregularity to the suture spacings (Pl. 1, fig. 6; Text-fig. 13). Part of the living chamber is preserved on several specimens of this species, however, implying this ammonoid was of small body size as an adult. The absence of any evidence of the living chamber and the more or less evenly spaced suture pattern of the nautiloid *Cymatoceras* n. sp. (Pl. 1, fig. 8), and the ammonoids *Engonoceras bravoense* Bose (Pl. 1, fig. 3) and *"Submantelliceras" brazoense* (Bose) (Pl. 1, figs. 9, 10; Text-fig. 14) indicate that these organisms are either juveniles or the preserved inner whorls of larger individuals.

The small body size of the Grayson heteromorph ammonoids is probably a consequence of a soft substrate. Heteromorph ammonoids such as *Scaphites* are mobile benthic organisms (Scott, 1940) and, therefore, the nature of the substrate affects their morphological adaptations. The Grayson heteromorphs probably remained small in size to prevent their foundering as they rested on the soft mud. Also, a small body size is beneficial for respiration under lowered oxygen tensions.

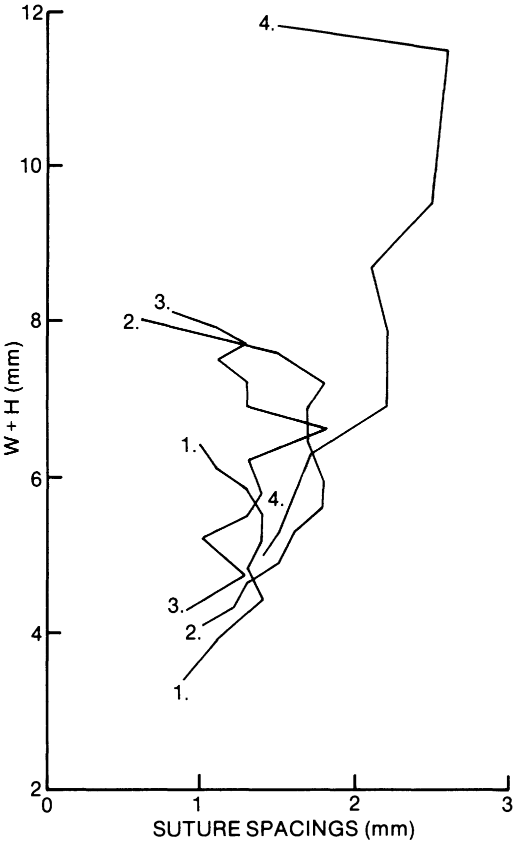
The squat shell morphology of *Adkinsia* suggests this necto-benthic ammonoid was not a good swimmer (Scott, 1940). It probably searched for prey swimming close to the bottom, resting occasionally. This mode of life subjected this ammonoid to the hazards of a soft mud substrate. The small body size of this organism is probably an adaptation to a soft substrate and the associated conditions.

The streamlined shell morphology of the mantellicerids and engonocerids suggests that these ammonoids were good swimmers (Scott, 1940). They probably searched for prey in the water column. The type of substrate present is not critical for this mode of life and, therefore, a small body plan as an adaptation to fluid substrate conditions did not evolve.

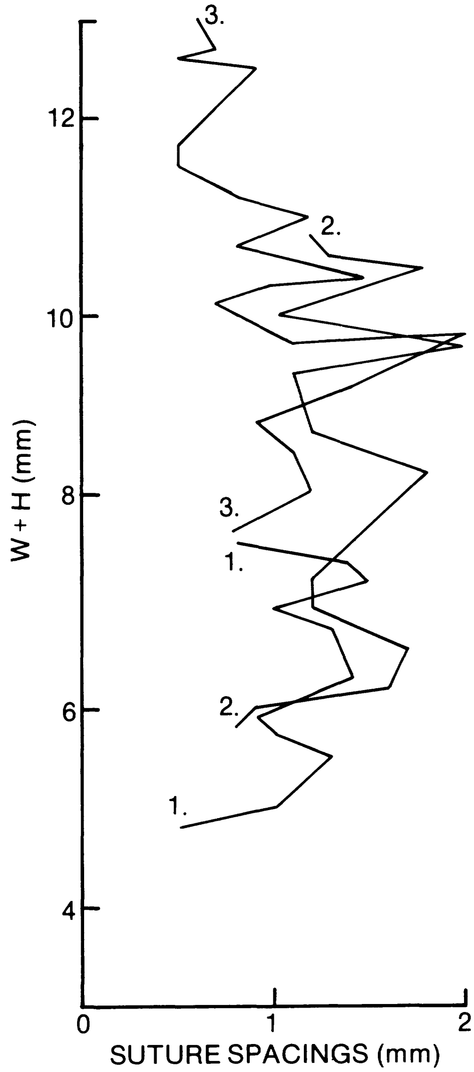
Condition and orientation of individuals in the fossil assemblage.—The Grayson fossils are well preserved, implying that they have had little or no transportation. The shells are not abraded or excessively broken. The spines

←

6—*Adkinsia bosquensis* (Adkins). Lateral view of TAMU 115, ×3.6.
7—*Scaphites subevolutus* Bose. Lateral view of TAMU 111, ×3.
8—*Cymatoceras* n. sp. Lateral view of TAMU 129, ×2.7
9,10—*"Submantelliceras" brazoense* (Bose). *9*, ventral view and *10*, lateral view of TAMU 124, ×3.2.



TEXT-FIG. *12*—Plot of suture spacings versus whorl width (W) + whorl height (H) for four specimens of the ammonoid *Scaphites subevolutus*.



TEXT-FIG. *13*—Plot of suture spacings versus whorl width (W) + whorl height (H) for three specimens of the ammonoid *Adkinsia bosquensis*.

are still evident on some of the echinoids. Numerous oyster and pectinid individuals are articulated. Oyster individuals from the middle claystone in north-central Texas appear to be in living position. There is no evidence of preferred orientation of any of the elongate fossils present.

Many of the tightly coiled taxa such as ammonoids and gastropods are preserved as pyritized internal molds. The number of pyritized macrofossils fluctuates vertically and laterally in the formation, but the lower and middle claystone in north-central Texas have the most pyritized fossils.

The pyritized macrofossils are probably a result of microreducing environments that developed within individual shells in the soft mud. When animals die in a soft substrate environment, their shells sink quickly into the mud prior to bacterial decomposition. Decay of the carcasses takes place in the mud, creating microreducing environments within the shells. The pyritized molds of the Grayson ammonoids, gastropods, infaunal bivalves and bivalves attached by a byssus are a result of such a process. In such an environment organisms that are not buried prior to decomposition would not be preserved as pyritized molds. The Grayson epifaunal bivalves that were cemented, anchored by supporting structures or secreted a gryphaeate lower valve are not usually pyritized.

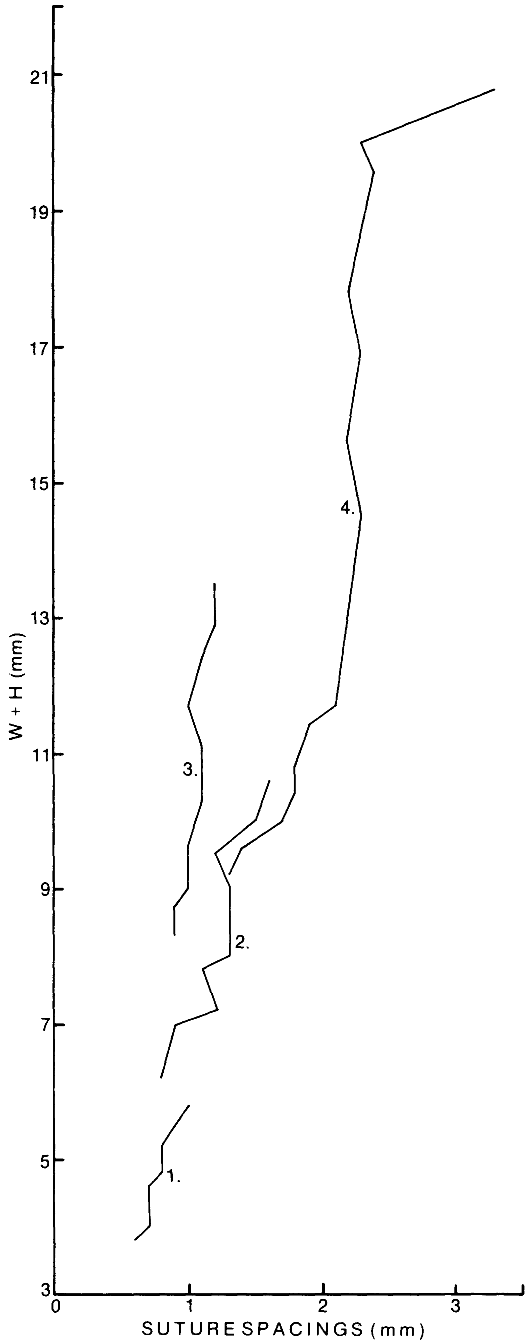
Trace fossils.—Trace fossils are present in the Grayson Formation, but a high degree of bioturbation is not evident. Horizontal tubular burrows 0.1 mm in diameter are present in the claystone and mudstone in north-central Texas. Many of these burrows are filled with pyrite. In north-central Texas, wispy burrows with indistinct boundaries form the predominant traces in the claystone. *Chondrites* is rare in the siltstone interbedded with the upper claystone. *Thalassinoides* is present in the laminated mudstone in southwest Texas and in the nodular wackestone interbedded with the upper claystone and siltstone interbedded with the basal claystone in north-central Texas.

The absence of extensive bioturbation and the presence of wispy burrows with indistinct boundaries in the claystone suggest that in north-central Texas, Grayson depositional conditions included a fluid substrate. Animals find it difficult to locomote and maintain burrows in sediments with high substrate fluidity. Movement of saturated sediments tends to collapse animal burrows and results in unstable conditions for infaunal organisms (Faas, 1972). Many burrowing organisms discriminate against these environments. Also, the nature of fluid sediments is not conducive to the preservation of burrows. The only traces that are commonly preserved in such sediments are wispy burrows with indistinct boundaries (Rhoads, 1970).

The shells contained in the claystone in north-central Texas are not extensively bored or encrusted. The oyster shells associated with the wackestone, however, are highly bored by clionid sponges and encrusted with membraniporids and serpulid worm tubes.

The absence of encrusting organisms on the shells contained in the Grayson claystone suggests that this mud formed a soft substrate. Encrusting animals such as bryozoans discriminate against soft substrates where clay and silt are suspended above the sediment-water interface (Alexander, 1975). The presence of encrusting bryozoans and annelids on the shells associated with the Grayson wackestone implies that these sediments formed a firm substrate.

Microfaunal composition.—The Grayson Formation contains a diverse and well preserved microfauna predominated by neritic benthic foraminifers. A high quality of preservation is indicated by spines being present on some of the planktonic foraminifers suggesting the microfossils have been subjected to little or no transportation. For a complete listing of the microfossils identified in this study see Mancini (1977, table 3).



TEXT-FIG. *14*—Plot of suture spacings versus whorl width (W) + whorl height (H) for four specimens of the ammonoid "*Submantelliceras*" *brazoense*.

The composition and diversity of the microfossil populations indicate that the Grayson sediments did not accumulate under low oxygen or abnormal salinity conditions but rather under normal marine inner to middle neritic conditions. Hyaline benthic foraminifers such as nodosariids, polymorphinids, buliminids, discorbids and anomalinids are the predominant benthic foraminifers. These foraminifers typically occur in present-day normal marine neritic environments (Bandy, 1964; Walton, 1964; Phleger, 1965). Miliolid benthic foraminifers are present in the Grayson Formation but are not abundant. The presence, but not abundance, of miliolids suggests normal salinities and not hypersalinities. Miliolids commonly are found in present-day nearshore environments but are particularly numerous in hypersaline environments (Murray, 1973). Agglutinated benthic foraminifers occur in the Grayson sediments, but the predominant forms are textulariids and verneuilinids rather than hyposaline types. Such forms are characteristic of Cretaceous inner to middle continental shelf environments (Burnaby, 1961; Sliter & Baker, 1972). The tests of the benthic foraminifers are not thin shelled, weakly ornamented or deformed. Typically, in low oxygen basins the benthic foraminiferal populations are comprised of individuals with weak ornamentation and thin shells (Harman, 1964). The reduction in calcium carbonate secretion is a response to these low oxygen conditions.

Planktonic foraminifers are relatively abundant throughout the Grayson Formation. At the Waco Spillway section, the percent of planktonic foraminifers increases from the lower claystone (34%) to the middle (42%) and upper (38%) claystone. This increase in planktonic foraminifers may be a result of the continuation of a marine transgression. The lower claystone may have accumulated in an inner neritic environment, whereas the middle and upper claystone probably accumulated in a middle neritic environment. In present-day marine environments, planktonic foraminifers are most abundant in offshore areas (Phleger, 1965). The Grayson heterohelicids, however, may have been neritic continental shelf planktonic forms.

The Grayson ostracode assemblage consists of forms which commonly occur in present-day normal marine environments (Puri & Hulings, 1957; Benson and others, 1961). At the Waco Spillway section, the middle claystone has the highest number of smooth-shelled (cytherellid) ostracodes. Cythereids are the predominant ostracodes in the lower and upper claystone. The abundance of smooth-shelled marine ostracodes (cytherellids) in the middle claystone may be a consequence of a soft substrate. Smooth-shelled marine ostracodes generally predominate in marine muds, whereas ornate marine ostracodes predominate in coarser, more calcareous sediments (Benson, 1961).

The maximum diameter of 100 specimens of *Valvulineria loetterlei* (Tappan) was measured for a sample from the lower, middle and upper claystone at the Waco Spillway section to determine if any vertical change occurs in the microfaunal population dynamics. This benthic foraminifer was selected because it consistently makes up 10% or more of the total benthic foraminiferal population. From the diameter measurements, size-frequency histograms and survivorship curves were constructed. Both indicate that there is no change from the bottom to the top of the section in population size distribution or mortality rate. The size-frequency histograms and survivorship curves are similar in shape to those illustrated in Text-figs. 4 and 5, respectively. The histograms and curves are illustrated in Mancini (1974, Ph.D. dissertation, Texas A&M). These moderately positively skewed size-frequency histograms and sigmoidal survivorship curves suggest that the foraminiferal populations consisted of a normal age distribution of a large number of juveniles, a moderate group of adults and a few gerontic animals.

Sedimentary features.—Sediment geochemistry and texture were evaluated to help determine the origin of the Grayson micromorphs. The amount of calcium carbonate, organic carbon and phosphate was measured to estimate the original productivity of the Grayson environment. Sulphur and iron percentages were determined to ascertain whether the sediments were deposited in a reducing environment. Iron, manganese, copper and zinc concentrations were determined to evaluate whether iron or other trace metals were present in excess, acting as possible stunting agents. The percent of clay in the rock was measured to estimate the potential fluidity of the original substrate.

At the Waco Spillway, the sediment geochemistry is comparable to that of a present-day nearshore mud as reported by Turekian & Wedepohl (1961). The average geochemical composition of the formation is iron (1.92%), manganese (450 ppm), zinc (48 ppm), copper (less than 50 ppm), phosphorus (630 ppm), sulphur (0.54%), organic matter (0.63%) and calcium carbonate (24.7%). These percentages fluctuate moderately from the bottom to the top of the section. See Mancini (1977, table 1) for the geochemical values for specific Grayson sediment samples from the Waco Spillway section. Iron and sulphur and, in some cases, organic material are concentrated in thin pyritic seams (Text-fig. 2). The red weathering mudstone at the top of the lower claystone is enriched in iron and manganese and deficient in sulphur. The white nodular wackestone at the top of the upper claystone is also enriched in manganese but is deficient in iron.

The Grayson micromorphs are most likely not a consequence of low oxygen conditions, abnormal salinities or excessive iron concentrations in the water. Excessive concentrations of iron, sulphur or organic matter are not present, nor is there a paucity of organic carbon, phosphorus or trace metals. Moderate to high concentrations of sulphur, iron and organic matter are common in environments characterized by low oxygen conditions (Berner, 1971; Presley and others, 1972). The iron and organic contents of hyposaline environments is generally high, whereas the trace metal concentration is usually low (Curtis, 1969).

The claystone at the Waco Spillway section consists of approximately 96% clay to medium silt and 4% medium silt to sand. Such a textural composition is characteristic of the lower, middle and upper Grayson claystone throughout north-central Texas. An average claystone sample from the basal claystone in north-central Texas consists of 82% clay to medium silt and 18% medium silt to sand. An average claystone sample from southwest Texas consists of 85% clay to medium silt and 15% medium silt to sand. See Mancini (1977, table 1) for the textural composition of specific claystone samples from the Waco Spillway section.

The Grayson substrate being chiefly composed of clay in north-central Texas indicates that these sediments had a high potential to form a soft substrate. Soft substrates in present-day environments are typically comprised of clay-size particles (Rhoads, 1970; Faas, 1972). The increase in the amount of silt and sand in the Grayson claystone in southwest Texas and in the basal claystone in north-central Texas suggests that these silty sediments had the potential to form a firm mud bottom. The pyritic seams associated with the middle claystone in north-central Texas (Text-fig. 2) probably formed a few centimeters below the sediment-water interface in the soft mud. These seams do not represent the surface sediments which were probably oxidized.

Paleogeographic isolation.—Grayson sediments represent a transgressive phase of a transgressive-regressive depositional cycle of the Texas Cretaceous (Young, 1972). Grayson sediments and fauna reflect uniform continental shelf conditions in the area between the Central Texas Platform and the Stuart City Reef Trend (Mancini, 1977). These depositional conditions are not conducive to the formation of barriers necessary for geographic isolation, and no evidence for the presence of barrier bars was observed in the Grayson exposures studied.

ORIGIN OF THE GRAYSON MICROMORPHS

The claystone of the Grayson Formation in north-central Texas contains a micromorph fauna. Micromorphs are rare to absent in the claystone from south-central and southwest Texas. The macrofossils found in the Grayson wackestone are not of small body size. The excellent preservation of the fossils implies that they have had little or no transportation.

The Grayson micromorphs are, in part, probably progenic organisms rather than stunted or juvenile animals. The composition and diversity of the fossil populations and the sediment geochemistry indicate that the Grayson claystone did not accumulate under low oxygen or abnormal salinity conditions but rather under normal marine inner to middle neritic continental shelf conditions. Excessive iron concentrations were not present in these waters because the sediment geochemistry is comparable to that of a present-day nearshore mud. The macrofossil populations are not composed primarily of juveniles. Although normal adult and gerontic animals are rare in some of the oyster and ammonoid populations, sexually mature individuals are present in these populations.

The small body size of some of the oysters and ammonoids is most likely an adaptive strategy evolved by these organisms for survival in a soft substrate environment. The presence of wispy burrows with indistinct boundaries in the claystone and the abundance of clay imply that these sediments had a high potential to form a soft substrate. Additional evidence suggesting a soft substrate includes: 1) the absence of extensive bioturbation in the claystone and the absence of encrusting bryozoans and annelids on the shells contained in the claystone, 2) the ostracode populations consisting of a high percentage of smooth-shelled cytherellids, 3) the macrofauna having a trophic structure dominated by epifaunal suspension-feeding bivalves with morphological adaptations for living on a soft bottom, and 4) the secretion of a gryphaeate lower valve by the oyster *Ilymatogyra arietina* from the Waco Spillway section.

Some of the small ammonoids and oysters are small adult animals. The presence of part of the living chamber and a suture pattern having the last few sutures more closely spaced imply that the ammonoids are adults. The development of mature smooth ornamentation at a smaller body size than normal by some of the *I. arietina* indicates adult oysters. These oysters are most likely progenic organisms because they became sexually mature at an earlier stage in their life history than the typical oyster. The age and size composition of these oyster populations is suggestive of populations that consist primarily of progenic animals. These populations consist of a large group of juveniles and a small group of adult and gerontic animals.

Populations composed predominantly of progenic organisms that inhabited a soft substrate environment where suitable attachment surfaces were rare have high juvenile mortality, then almost constant mortality for the adult and gerontic animals (Mancini, 1978). The survivorship curves for the Grayson oyster populations are sigmoidal suggesting high mortality for juveniles, lower mortality for adults and then increased mortality for gerontic individuals. The Grayson oysters experienced the high juvenile mortality common in a soft substrate environment. The high juvenile mortality reflects competition among the juveniles for available settling space on a soft substrate. The secretion of a gryphaeate lower valve by these oysters, however, provided an adaptation for improved survival on a soft substrate. The reduced mortality for the adult oysters may reflect this adaptation. Chance alone no longer determined which of these oysters would be overturned by vagrant animals and sink into the mud or have their respiratory and feeding mechanisms fouled by sediment particles agitated into suspension through turbulence or biogenic activity. The increased mortality for the gerontic oysters may reflect the common hazard for all animals living on a soft substrate, that is, the sinking into the soft mud as they increase in size.

CONCLUSIONS

1) The claystone of the Grayson Formation in north-central Texas contains a micromorph fauna.

2) The sedimentary and biogenic features contained in the claystone indicate this formation had the potential to form a fluid substrate, and the faunal composition indeed suggests Grayson depositional conditions included a soft substrate.

3) The small body size of some of the oysters and ammonoids is most likely an adaptive strategy evolved by these organisms for survival in a soft substrate environment.

4) The specimens of the oyster *Ilymatogyra arietina* (Roemer) from the Waco Spillway section are most likely progenic individuals because they became sexually mature at an earlier stage in their life history than the typical oyster. The secretion of a gryphaeate lower valve by these oysters provided an adaptation for living on a soft bottom.

5) Progenesis is one mechanism by which organisms can adapt to a soft substrate.

6) Grayson pyritized specimens are probably a result of microreducing environments that developed within individual shells in the soft mud.

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