

# FORAMINIFERAL PALEOECOLOGY AND PALEOCEANOGRAPHY OF THE GREENHORN CYCLE ALONG THE SOUTHWESTERN MARGIN OF THE WESTERN INTERIOR SEA

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**ABSTRACT:** Foraminifera in shales and mudrocks of the Greenhorn Cycle (late Cenomanian-middle Turonian age) in the Cretaceous Western Interior Basin were strongly influenced by sea level change. This long-term record of third-order sea level rise and fall is superposed by fourth-order relative sea level cycles as delimited by carbonate and sedimentological data. The study interval includes the Cenomanian-Turonian boundary and the early Turonian record of the highest stand of sea level in the western interior. We document stratigraphic variations in foraminiferal assemblages and their response to changing sea level for one drill core through the Tropic Shale (Escalante, Utah) and two outcrop sections of the Mancos Shale (Lohali Point, Arizona; Mesa Verde, Colorado) from the Colorado Plateau. The three sections record deposition along the southwestern margin of the Greenhorn Sea and provide a temporal and spatial framework for interpretations of paleoecology and paleoceanography.

Earlier studies demonstrate that fluctuations in planktic foraminifera and calcareous and agglutinated benthic foraminifera track the transgression and regression of the Greenhorn Cycle. Results of assemblage analyses presented here show that benthic taxon dominance also correlates to fourth-order sea level changes, and to the type of systems tract. Assemblages of calcareous benthic foraminifera are dominated by two species, *Gavelinella dakotensis* and *Neobulimina albertensis*. *Neobulimina*, an infaunal taxon, dominated during the late transgression and highstand of the Greenhorn Sea (early Turonian) when warm, normal salinity, oxygen-poor Tethyan waters advanced northwards into the seaway. In contrast, the epifaunal/shallow infaunal taxon *Gavelinella* proliferated briefly during times of water mass renewal and when deposition of organic matter increased at the transition between fourth-order cycles. Peaks in abundance of other calcareous benthic species delimit transgressive pulses prior to the spread of oxygen-poor Tethyan water masses. These broad-based correlations may result from an intricate relationship among changing water masses, flux of terrestrial and marine organic matter, sedimentation rates, and benthic oxygenation.

Regression of the Greenhorn Sea resulted in a greater restriction of oceanic circulation and in the withdrawal of Tethyan waters that were replaced by cooler, lower salinity water masses of Boreal affinity. An abrupt change to dominance by agglutinated benthic foraminifera and loss of nearly all planktic foraminifera marks this paleoceanographic event. Enhanced biological productivity accompanied regression in south-central Utah. Depauperate benthic foraminiferal assemblages reflect the stress of low-oxygen conditions despite an abundance of food. Enhanced salinity stratification during later stages of regression may have reduced ventilation on the seafloor and led to dysoxic bottom waters.

Sea level change helped produce distinctive assemblages of benthic foraminifera that can be used to delimit successive systems tracts. Foraminiferal assemblages also provide insight into their evolutionary responses to rapidly changing paleoenvironments. Our results indicate no evolution in the foraminiferal biota of the study sections, which we think points to evolutionary stasis.

## INTRODUCTION

The Late Cretaceous was a time of dynamic change in the marine environment with much of it recorded in shale and limestone sequences of the Western Interior Basin of North America. Sediments accumulated in an extensive epicontinental seaway and provide a thick stratigraphic record for the interpretation of Late Mesozoic paleoenvironments. Many workers have studied the depositional and tectonic history of these sequences. Considerable attention has also focused on reconstructing the seaway's climatic and oceanographic history, as revealed by sedimentology, geochemistry, and biotic composition.

Planktic and benthic foraminifera furnish useful paleoecologic data for interpreting Cretaceous paleoenvironments in the Western Interior Sea. This includes information on salinity, productivity, stratification of ancient water masses, and benthic oxygenation (e.g., Eicher and Worstell, 1970; Frush and Eicher, 1975; Eicher and Diner, 1985; Leckie et al., 1991; Caldwell et al., 1993; Fisher et al., 1994). Foraminifera provide critical information for testing paleoceanographic and sequence stratigraphic models. This contribution describes the paleoecology of foraminiferal assemblages in three upper Cenomanian-middle Turonian sections (Greenhorn Cycle) from the southwestern side of the "Greenhorn Sea". We also show the usefulness of foraminifera for understanding and interpreting relationships between sea level change, productivity, and benthic ventilation in ancient marine environments.

## Geologic Setting

The Western Interior Sea covered most of the west-central North American craton during the Late Cretaceous. This was a time of warm greenhouse (CO<sub>2</sub>-rich) climate, high global sea level, and widespread burial and preservation of organic matter. Six third-order tectonoeustatic cycles of marine transgression and regression are recorded in Cretaceous strata of the Western Interior (Kauffman, 1977, 1984, 1985; following the terminology of Vail et al., 1977). The best developed and most extensive of these cycles is the early Cenomanian-middle Turonian Greenhorn Cycle.

The early Turonian was the time of the highest sea level of the first-order Mesozoic-Cenozoic, tectonoeustatic cycle (Hancock and Kauffman, 1979; Haq et al. 1987). The seaway reached its maximum extent during early Turonian time. Tectonic and tectonoeustatic controls were tightly coupled with sedimentation patterns within the western interior (Kauffman, 1977, 1985). Warm southern water masses invaded the Western Interior Sea during transgressive episodes (Kauffman, 1984; Kauffman and Caldwell, 1993). With transgression came the mixing and/or juxtaposition of very different water masses, that is, cool, northern Boreal waters, and warm, southern Tethyan waters. The interaction of these water masses was probably also influenced by north-south and east-west differences in evaporation, precipitation, and runoff, as well as seasonality and the movement of storms across the seaway (Parrish et al., 1984; Glancy et al., 1986, 1993;

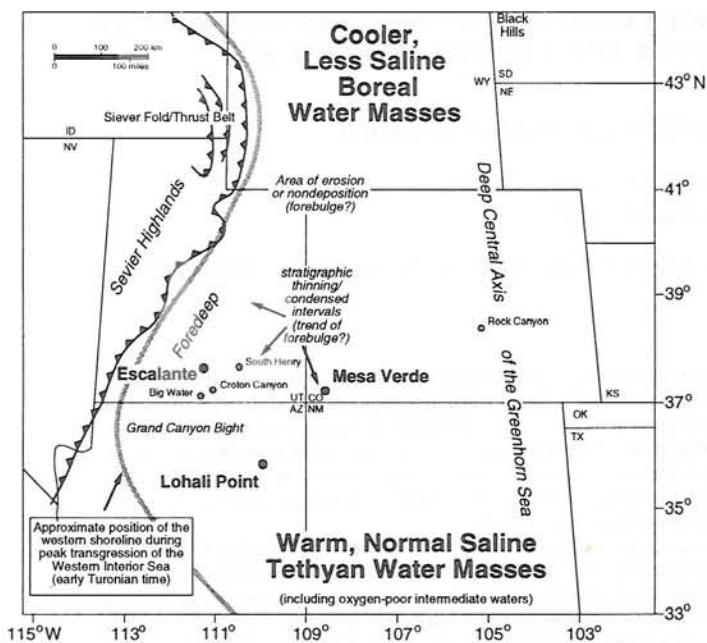


FIG. 1.—Map of the four corners area of Utah, Colorado, New Mexico, and Arizona showing the location of the three sections studied here: the Escalante (ES) core was drilled on the northern edge of the Kaiparowits Plateau near Escalante, Utah; the Lohali Point (LP) section is located on the eastern side of Black Mesa in northeastern Arizona; and the Mesa Verde (MV) section is located near the entrance to Mesa Verde National Park, between Cortez and Mancos, Colorado. Also shown is the approximate position of the western shoreline of the Greenhorn Sea at the time of peak transgression in the early Turonian (after Molenaar, 1983).

Ericksen and Slingerland, 1990; Hay et al., 1993; Jewell, 1993; Parrish, 1993; Slingerland et al., 1996). Water mass boundaries and circulation patterns fluctuated with changes in relative sea level, climate, and changes in the physiographic size and shape of the seaway. Many rivers provided fresh water, especially along the tectonically active western margin of the seaway. These contrasts in water mass were best developed close to peak transgressive episodes. Rhythmic bedding of limestone/chalk and marlstone/calcareous shale occurred during these times (e.g., Pratt, 1984; Barron et al., 1985; Arthur et al., 1985; Eicher and Diner, 1989; Sageman et al., 1997).

#### Previous Foraminiferal Studies

Cenomanian-Turonian rocks of the Western Interior of the United States and Canada contain an excellent, well documented foraminiferal record (e.g., Tappan, 1940; Cushman, 1946; Young, 1951; Jones, 1953; Fox, 1954; Frizzell, 1954; Eicher, 1965, 1966, 1967, 1969; Stelck and Wall, 1954, 1955; Wall, 1960, 1967; Lamb, 1968; Eicher and Worstell, 1970; Hazenbush, 1973; Lessard, 1973; Frush and Eicher, 1975; North and Caldwell, 1975; Caldwell et al., 1978, 1993; McNeil and Caldwell, 1981; Eicher and Diner, 1985; Leckie, 1985; Leckie et al., 1991 and this volume; Olesen, 1991; Fisher et al., 1994; Schroeder-Adams et al., 1996). In the United States, many of these studies focused on the central and eastern portions of the seaway (e.g., Eicher and Worstell, 1970) and there are less published data for the western margin. In addition, although the taxonomy and to a lesser extent the spatial distributions of Cenomanian-Turonian foraminifera were studied (e.g., Caldwell et al., 1978, 1993; Eicher and

Diner, 1985), the paleobiogeography and paleoecology of these biotas were not evaluated in the context of recent advances in our understanding of foraminiferal biology and ecology.

We present new paleoecologic interpretations based on upper Cenomanian-middle Turonian (Greenhorn Cycle) foraminiferal assemblages from the Colorado Plateau. This, and a complementary study by Leckie et al. (this volume), represent the first comprehensive paleoecologic analyses of foraminiferal assemblages from this southwestern region. Our data are interpreted with the aid of recent conceptual models of microhabitat ecology based on living benthic foraminifera (e.g., Corliss, 1985; Corliss and Chen, 1988; Corliss and Emerson, 1990; Jorissen et al., 1995), and then used to deduce paleoenvironment in relation to water mass interactions, affinities, and sea level change within the Greenhorn Sea.

#### Objectives

Our primary objective was to determine the response of foraminifera in an atypical marine environment stressed by sea level change in a dynamic depositional system. Questions that we sought to answer were: (1) Which foraminiferal taxa dominate Greenhorn assemblages and why?, (2) What kinds of paleoenvironmental conditions might exclude other taxa?, (3) Can some of the paleoecologic constraints acting on foraminiferal communities be established? In particular, are certain benthic taxa indicative of benthic oxygen levels?, (4) Can changes in foraminiferal assemblage structure be used to recognize and constrain third-order and fourth-order cycles of relative sea-level change?, (5) Can foraminifera be used to provide ground-truth data supporting climatic and paleoceanographic models for the Western Interior Sea? (6) And in a broad sense, what are the evolutionary responses of individual taxa and communities to rapid changes in paleoenvironmental conditions induced by changes in sea level?

#### MATERIALS AND METHODS

Foraminiferal assemblages were studied from three localities representing a transect across the southwestern side of the Greenhorn Sea: a cored section of Tropic Shale near Escalante, Utah (ES) on the Kaiparowits Plateau and two outcrop sections of Mancos Shale, one at Lohali Point, Arizona (LP) in the eastern Black Mesa Basin and the other near Mesa Verde National Park, Colorado (MV) on the Four Corners Platform (Fig. 1). These three stratigraphic sections allow a regional comparison of foraminiferal assemblage composition. This type of spatial comparison provides a comprehensive approach for analyzing biotic trends within the seaway and permits reliable interpretations of paleoecology and paleoenvironment.

We use foraminiferal assemblages to infer paleoenvironment. One-hundred and ninety-three samples from the Mancos and Tropic Shales were analyzed for both planktic and benthic foraminifera. The interval contained within these samples is approximately 3.5 million years. Foraminiferal assemblage data collected for each sample included: (1) planktic to benthic ratio (% planktics), (2) planktic morphotype analysis (that is % biserial, triserial, trochospiral, planispiral, and keeled morphologies), and (3) abundance of major benthic species (*Neobulimina albertensis* and *Gavelinella dakotensis*) or groups of taxa (agglutinated taxa and other calcareous benthics). Leckie (1985), West et al. (1990), and Leckie et al. (1991 and this volume) demonstrate the utility

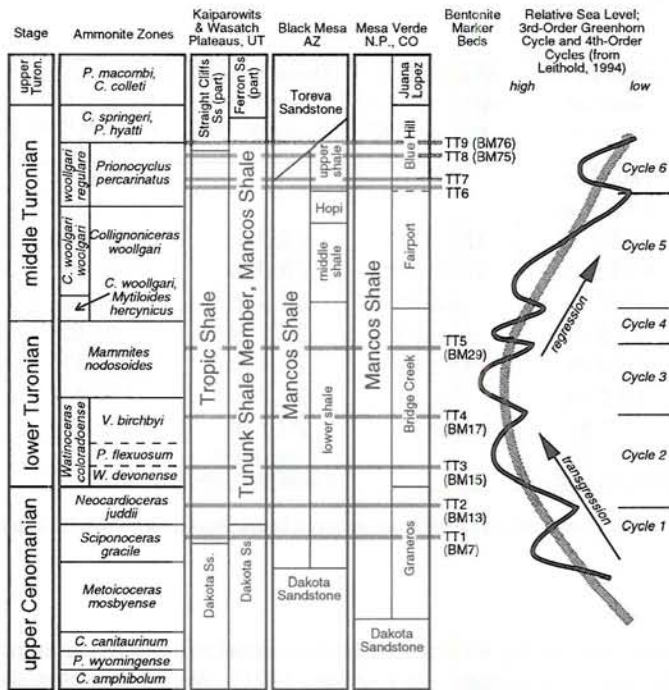


FIG. 2—Time-stratigraphic relationships and proposed correlation of rock units of the Greenhorn Cycle on the southwestern side of the Greenhorn Sea. Ammonite biostratigraphy is after Kirkland (1991) and Kauffman et al. (1993). Elder (1985) and Kirkland (1991) included *Vascoceras birchbyi* and *Pseudospidoceras flexuosum* as subzones of the *Watinoceras* Zone. Stratigraphy: southern Utah, Leithold (1994); Black Mesa, Kirkland (1991); Mesa Verde, Kirkland et al. (1995), Leckie et al. (1997). Bentonite marker beds: TT (Tropic-Tununk) from Leithold (1993, 1994) and BM (Black Mesa) from Kirkland (1991) (Table 1). Kirkland (1991) notes the concurrence of *P. percarinatus* and *C. woollgari regulare* in the Hopi Sandy Member of the Mancos Shale in Black Mesa and places the boundary between the *C. woollgari woollgari* and *C. woollgari regulare* Subzones within the Hopi interval. We correlate the Hope Sandy Member with the regressive phase of Cycle 5 in southern Utah, which Leithold (1994) interpreted as a forced regression.

of this type of data for paleoenvironmental analysis of Cenomanian-Turonian age rocks from the Western Interior. Foraminiferal assemblage data are based on counts of the >63mm size fraction of approximately 200-300 specimens where practical. Many samples from the middle Turonian parts of the sections (Cycles 5 and 6) contain depauperate benthic foraminiferal assemblages. The numbers of foraminifera picked from these latter samples are based on one or two trays of a sample split (see Appendices 1-3). Rare species and other biogenic and mineral components were also examined in all of the samples. Additional details on sample processing, picking, and counting methods can be found in Leckie et al. (1991).

#### STRATIGRAPHY

##### *Escalante Core (ES)*

A 695 ft.-thick-section (212 m) of Tropic Shale was cored near the town of Escalante in south-central Utah (Fig. 1). The Tropic Shale consists primarily of calcareous shale and mudstone representing muddy prodeltaic depositional environments of the western margin of the Greenhorn Sea (Leithold, 1993, 1994; Leithold and Dean, this volume). It conformably overlies nonmarine and marginal marine facies of the Dakota Sandstone

near the Kaiparowits Plateau (Leithold, 1994). Its upper contact grades with the overlying shallow marine and deltaic deposits of the Tropic Canyon Member of the Straight Cliffs Formation (Fig. 2). The contact with the Dakota Sandstone is placed at about 835 ft. (255 m) in the Escalante core; the contact with the Straight Cliffs Formation is tentatively placed at about 140 ft. (43 m) based on the first meter-thick sandstone in the Tropic/Straight Cliffs transition (Leithold, pers. commun., 1996). Samples representing the transgression of the Greenhorn Sea and the early phases of its regression were examined in this study.

Leithold (1994) recognized six fourth-order depositional sequences superposed on the third-order transgressive-regressive Greenhorn Cycle (Fig. 2). The depositional sequences consist of fifth-order parasequences, of which at least 37 were delimited by Leithold (1994) in the Tropic Shale and correlative Tununk Shale Member of the Mancos Shale in southern Utah. Cycles 1-3 record the transgression of the Greenhorn Sea. The highest percentages of carbonate occur in Cycle 3. This interval in the lower Turonian *Mammites nodosoides* Zone may represent peak transgression (Leithold, 1994). Cycle 4 records the highest and early phase of regression. During Cycle 5, the shoreline was displaced rapidly eastward during a major regressive phase. A rise of relative sea level (renewed subsidence?) forced the shoreline to rapidly retreat westward and then prograde during Cycle 6. According to Leithold (1993, 1994) this latter flooding event was associated with anoxic bottom waters. Leithold and Dean (this volume) note the similarity between the stratigraphy of the Escalante core and that of Leithold's (1993, 1994) Big Water section, which is located on the southern rim of the Kaiparowits Plateau (Fig. 1). At Big Water there is a disconformity in the upper part of Cycle 5 (topset beds are truncated) due to subaerial or shallow subaqueous erosion as the shoreline was displaced rapidly eastward (Leithold, 1994). However, there is no evidence of this disconformity in the Escalante core (Leithold and Dean, this volume).

##### *Lohali Point Section (LP)*

LP is located on the eastern side of the Black Mesa in north-eastern Arizona. The Mancos Shale at LP is 203 m thick. The shale is underlain disconformably by the upper Cenomanian Dakota Sandstone and overlain conformably by the middle Turonian Toreva Sandstone (Fig. 2) (Kirkland, 1991). Kirkland (1991) distinguished three informal members of the Mancos Shale and formally proposed the Hopi Sandy Member for the numerous sandstone beds between the middle and upper shale members. The lower shale member is the most carbonate-rich interval of the Mancos at LP. This unit records the transgression of the Greenhorn Sea and its maximum extent during early Turonian time (Elder, 1991; Kirkland, 1991; Leckie et al., 1991), and it correlates to Utah Cycles 1-4 of Leithold (1994). The middle shale member correlates to the transgressive and early regressive, lower part of Cycle 5 in the Tropic Shale and in the Tununk Member of the Mancos Shale in the southern Utah sections. We correlate the Hopi Sandy Member to the regressive upper part of Cycle 5. The upper shale member reflects an abrupt relative rise of sea level—perhaps subsidence—and its subsequent fall, which correlates to Cycle 6 in Utah (Kirkland, 1991; Leckie et al., 1991).

##### *Mesa Verde Section (MV)*

The MV section is near the northern edge of Mesa Verde National Park in the southwestern corner of Colorado. This sec-

TABLE 1.—BENTONITE BEDS<sup>1</sup>

Utah Bentonite	<i>Escalante</i>	Black Mesa	Black Mesa	<i>Lohali Point</i>	Mesa Verde	<i>Mesa Verde</i>	Rock Canyon
Marker Beds	<i>Core</i>	Basin, AZ	Basin, AZ	<i>Section</i>	Nat'l. Park, CO	<i>Section</i>	Pueblo, CO
Leithold, 1994	Kauffman and Leithold, unpubl.	Kirkland, 1991	(C/T interval only) Elder, 1987	Kirkland, 1991	Leckie et al., 1997	Leckie et al., 1997	Kauffman, Pratt et al., 1985
<b>TT9</b>	<b>273' (83.2 m)</b>	BM76		<b>164.4 m</b>			PF34?
<b>TT8</b>	<b>309' (94.2 m)</b>	BM75		<b>154.1 m</b>			PF31/33?
<b>TT7</b>	<b>329' (100.3 m)</b>	Unit 183?		<b>120.1 m</b>	Unit 171?	<b>71.0 m</b>	PF30/31?
<b>TT6</b>	<b>339' (103.4 m)</b>	Unit 182?		<b>119.9 m</b>	Unit 169?	<b>70.0 m</b>	PF24/26?
<b>TT5</b>	<b>657' (200.3 m)</b>	BM29		<b>35.2 m</b>	Unit 72	<b>27.8 m</b>	PBC32
<b>TT4</b>	<b>749' (228.5 m)</b>	BM17	D	<b>25.0 m</b>	Unit 53	<b>25.2 m</b>	PBC20
<b>TT3</b>	<b>771' (235.1 m)</b>	BM15	C ("boundary")	<b>16.4 m</b>	Unit 49	<b>24.4 m</b>	PBC17
<b>TT2</b>	<b>804.5' (245.3 m)</b>	BM13	B ("Neocard")	<b>13.2 m</b>	Unit 44	<b>23.2 m</b>	PBC11
<b>TT1</b>	<b>824.5' (251.4 m)</b>	BM7	A4 ("Skip")	<b>7.2 m</b>	Unit 36	<b>20.7 m</b>	PBC5
	830' (250 m) depth in core (feet/m)		A1	meters above Dakota Sandstone		meters above Dakota Sandstone	

<sup>1</sup>Tentative correlation of bentonite beds TT1-TT9 of Leithold (1993, 1994) to bentonites of Black Mesa and the Lohali Point section at Black Mesa (Elder, 1987; Kirkland, 1991), and to the Mesa Verde section (Leckie et al., 1997).

tion is the principal reference section of the Mancos Shale in its type area (Kirkland et al., 1995; Leckie et al., 1997). The Greenhorn Cycle is 141 m thick at MV and is represented by the Graneros, Bridge Creek, Fairport, and Blue Hill Members of the Mancos Shale (Fig. 2). Increasing carbonate content and an overall fining upwards sequence in the Graneros Shale Member indicate transgression of the Greenhorn Sea. The interbedded calcareous shale, limestone, and calcarenite of the Bridge Creek Limestone Member record peak transgression and high stand. Carbonate content drops off sharply in the middle and upper parts of the Fairport Shale Member (Leithold, pers. commun., 1997). We correlate this drop in carbonate in the Fairport to the Hopi Sandy Member of the Mancos Shale at LP and the major regressive episode (Cycle 5) along the southwestern side of the seaway. The Blue Hill Shale Member records an episode of relative sea level rise and subsequent fall with regression of the Greenhorn Sea during the middle Turonian, and it correlates to the upper shale unit at LP and to Leithold's Cycle 6 in south-central Utah.

#### Marker Beds and Correlation

Macrofossil assemblages and numerous bentonite beds (e.g., TT1-TT5) provide reliable correlation through the transgressive phase of the Greenhorn Cycle, particularly in the upper Cenomanian *Sciponoceras gracile* to lower Turonian *Mammites nodosoides* zones (e.g., Cobban and Scott, 1972; Kauffman, 1977; Elder, 1985, 1987, 1991; Elder and Kirkland, 1985; Kirkland, 1991; Leithold, 1993, 1994; Leckie et al., 1997) (Fig. 2). This interval correlates to Cycles 1-4 of the Tropic Shale in southern Utah (Leithold, 1993, 1994), the lower shale unit of the Mancos Shale in Black Mesa (Kirkland, 1991), and to the upper Graneros and Bridge Creek Members of the Mancos Shale at Mesa Verde (Kirkland et al., 1995; Leckie et al., 1997).

Regression of the Greenhorn Sea began in early middle Turonian time, which correlates to the *Collignonicerias woollgari* zone. Cycle 5, in the southern Utah sections, records a forced regression. According to Leithold (1994), the shoreline migrated eastward at least 150 km during this fourth-order cycle and perhaps as much as 300 km based on the distribution of the correla-

tive Coon Spring Sandstone Bed in eastern Utah and westernmost Colorado (Molenaar and Cobban, 1991). We propose that the Hopi Sandy Member of the Mancos Shale in northeastern Arizona (Black Mesa Basin) represents the same regressive event. The Black Mesa sections (Kirkland, 1991) are located south and southeast of the southern Utah sections (Leithold, 1993, 1994) and at similar or slightly more distal locations relative to the shoreline. Therefore, regressive deposits could be roughly isochronous between the two areas. The correlation of the Hopi Sandy Member with the regressive part of Leithold's Cycle 5 is supported by (1) the relatively coarse ammonite biostratigraphy available in the regressive phase of the Greenhorn Cycle, and (2) by the foraminiferal population data presented here.

If this lithostratigraphic correlation is correct, then marker bentonite beds TT6-TT9 in southern Utah likely correlate to bentonite beds Unit 182 and Unit 183 at LP and marker bentonite beds BM75 and BM76 in Black Mesa (Table 1). The first occurrence of *Prionocyclus hyatti* is between bentonites TT8 and TT9 in southern Utah (Leithold, 1994) and between bentonites BM75 and BM76 in Black Mesa (Kirkland, 1991), supporting the proposed correlation. However, the correlation of these marker beds to MV is more problematic for several reasons: (1) the Mesa Verde section lies further offshore and lithofacies changes were perhaps diachronous relative to southern Utah and Black Mesa, (2) macrofossil zones are of broader duration, diversity is lower, and the paucity of adult ammonite specimens in this part of the Greenhorn Cycle renders biostratigraphy less robust than in the transgressive upper Cenomanian-lower Turonian interval, and (3) sandy regressive deposits representing distal equivalents to the Hopi Sandy Member or Coon Spring Sandstone Bed are not present in the MV section (Leckie et al., 1997).

The Blue Hill Shale Member of the Mancos Shale at MV is correlated to the upper shale member at Black Mesa based primarily on the distinctive noncalcareous shale, paucity of macrofossils, and sharp drop in bentonite/limonite frequency. Bentonite correlations between LP and MV in Hopi Sandy/Blue Hill equivalents must be considered tentative due to the paucity of macrofossils. Despite the uncertainties in exact bentonite correlations between ES/LP and MV, the foraminiferal population data presented below help to delimit the distal equivalents of Cycle 5 and the Hopi Sandy Member.

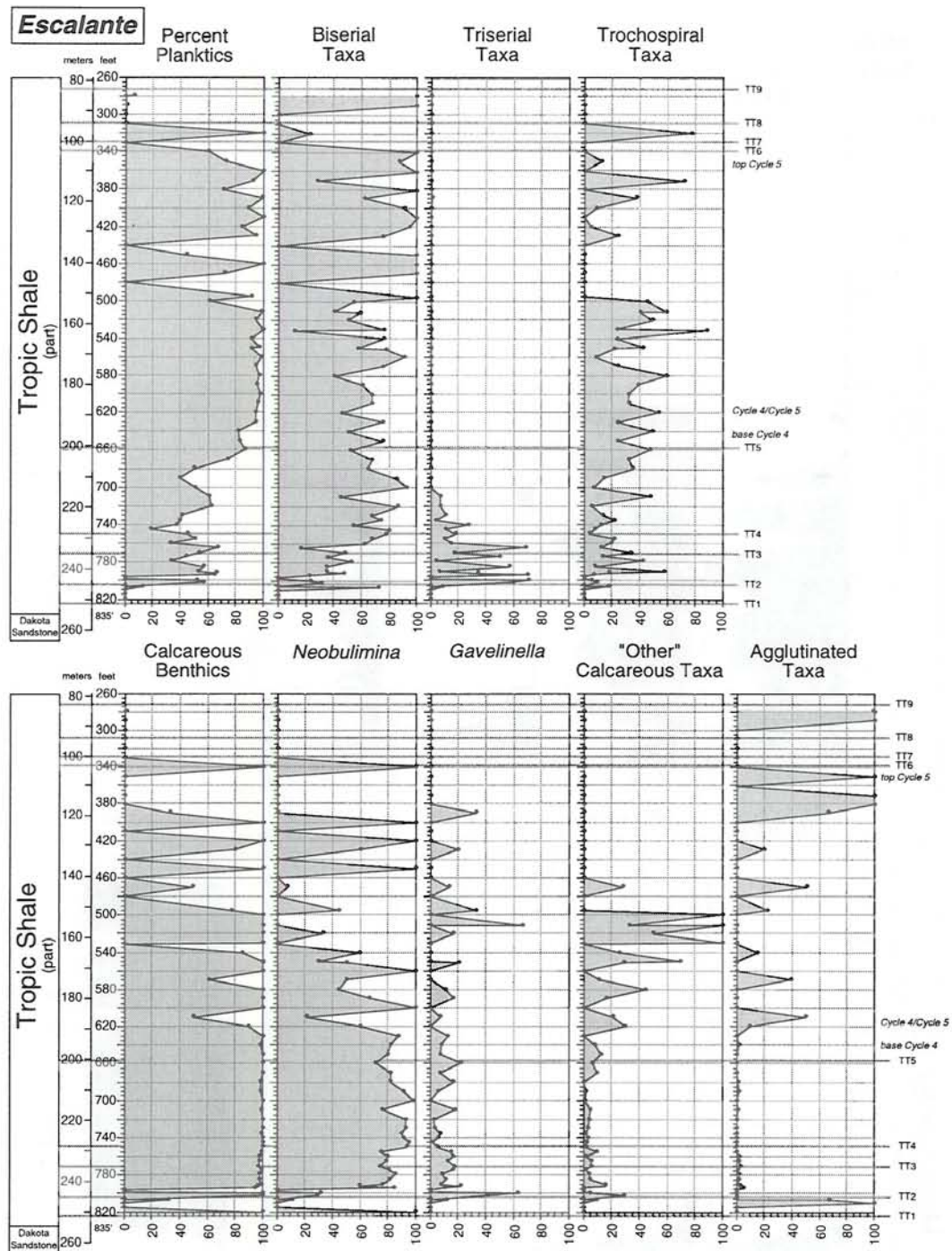


FIG. 3—Foraminiferal data for much of the Greenhorn Cycle in the Escalante core. Thickness corresponds to depth in the core (in feet). Top panel: planktic foraminiferal data include the proportion of planktics to total foraminifera (percent planktics), biserial taxa (*Heterohelix* spp.), triserial (*Guembelitra cenomana*), and trochospiral taxa (species of *Hedbergella* and *Whiteinella*). Bottom panel: benthic foraminiferal data include the proportion of calcareous benthics to total benthic foraminifera (percent calcareous benthics), *Neobulimina albertensis* (a common infaunal calcareous benthic), *Gavelinella dakotensis* (a common epifaunal/shallow infaunal calcareous benthic), other calcareous benthic taxa (e.g., *Cassidella tegulata*, *Buliminella fabilis*), and the proportion of agglutinated benthics to total benthic foraminifera. Bentonite marker beds and the intervals that correlate to Cycles 4 and 5 are shown (after Leithold, 1994; Leithold and Dean, this volume; Leithold, pers. comm., 1996).

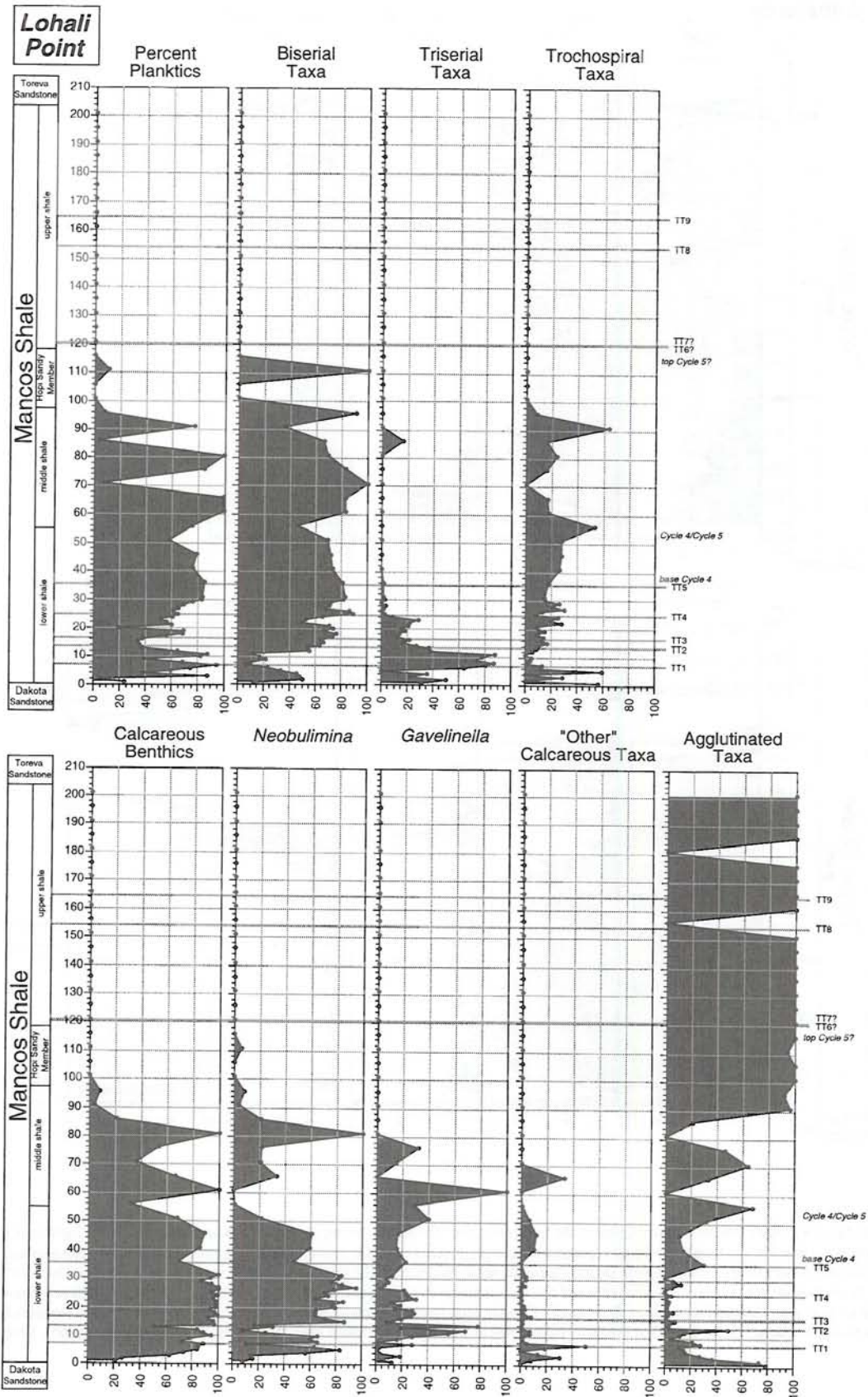


Fig. 4—Foraminiferal data for the Greenhorn Cycle at the Lohali Point section. Thickness corresponds to meters above the Dakota Sandstone. Top panel: planktic foraminiferal data; bottom panel: benthic foraminiferal data (for details refer to Figure 3). Proposed correlation to Cycles 4 and 5 of southern Utah (Leithold, 1994).

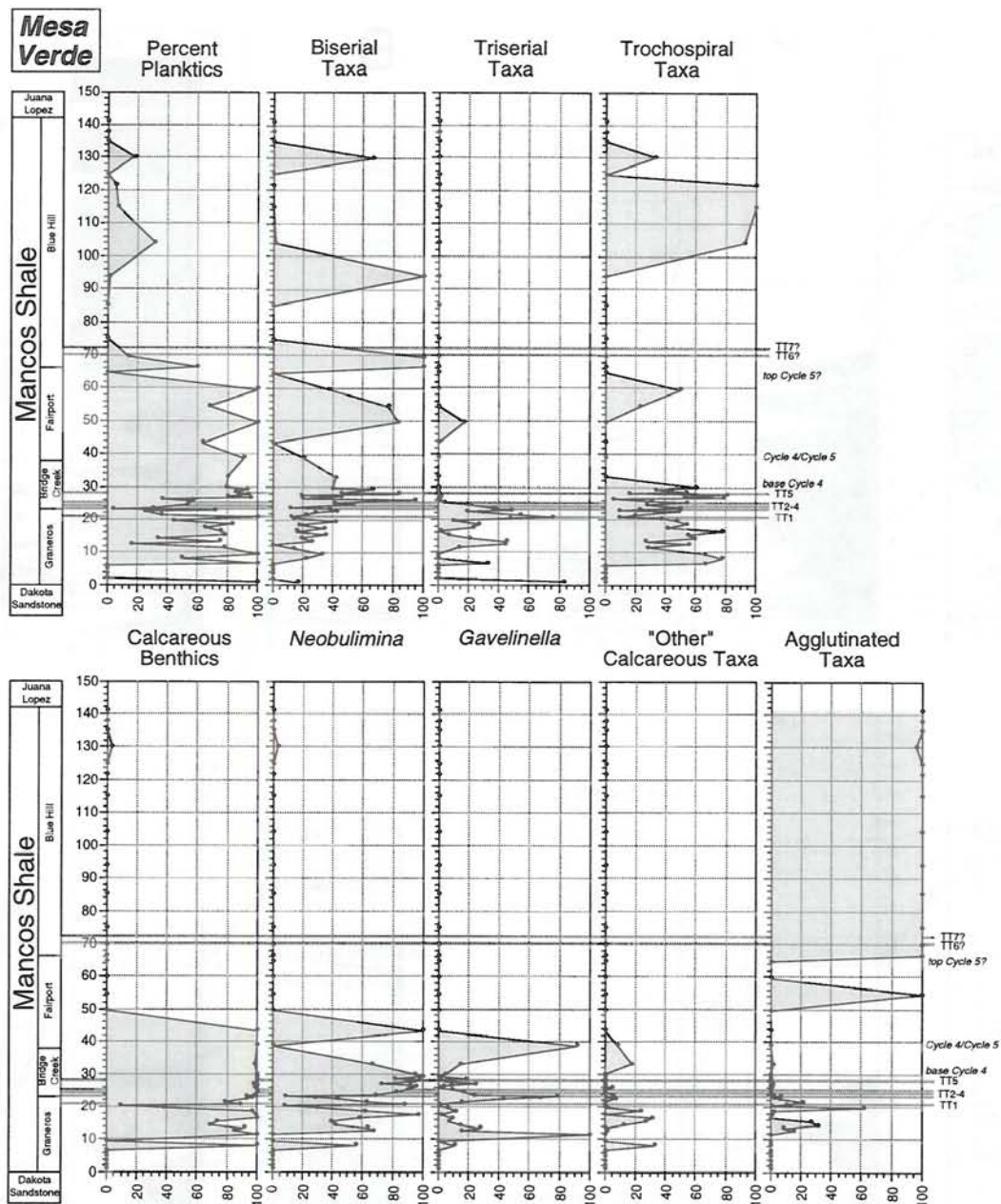


FIG. 5—Foraminiferal data for the Greenhorn Cycle at the Mesa Verde section. Thickness corresponds to meters above the Dakota Sandstone. Top panel: planktic foraminiferal data; bottom panel: benthic foraminiferal data (for details refer to Figure 3). Proposed correlation to Cycles 4 and 5 of southern Utah (Leithold, 1994).

## RESULTS

### Planktic Foraminifera

Major biotic trends in the planktic foraminiferal assemblages for all three sections analyzed are expressed as percentage data (Figs. 3, 4, 5; see Appendices for raw data tables). The first appearance of planktic foraminifera is diachronous from east to west, occurring first at MV, then at LP, and finally at ES (Fig. 6). At all three sites the foraminifera appear suddenly and abundantly within the sections, accounting for 60-90% of the total assemblage. The proportions of planktics to benthics fluctuate during transgression but stabilize during highstand (Cycle 4). Fluctuations during the transgression (Cycles 1-3) may reflect dynamic environmental shifts associated with the numerous fifth-

order parasequences superposed on the fourth-order cyclicity (Leithold, 1994; O.L.O. West, in prep.). Relative abundance of planktics increases offshore from ES to LP to MV. In the upper Cenomanian there is a decrease in planktic foraminifera at each locality followed by recovery in the lower Turonian. They then decline in abundance after TT6, but disappear sooner at LP than at the other sites.

Analysis of percent planktic morphotypes reveals that the first occurrence of biserial, triserial, and trochospiral morphotypes is also diachronous. Biserial taxa (*Heterohelix*) are most abundant in the lower Turonian (above TT4; Cycle 3) at all three sites and account for the majority of the increase seen in total planktics through the lower Turonian. In contrast, triserial taxa (*Guembelitra*) appear first at MV and LP near TT1 in high abundances, followed by a sharp decline in abundance below TT2. At ES, they occur later. Populations at this site fluctuate more than

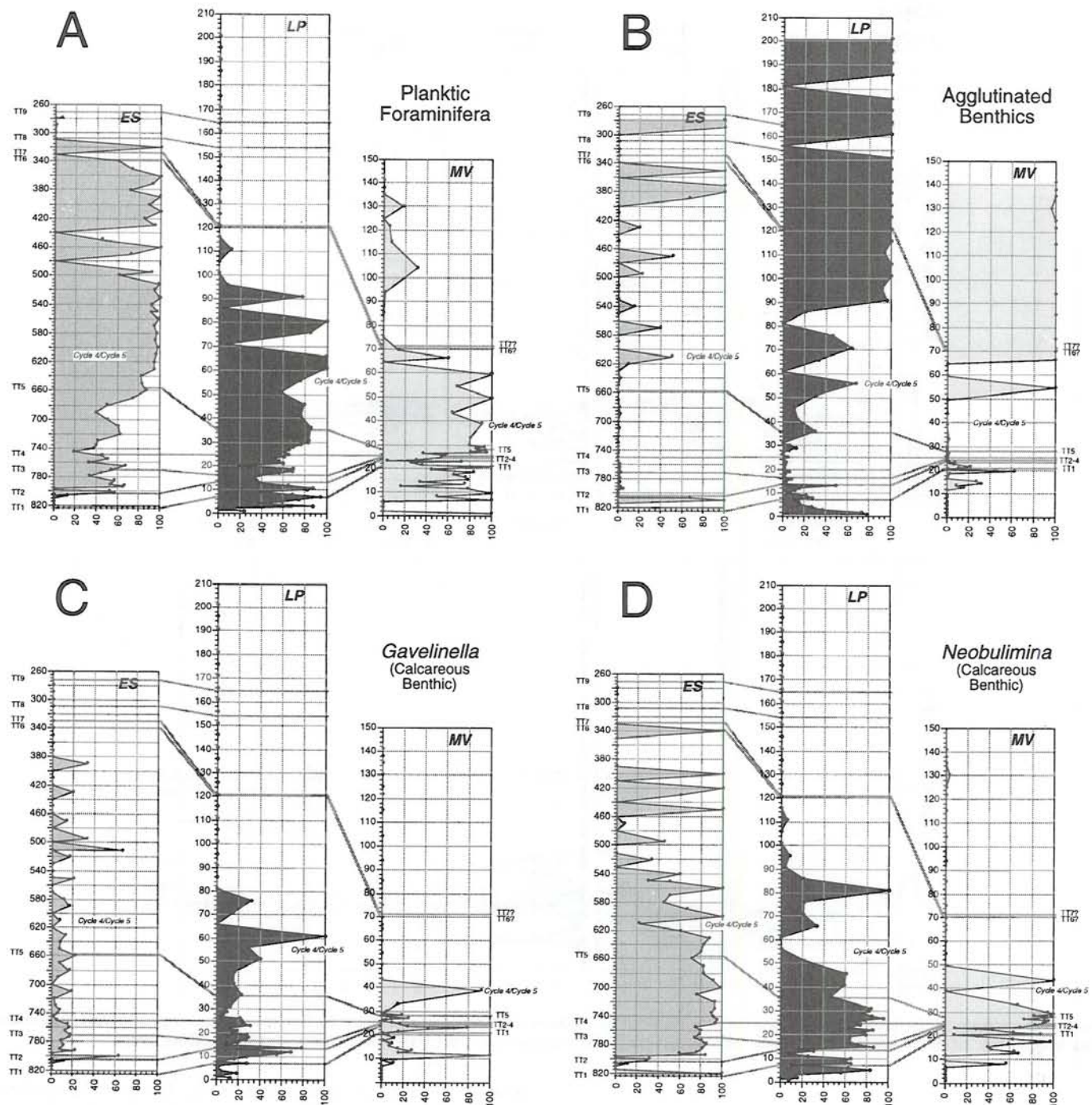


FIG. 6—Correlation of the Escalante core with the Lohali Point and Mesa Verde outcrop sections showing the stratigraphic distribution of planktic foraminifera, agglutinated benthic foraminifera, and the calcareous benthic species *Gavelinella dakotensis* and *Neobulimina albertensis*. Note the following: (A) the increase in relative abundance of planktic foraminifera between TT4 and TT5 in all three sections corresponding to the approach of peak transgression in Cycle 3, (B) agglutinated benthics are very subordinate to calcareous benthics until the onset of regression of the Greenhorn Sea; in particular, the regressive phase of Cycle 5 (below TT6), represented by the Hopi Sandy Member of the Mancos Shale at Lohali Point, marks the shift to agglutinated dominance in benthic foraminiferal assemblages, (C) the two correlative acmes of *Gavelinella*: one near TT2 corresponds with the transition from Cycle 1 to Cycle 2, and the other above TT5 corresponds with the transition between Cycle 4 and Cycle 5 (each acme precedes a shift to *Neobulimina* dominance), and (D) the dominance of *Neobulimina* throughout Cycles 2, 3, and 4 in all three sections at a time when the seaway was at or near its maximum extent; a short-lived recovery also occurs in the transgressive part of Cycle 5 at all three sections (between TT5 and TT6).

at the other two sites and persist longer. Trochospiral taxa (species of *Hedbergella* and *Whiteinella*) exhibit high variability at all three sites. The high stratigraphic occurrence of relatively abundant trochospiral morphotypes at MV is an artifact due to very small population numbers.

All three sites are dominated by biserial and triserial taxa,

but there is a brief period of trochospiral dominance in the upper Cenomanian (below TT1) at LP and MV. In the uppermost Cenomanian (*Neocardioceras* Zone) there is a decrease in triserial taxa and a coincident increase in the abundance of biserial taxa. This turnover is attributed to the invasion of southern water masses, and perhaps heightened marine productivity, as water



mass mixing proceeded across the southwestern side of the seaway (Leckie et al., this volume). No keeled taxa were recorded for ES and LP and only two specimens were found at MV in the upper Cenomanian.

#### *Benthic Foraminifera*

Major biotic trends in the benthic foraminiferal assemblages for all three sections are expressed as percentage data (Figs. 3, 4, 5; see Appendices for raw data tables). Within the upper Cenomanian and basal Turonian (TT1-TT4), benthic assemblages show similar stratigraphic trends at ES, LP, and MV. There is a sharp increase in relative abundance of *Gavelinella dakotensis* in the upper Cenomanian (near TT2), followed by a rapid shift to dominance by *Neobulimina albertensis* (between TT2 and TT3) near the Cenomanian-Turonian boundary (Fig. 6). The *Neobulimina* abundance is sustained until shortly after TT5, and the dramatic change in taxon dominance is approximately isochronous at all three western sites. This ecologic shift from a *Gavelinella* acme to *Neobulimina* dominance, is also documented at Rock Canyon, Colorado, in the central part of the seaway (Leckie et al., 1991, this volume) and is the basis for our positioning of the Cenomanian-Turonian boundary at approximately 242 m (795 ft) in the ES core.

Benthic foraminiferal numbers drop off markedly after Cycle 3 and again after Cycle 4 in the middle Turonian (Fig. 7). Between TT5 and TT6 at MV and LP, there is a second short-lived increase in *Gavelinella* (Figure 6) that is roughly isochronous and associated with a concurrent increase in other calcareous benthics at ES and LP. An abrupt decline in overall dominance of this taxon abruptly follows and later abundances are more variable. At ES, no increase in *Gavelinella* is observed, perhaps due to the depauperate nature of benthic foraminifera in the samples. However, planktic foraminifera are abundant in the same samples, which indicates that sediment dilution and dissolution cannot account for the paucity of benthics. Other nearshore sections are being studied to test this idea. *Neobulimina* dominates benthic assemblages through Cycles 1-4 and makes an attenuated reappearance at all three sites within the lower part of Cycle 5 (Fig. 6).

Other calcareous benthic foraminifera are present in very low abundance throughout all three sections. Diverse calcareous taxa characteristic of the benthonic zone of Eicher and Worstell (1970) are notably absent. Calcareous benthic assemblages are dominated at different times by one of only two calcareous taxa, *Gavelinella* or *Neobulimina*.

Agglutinated taxa suddenly appear in abundance at all three localities following the reappearance of *Neobulimina* in Cycle 5, which marks a shift from calcareous-dominated to agglutinated-dominated benthic assemblages. Agglutinated taxa are highly variable and less abundant at ES than at LP while at MV, some samples lack benthic foraminifera below TT6. The interval above TT6 correlates to Cycle 6 and regression of the Greenhorn Sea. Benthic foraminiferal assemblages are dominated almost exclusively by agglutinated taxa through this interval.

#### DISCUSSION

##### *Overview*

Foraminiferal paleoecology is widely applicable for reconstructing paleoenvironments. It is of special value in

paleoceanographic studies for inferring water mass affinities and for tracking changes in sea level within the Western Interior Sea. In epicontinental seas, oceanographic variables fluctuated significantly through time but may also have been amplified by enhanced seasonality, climatic cyclicality, and mixing of different water masses. Because foraminifera are sensitive to these oceanographic factors, attendant changes in foraminiferal assemblages can be used to track water mass evolution both temporally and spatially. For example, different water masses, defined qualitatively in terms of salinity, temperature, origin, and oxygenation can be deciphered from planktic and benthic foraminiferal assemblages and paleobiogeography (see Leckie et al., this volume).

A major aim of this study was to apply foraminiferal paleoecologic analysis to questions about water masses in the southwestern region of the Western Interior Sea during the deposition of the Greenhorn Cyclothem. This period is represented by a major transgressive-regressive episode that records the advance and retreat of the Greenhorn Sea (Fig. 2). Some contention surrounds the paleoenvironmental conditions that existed during deposition of the Greenhorn Cycle. Most workers agree that bottom waters became oxygen-deficient at times during transgression and regression but the cause, severity, and distribution of oxygen deficiency are uncertain.

Some authors (e.g., Pratt, 1984; Arthur et al., 1985; Barron et al., 1985; Pratt et al., 1993; Savrda and Bottjer, 1993) propose that a low-salinity surface layer resulting from fluvial discharge from the western highlands and driven by cyclic changes in climate, led to density stratification and reduced benthic ventilation in the Greenhorn Sea. Others favor this freshwater cap scenario in combination with the incursion of an oxygen minimum zone during eustatic sea level rise that was concomitant with a global oceanic anoxic event (e.g., Leckie et al., 1991; Sageman et al., 1997). Benthic oxygen stress can also result from high biological productivity in surface waters. Along the western margin, particularly during the regressive episode of Cycle 5, high productivity created oxygen-poor benthic conditions due to the high flux of marine organic matter (Leithold, 1993, 1994; Leithold and Dean, this volume). We tried to test these paleoenvironmental interpretations using foraminiferal data. We assessed the conditions in the water column and at the sediment surface by analyzing foraminiferal assemblages within a modern ecologic and sequence stratigraphic framework.

Previous studies of ancient communities of both macrobiota and microbiota in the Western Interior, found that the communities have high species dominance and low species diversity. Our data indicate that this also holds true for the foraminiferal communities along the southwestern side of the Greenhorn Sea. This may indicate that the salinity of the seaway was lower than normal or that low oxygen conditions were widespread in the basin at times. For example, salinity stratification, combined with enhanced productivity due to elevated fluvial input and/or incursion of warm, oxygen-poor waters into the seaway with transgression may have reduced benthic ventilation, resulting in dysoxia or anoxia of bottom waters and underlying sediments.

At all three sections, planktic and benthic foraminiferal diversity are low and there is an inverse correlation between foraminiferal abundances and diversity. This may be because high total abundances result from an increase in one or a few species. This especially seems to be the case for the benthic assemblages. Planktic foraminiferal assemblage structure clearly reflects the transgression and regression of the third-order Greenhorn Cycle.

Of more significance, perhaps, patterns of benthic foraminiferal succession within the sections correlate broadly to fourth-order cycles of relative sea level (cycles 1-6 of Leithold, 1994) that are superposed on the Greenhorn Cycle.

#### *Planktic Foraminiferal Paleocology*

Analysis of assemblage structure of planktic foraminifera provides key data for understanding ancient oceans. For example, Leckie (1987) showed that there are marked differences in the composition of low-latitude, open-ocean planktic assemblages and epicontinental sea assemblages. Planktic foraminifera reveal the nature of the upper water column. When used in conjunction with information on bottom waters garnered from benthic foraminiferal data, they provide a powerful tool for paleoceanographic reconstruction (Leckie et al., 1991, also this volume).

Our results indicate that the percentage of planktic foraminifera fluctuates between samples in the upper Cenomanian (Fig. 6). Diversity is low (4-5 species), with the epicontinental sea taxa *Heterohelix* and *Guembelitra* comprising more than 70% of specimens. These surface-dwelling genera indicate shallow marine environments (Leckie, 1987; Leckie et al., 1991). The diachronous appearance of planktic taxa records the advance of warm, normal marine southern waters as the Greenhorn Sea transgressed rapidly across the region. For example, *Guembelitra* appears to be absent from the nearshore ES site until just after bentonite bed TT2 while the percentage of this morphotype at LP and MV approaches 80% between TT1 and TT2. After TT4, during the early Turonian, this morphotype virtually disappears from assemblages at all three sites. The planispiral genus *Globigerinelloides* is restricted to the upper Cenomanian *Sciponoceras* Zone. Species of *Globigerinelloides* are characteristic of more open marine pelagic environments and indicate the establishment of normal marine conditions coincident with peak transgression. The fluctuation of the planktic to benthic ratio during transgression suggests that conditions were stressful in the upper water column at this time. We suggest that a combination of lowered salinity and high rates of sedimentation from increased fluvial input caused fluctuations in planktic populations. The effects of these factors would be especially pronounced in nearshore environments; indeed, at the Escalante site, planktic to benthic proportions are lower during transgression than at the more offshore locales.

Based on the percentage of morphotype groups, we interpret planktic assemblages as characteristic of particular oceanographic environments. Higher ratios of trochospiral and keeled morphotypes indicate a more open marine environment, while assemblages dominated by biserial *Heterohelix* likely indicate stressful conditions (Leckie, 1985, 1987; Leckie et al. 1991, and this volume). The increased abundance of this morphotype suggests less saline conditions in the upper water column and/or oxygen-poor waters associated with salinity stratification. An alternative explanation is that *Heterohelix* was associated with the incursion of Tethyan water masses into the seaway and perhaps, in particular, with low-oxygen conditions including stratification and enhanced productivity (Leckie et al., this volume). The rapid rise to dominance of this genus during the Cenomanian-Turonian Oceanic Anoxic Event (Cycle 2) and its continued dominance through peak transgression and highstand (Cycles 3 and 4) supports this hypothesis.

Through the lower Turonian, there is an increase up section in planktic foraminiferal abundance and diversity (Leckie et al., 1991; Olesen, 1991). A similar trend is seen in sections from the more distal, central part of the seaway (Eicher and Worstell, 1970; Eicher and Diner, 1985). Sustained maximum abundances at all three sites occur within Cycle 3 and Cycle 4 of Leithold (1994). During this interval of peak transgression and highstand, planktic foraminifera comprise 60-100% of foraminiferal assemblages and there is a general increase in trochospiral morphotypes (*Whiteinella* and *Hedbergella*) representative of the open marine, shallow-water biota of Leckie (1987).

Abundant fecal pellets and a marked decrease in bioturbation intensity in Cycle 5, during the early middle Turonian, particularly at ES (Leithold and Dean, this volume), point to enhanced productivity and oxygen depletion in the benthos associated with regression of the Greenhorn Sea. Elevated proportions of the biserial planktic foraminifera through this interval further support the association of *Heterohelix* with unstable pelagic conditions, which include reduced salinity, high productivity, and oxygen reduction in the water column. Boreal waters pushed southward with the withdrawal of warm, normal marine Tethyan waters during the late regressive phase of the Greenhorn Cycle. Associated with this major change in water masses (Fig. 6), planktic foraminifera were very rare in the southwestern seaway during Cycle 6.

#### *Benthic Foraminiferal Paleocology*

Benthic foraminifera are sensitive indicators of change in the marine environment. Benthic foraminiferal microhabitats in modern taxa are primarily determined by a delicate interplay between the amount of organic matter and oxygen present in the sediment and at the sediment-water interface. Epifaunal foraminifera (those that live on top of the sediment) and infaunal forms (those living within the sediment) also have distinctive morphologies that are related to their life habit (e.g., Corliss, 1985; Corliss and Chen, 1988; Corliss and Emerson, 1990; Corliss and Fois, 1991; Jorissen et al., 1995). By analogy, fossil benthic foraminifera can be used to indicate the amount of organic matter and/or degree of oxygenation within sediments and at the sediment-water interface in ancient marine systems.

We find the conceptual model of Jorissen et al. (1995) to be especially useful for interpreting benthic foraminiferal paleoecology in our sections. This model explains microhabitats of benthic foraminifera in terms of trophic conditions and oxygen concentrations. The model states that foraminiferal microhabitat preferences are a function of the negative interplay between oxygen and food availability that results from differences in the downward organic flux. Jorissen et al. (1995) posit that, under oligotrophic conditions, microhabitat depth is controlled by the availability of food particles, but in eutrophic settings, it is limited by a critical oxygen level. A similar interpretation was also proposed by Corliss and Emerson (1990) to explain differences in microhabitats in the northwest Atlantic.

In a transect across the Adriatic Sea, Jorissen et al. (1995) found that shallow microhabitats are oxygen-controlled on the shelf and upper slope areas, while in the deeper parts of the basin, the availability of food and not oxygen, determines the depth at which foraminifera live. This model offers a logical approach to paleoenvironmental reconstruction based on benthic foraminifera, and we think that it provides a useful framework within which to interpret benthic foraminiferal paleoecology of the West-

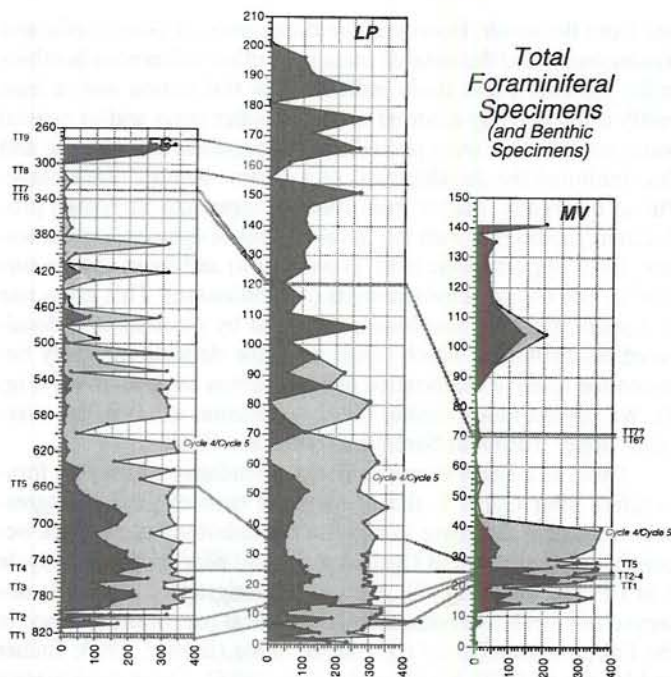


FIG. 7.—Number of foraminiferal specimens picked and counted in the Escalante core and in the Lohali Point and Mesa Verde outcrop sections. Light stipple = total foraminifera (benthics and planktics), dark stipple = benthic foraminifera. Because assemblages are based on counts of sample splits (less than one picking tray for samples containing abundant foraminifera and no more than two trays for samples containing fewer specimens), these plots represent a proxy for foraminiferal abundance in the >63 $\mu$ m fraction.

ern Interior.

Our results indicate that along the southwestern margin of the Western Interior Sea, a low species diversity and high species dominance foraminiferal biota prevailed during deposition of the Greenhorn Cycle. Two calcareous species dominate the benthic foraminiferal assemblages at all three study sections: *Gavelinella dakotensis* and *Neobulimina albertensis*. Two distinct benthic habitat characteristics, infaunal or epifaunal, are recognized by biologists. Leckie et al. (1991, and this volume) interpret *Gavelinella dakotensis* as an epifaunal species and *Neobulimina albertensis* as an infaunal species. However, as discussed by Jorissen et al. (1995), it is almost impossible to determine whether smaller foraminifera are strictly epifaunal. Buzas et al. (1993) argued that when dealing with soft sediments, a real substrate does not exist and that all benthic foraminifera are infaunal. Indeed, Linke and Lutze (1993) argued that we should not classify foraminiferal microhabitats as static, but instead think of them as the expression of a dynamic adaptation for acquiring food. In line with this more realistic approach to microhabitat determination, we interpret *Gavelinella* as an epifaunal/shallow infaunal taxon and *Neobulimina* as an infaunal taxon.

Within our study sections, we see clear-cut and coherent alternations between short-lived *Gavelinella*-dominated assemblages and those dominated by *Neobulimina*. We suggest that this alternation in taxon dominance indicates an ecologic shift that was caused by changes in the dynamic relationship between microhabitat depth and organic flux, and that it was intimately related to fluctuations of sea level, flux of organic matter, and water mass characteristics of the seaway. Changes in relative sea level not only influenced water mass distribution and circula-

tion, but also affected marine productivity by delivering nutrients and terrestrial organic matter to the seaway.

The rapid transgression of the Greenhorn Sea during the late Cenomanian opened new benthic niches in the core of the seaway, as relatively well oxygenated, normal marine waters invaded from the south. These niches were filled by diverse assemblages of calcareous benthics ("benthonic zone" of Eicher and Worstell, 1970) that immigrated to the Greenhorn Sea with the incursion of warm, Tethyan water masses. The benthonic zone is well developed in offshore sites such as Rock Canyon, Colorado (Fig. 1; Eicher and Worstell, 1970; Frush and Eicher, 1975; Eicher and Diner, 1985; Leckie, 1985). In contrast, in our nearshore sections along the southwestern margin of the seaway, benthic diversity is very low and the diagnostic species of the benthonic zone are not present. This very poor expression of the benthonic zone is perhaps due to the diachronous nature of the transgression. Water mass characteristics such as temperature and salinity or other factors such as water clarity, water depth, and organic character or content of the sediments, may account for the absence of the benthonic zone on the western margin during the time of the *Sciponoceras* zone.

An increase in abundance of the epifaunal-shallow infaunal species *Gavelinella dakotensis*, which dominates assemblages just prior to the Cenomanian-Turonian boundary (Fig. 6), is present at all locales of the southwestern margin and the central part of the seaway (Leckie et al., this volume). We call this the *Gavelinella* acme. We interpret *Gavelinella* as an opportunistic pioneer species capable of taking advantage of the combination of both new niches opened by the incursion of the transgressing seaway and sporadic input of terrestrial and marine detrital organic matter, which coincide with fourth-order, transgressive-regressive pulses. The *Gavelinella* acme developed at the end of Cycle 1 and/or start of Cycle 2. A putative second acme smaller in magnitude developed at the transition from Cycle 4 to Cycle 5 (Fig. 6). There are problems in interpreting data for this latter transition due to the paucity of benthic foraminifera (Figure 7).

According to Gooday (1993), sudden inputs of phytodetritus from plankton blooms promote opportunistic epifaunal taxa because they thrive on high-quality food and reproduce rapidly. This results in a biota with strong epifaunal dominance. Pulses of phytodetritus would be common along the western margin of the seaway, as numerous rivers drained into it. Fluvial input delivered both terrestrial organic matter and nutrients, which stimulated plankton blooms. In shallow, marginal marine environments, this provided a plentiful source of food for opportunistic epifaunal-shallow infaunal species, which could outcompete other species and rapidly prosper. As long as bottom waters remained oxygenated these taxa dominated benthic assemblages when food was abundant. However, a reduction in these food pulses kept more opportunist taxa (like *Gavelinella dakotensis*) in check allowing other species to flourish. We think that this reduction in food supply coupled with well-oxygenated bottom waters, accounts for the high diversity of the benthonic zone from the central and eastern part of the seaway.

We propose that the *Gavelinella* acme in our sections resulted from rapid multiplication of this opportunistic, epifaunal-shallow infaunal taxon in response to sudden inputs of food. In all sections we see a *Gavelinella* acme in the uppermost Cenomanian and a smaller one at LP and MV in the lower middle Turonian. Both acmes coincide with the end of regressive pulses or the start of transgressive pulses of Leithold's (1994) fourth-order cycles (Fig. 8). Increased riverine influx associated with

fourth-order regressions provided pulses of organic matter from plankton blooms and high sedimentation rates, which may have precluded infaunal microhabitats. Because of its epifaunal-shallow infaunal microhabitat, *Gavelinella* could take advantage of fresh, easily metabolized food fragments concentrated at the sediment surface. We suggest that benthic bottom waters were mesotrophic and oxygenated at these times. Under these conditions benthic assemblages were food-dominated; that is the availability of organic matter, and not oxygen, determined the microhabitat depth (Corliss and Emerson, 1990; Jorissen et al., 1995). However, if rates of productivity and sedimentation are too high, oxygen depletion at the seafloor may greatly limit benthic foraminiferal proliferation, despite the abundance of food. This may account for the absence of a second *Gavelinella* acme at ES.

Across the Cenomanian-Turonian boundary the dominance of *Gavelinella* in the benthic assemblages at all sections declines due to an abrupt increase in the infaunal species *Neobulimina albertensis* (Figs. 6, 8). As mentioned previously, we think that this alternation in taxon dominance indicates an ecologic shift. It occurs at all three sites and indicates paleoceanographic change associated with the Cenomanian-Turonian boundary interval (Leckie et al., this volume). We interpret the shift from *Gavelinella*-dominated assemblages to those dominated by *Neobulimina* as indicative of a change in which microhabitat is controlled by a critical oxygen level instead of food availability.

*Neobulimina* is very abundant and dominates the foraminiferal assemblages of Cycles 2-4 of Leithold (1994) (Figs. 3, 4, 5). Dominance of this taxon also correlates to the approach of peak transgression of the Greenhorn Sea in the early Turonian (Figure 8). Based on planktic foraminiferal assemblage structure and carbonate data, peak transgression occurred within Cycle 3 (Leckie et al., 1991; Leithold, 1994; Leithold and Dean, this volume). During this time the southern portion of the seaway was dominated by a warm, perhaps oxygen-poor Tethyan intermediate water mass (Leckie et al., 1991, this volume). Primary productivity may also have increased based on the abundance of *Heterohelix* in the planktic assemblages (Figs. 3-5).

According to the model of Jorissen et al. (1995), shallow microhabitats are oxygen-controlled in eutrophic settings on shelf and upper slope areas, which leads to a shallowing of microhabitat depth and a decrease in the size of the infaunal niche. Progressing from an oligotrophic to a mesotrophic environment, the depth of foraminiferal microhabitats becomes deeper and the size of the infaunal niche gets larger as food supplies increase. This will obviously result in an increase in the percentage of infaunal species in an assemblage. Jorissen et al. (1995) argue that in oxygen-controlled environments, the increasing oxygen-stress preferentially eliminates the less resistant epifaunal-shallow infaunal taxa. The net result, is a continued rise in the percentage of infaunal species until they approach 100% in highly dysoxic environments such as sapropels (e.g., Verhallen, 1990). Under such oxygen-poor conditions, infaunal taxa will most likely live at the surface of the sediment rather than within it (Jorissen et al., 1995). Some benthic foraminifera may be facultative anaerobes (Bernhard, 1989, 1993, 1996; Sen Gupta and Machain-Castillo, 1993), and it is possible that this may have been the case for *Neobulimina* (West et al., 1993). This ability facilitates survival when bottom waters are anoxic. The possibility that this taxon also harbored bacterial chemosymbionts should not be ruled out; chemoautotrophy is a viable trophic strategy in anaerobic, sulfide-rich sediments (West, 1993).

Other calcareous taxa immigrated to the Western Interior

Sea from the south. However, the dominance of *Gavelinella* and *Neobulimina* and the notable paucity of other calcareous benthics in the sections under study indicates that this region was at least partly influenced by a cooler northern water mass and/or coastal water masses, that were periodically hyposaline and dysoxic and thus inhibited the development of a diverse benthic assemblage. Pulses of organic matter from riverine input and increased productivity, combined with the development of dysoxic bottom waters, favor opportunistic taxa (*Gavelinella*) and those able to survive in low oxygen environments (*Neobulimina*). This gives rise to a succession of *Gavelinella* followed by *Neobulimina* dominated assemblages, which result from the delicate interplay between the relative importance of food versus oxygen levels (Fig. 8). We predict that a similar biotic succession exists in the overlying upper Turonian-Santonian Niobrara Cycle.

There is a sharp decrease in the abundance of benthic foraminifera after Cycle 3, that is after the time of peak transgression. A further decrease in benthic foraminiferal abundance occurs in the upper part of Cycle 4 at ES and near the base of Cycle 5 at LP and MV (Fig. 7). A similar stratigraphic pattern is observed in correlative rocks from the central part of the seaway, in the Fairport Member of the Carlile Shale (Eicher, 1966; Eicher and Worstell, 1970; Eicher and Diner, 1985). These depauperate benthic assemblages are associated with abundant fecal pellets in the shale and relatively abundant planktic foraminifera through the interval of Cycle 4 and the lower part of Cycle 5 (Fig. 6). The presence of abundant planktics rules out the possibility that the benthic assemblages were diluted or dissolved.

We think that low benthic abundances were caused by the combined effects of changing benthic water mass - perhaps the retreat of Tethyan water masses and increasing influence of Boreal waters? - and renewed oxygen depletion in bottom waters associated with high productivity and high sedimentation rates along the western margin. These changes were concomitant with the major Coon Spring-Hopi regression of Cycle 5 (Leithold, 1994) (Fig. 8). Increased productivity is indicated by the abundant planktic foraminifera and fecal pellets and an increase in the flux of marine organic carbon documented at ES (Leithold and Dean, this volume). With an increase in productivity one would expect to see an increase in benthic foraminifera. This begs the question of why no such increase is seen. We suggest that high productivity in surface waters, coupled with higher sedimentation rates, resulted in rapid depletion of benthic oxygen. A marked decrease in bioturbation intensity upward through the shale of Cycle 5 at ES further supports an interpretation of benthic oxygen depletion (Leithold and Dean, this volume). Benthic foraminifera are unable to proliferate under anoxic conditions even though food was abundant.

Following the minor increase in *Gavelinella* seen at the Cycle 4/Cycle 5 transition at LP and MV, the relative abundance of *Neobulimina* near the base of Cycle 5 increases at all three sites (Fig. 6). This trend is associated with increased carbonate values in the lower part of Cycle 5 at all three sites (Leithold and Dean, this volume; Leithold, pers. commun., 1997; McCormic, pers. commun., 1997) and in correlative rocks of the basal Fairport Member of the Carlile Shale in the central part of the seaway (Glenister and Kauffman, 1985) (Fig. 2). We interpret this as indicative of the final influence of Tethyan water masses during the Greenhorn Cycle.

Within Cycle 5 strata (below TT6) there is a clear shift from calcareous-dominated to agglutinate-dominated benthic assemblages with more northern affinities (Fig. 6). At LP, the shift in

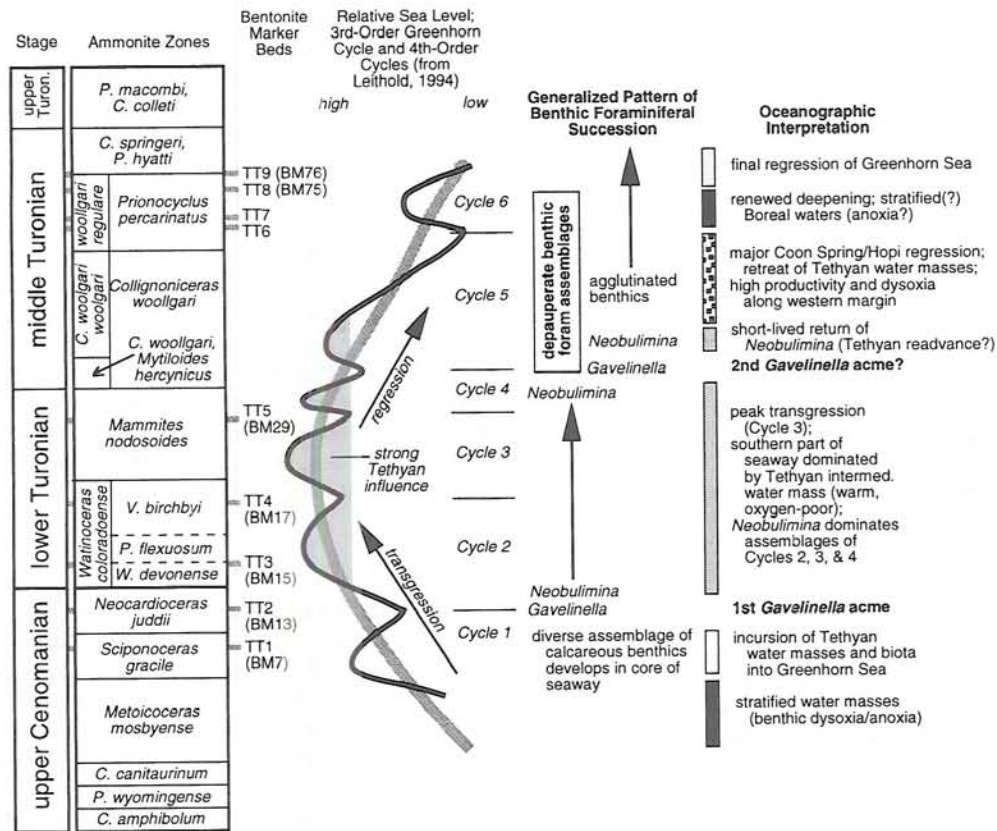


FIG. 8—General trends in benthic foraminiferal populations relative to the fourth-order transgressive-regressive cycles of Leithold (1994). Calcareous benthics are common on the southwestern side of the Greenhorn Sea during transgression and highstand (late Cenomanian-early Turonian), when the seaway was strongly influenced by a southern water mass. Agglutinated benthics characterize the seaway during regression (middle Turonian) which reflects the displacement of Tethyan waters by cooler, less saline water masses from the north. The calcareous benthics display a pattern of succession through the fourth-order cycles. However, these cycles of succession are masked by *Neobulimina* dominance when the seaway is large and dominated by an oxygen-poor Tethyan water mass (Cycles 2, 3, and 4). A major regression during Cycle 5 (Coon Spring/Hopi) brings the strong Tethyan influence to an end and Boreal water masses dominate the seaway for the remainder of the Greenhorn Cycle.

foraminiferal assemblages corresponds with the middle shale-Hopi Sandy Member contact of the Mancos Shale. This dramatic shift in benthic foraminiferal communities is very similar to the trends documented in the central part of the seaway (Eicher, 1966; Eicher and Worstell, 1970; Eicher and Diner, 1985). We interpret this shift as representing the continued displacement of Tethyan waters by Boreal water masses across the southwestern side of the seaway, coincident with an early phase of regression of the Greenhorn Sea (Fig. 8).

Cycle 6, which correlates to the upper shale member of the Mancos Shale at LP and to the Blue Hill Member of the Mancos at MV, records the final regression of the Greenhorn Sea that led to restricted circulation of less saline and, perhaps, stratified Boreal waters. These conditions are indicated by very low carbonate in the shale and its equivalents from the central part of the seaway (Blue Hill Member of the Carlile Shale; Glenister and Kauffman, 1985; Leithold, 1994; Leithold and Dean, this volume), depauperate assemblages of benthic molluscs and ammonites (Glenister and Kauffman, 1985; Kirkland, 1991; Leckie et al., 1997), very rare and sporadic planktic foraminifera, and benthic foraminiferal assemblages dominated exclusively by agglutinated taxa.

#### Sequence Stratigraphy

Benthic foraminiferal taxon dominance can be used to de-

limit fourth-order sequence stratigraphic systems tracks within the third-order Greenhorn Cycle. We find that diagnostic benthic taxa characterize the systems tracks recognized by Leithold (1994) (Fig. 9). During Cycle 1 of the transgressive phase of the Greenhorn Cycle, the transgressive systems tract (TST) is marked by a mixed calcareous and agglutinated assemblage, which is equivalent to the benthonic zone (Eicher and Worstell, 1970) further out in the basin. The thin, highstand systems tract (HST) and the shelf margin system tract (SMST), are characterized by *Neobulimina* and *Gavelinella* respectively (see also Leckie et al., this volume). Within Cycle 2, the TST, HST, and SMST are all dominated by *Neobulimina*; which indicates rising sea level and the incursion of an oxygen minimum zone of Tethyan affinity (Leckie et al., this volume). Cycles 3 and 4 are associated with peak transgression and highstand of the Greenhorn Sea. Continued persistence of a warm, oxygen-poor Tethyan water mass is indicated by the high abundances of *Neobulimina*. A similar pattern of biotic succession is repeated in the regressive deposits prior to the final retreat of Tethyan waters, where again *Gavelinella* is diagnostic of the SMST of Cycle 4 and *Neobulimina* is characteristic of the TST of Cycle 5. This pattern is what one might predict for a transgressive-regressive succession, but further testing is needed. For example, the *Gavelinella* acmes at the Cycle 1/2 and Cycle 4/5 transitions may prove to characterize a broader spectrum of systems tracks including late HST, SMST, and early TST. Agglutinated benthics

### Third-Order Greenhorn Cycle

Transgression			Regression		
4th-Order Cycle	Diagnostic Foraminifera	Systems Track	4th-Order Cycle	Diagnostic Foraminifera	Systems Track
Cycle 2	<i>Neobulimina</i>	SMST	Cycle 6	agglutinated benthics; very rare planktics agglutinates plus rare planktics and/or calcareous benthics	HST
		HST			TST
Cycle 1	<i>Gavelinella</i>	TST	Cycle 5	agglutinated benthics	HST
		SMST			TST
		HST			SMST
	<i>Neobulimina</i>	TST	Cycle 4 (part)	<i>Gavelinella</i>	
	mixed calcareous & agglutinated benthics				

FIG. 9—Correlation of foraminiferal assemblages to the fourth-order cycles of Leithold (1994) and their preliminary sequence stratigraphic interpretation. TST = transgressive systems track, HST = highstand systems track, SMST = shelf margin systems track (Van Wagoner et al., 1988). *Gavelinella* is associated with the transition from Cycle 1 to Cycle 2 and possibly with the transition from Cycle 4 to Cycle 5. We tentatively correlate these occurrences with the SMST. Influx of planktic and/or calcareous benthic foraminifera is associated with the TST of Cycles 1 and 6, while the advance of warm, oxygen-poor waters during deposition of Cycle 2, 3, and 4 accounts for the dominance of *Neobulimina* in both transgressive and regressive phases of these cycles (that is TST, HST, and SMST). Regression of the Greenhorn Sea and the retreat of Tethyan water masses accounts for the shift to agglutinated benthic foraminiferal assemblages in the upper part of Cycle 5 (HST) and in Cycle 6.

characterize the HST and TST at the top of Cycle 5 and within Cycle 6. This is the expression of the influence of Boreal waters and the removal of Tethyan water masses from the region.

#### Evolutionary Response to Changing Sea Level

The Western Interior Sea represents a dynamic environment. Such a system with rapid changes in environmental conditions might be expected to elicit a correspondingly rapid evolutionary response in the biota and induce speciation within the dominant lineages. However, our data show that the foraminiferal assemblages remained stable. Benthic foraminifera show a pattern of no change in terms of species diversity; the same species persist throughout the sections. Although the assemblages track environmental change in terms of species dominance and composition there appears to be no evolution within the individual species lineages or change in the composition of the foraminiferal assemblages across the study area. Although environment seems to determine which assemblage dominated at any point in time throughout the sections, the same distinctive species and foraminiferal communities persisted, which indicates a pattern of evolutionary stasis.

A perusal of recent paleobiological literature reveals a surge of renewed interest in this well-recognized pattern of long periods of stasis and evolutionary stability disrupted by episodes of geologically rapid evolutionary change (Ivany and Schopf, 1996). Recent research reveals that stasis and episodes of rapid evolutionary turnover may occur concurrently in entire communities (Brett, 1995). Stasis is now seen as a pattern of linked stability and linked change where the principle unit of selection is the community/ecosystem rather than individual species. This pattern emerging from the fossil record is reframed in terms of community and group selection and is called coordinated stasis (Brett

and Baird, 1995).

All studies to date documenting coordinated stasis in the fossil record were done on higher metazoa. A major unanswered question is, does stasis manifest differently in the fossil record of microorganisms than in the fossil record of animals. For example, studies conducted of coordinated stasis in animals reveal consistent change in taxonomic composition in recurring fossil assemblages and no change in species composition during periods of stasis (Brett and Baird, 1995; Leiberman et al., 1995). Also, morphological stasis is thought to be a response to widely fluctuating physical environments on geological timescales (Sheldon, 1996). Is this the case for the microbiota? Study of the relationship between the dynamic environmental and depositional conditions manifest in Upper Cretaceous strata of the Western Interior Sea, and the evolutionary response of the foraminifera of this large epicontinental sea, provide an ideal opportunity to test for stasis in the microbiota (O.L.O. West, in prep.).

#### CONCLUSIONS

1. Foraminiferal assemblages and swings in species dominance are closely linked to third- and fourth-order transgressive and regressive episodes in the Cenomanian-Turonian Greenhorn Cycle. Cyclic changes in benthic species dominance (i.e., *Gavelinella* versus *Neobulimina*) are recorded in sequences of the southwestern margin of the Western Interior Sea. Diagnostic foraminiferal taxa can be used to delimit several of the six fourth-order, transgressive-regressive cycles and systems tracks recognized by Leithold (1994). A *Gavelinella* acme at all study sites is associated with the transition from regressive to transgressive pulses of fourth-order cycles. The epifaunal-shallow infaunal species *Gavelinella dakotensis* indicates more normal marine waters, higher benthic oxygen levels, and pulses of organic matter into the system. Assemblages dominated by *Neobulimina albertensis* are associated with the late transgressive and highstand phases of the third-order Greenhorn Cycle of the early Turonian, when a warm, oxygen-poor intermediate water mass of Tethyan affinity spread across much of the southern seaway. Under these presumed dysoxic conditions, a critical level of oxygen was more important than food; low-oxygen tolerant infaunal taxa could proliferate and exclude epifaunal-shallow infaunal taxa that require higher oxygen levels. *Neobulimina* may also have been a facultative anaerobe and thus preadapted to survive in low-oxygen conditions.

2. We see a pattern of regional biotic change that signals paleoenvironmental change across the Cenomanian-Turonian boundary. We think it results from the expansion of an oxygen minimum zone and increased primary productivity at the Cenomanian-Turonian boundary. We place the boundary at approximately 242 m (795 ft) in the Escalante core on the basis of an ecologic shift from epifaunal-shallow infaunal-dominated foraminiferal assemblages (*Gavelinella*) to infaunal-dominated assemblages (*Neobulimina*).

3. Regression in Cycle 5 (early middle Turonian) increased productivity along the western margin. This led to the development of dysoxic bottom waters, which resulted in depauperate benthic foraminiferal assemblages despite an abundance of food.

4. The transition from calcareous-dominated to agglutinate-dominated assemblages within Cycle 5 indicates the displacement of Tethyan water masses that invaded the Western Interior Basin during eustatic sea level rise by cooler, less saline northern waters of Boreal affinity. This displacement is associated with

increased sedimentation rates, freshwater runoff from the western highlands, and perhaps the development of salinity stratification and dysoxic bottom waters further out in the basin.

5. Variations in foraminiferal assemblage composition result from changes in salinity, oxygenation, and perhaps temperature, that followed from changing sea level and coincident variability in freshwater runoff and productivity. The Greenhorn Sea was influenced by Tethyan water masses during transgression that eventually were displaced by Boreal waters. Foraminiferal data from the southwestern margin support the paleoceanographic model of Slingerland et al. (1996), which posits that estuarine circulation with a strong counterclockwise gyre occupied the entire north-south extent of the seaway.

6. Our initial results on the evolutionary response of foraminifera to changing sea level indicate that the Western Interior provides an outstanding model system for testing and refining evolutionary concepts. In particular, foraminiferal communities could help us test how coordinated stasis, which has mainly been studied in macrobiotic communities, may manifest in the microbiota.

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APPENDIX 1.—ESCALANTE DATA

Sample Number	279.08	280.06	290.10	299.81	310.00	320.04	330.00	340.00	350.21	361.09	371.06	381.09	389.50	400.08	410.04	420.02	429.83	440.10	450.05	460.06	470.00	479.86	494.97	500.10	511.10	511.28	520.10	
Raw Data																												
<b>Planktic Morphotypes</b>																												
Biserial	22	2	2	0	0	5	0	3	7	13	7	5	196	30	5	253	65	0	8	26	210	0	98	6	132	56	54	
Triserial	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Trochospiral	0	0	0	0	17	0	0	1	0	18	0	117	3	0	13	21	0	0	0	0	0	0	0	5	191	38	52	
Planispiral	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Keeled	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>Benthic Morphotypes</b>																												
Calcareous Other	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	0	0	0	7	2	1	3
Neobulimina	2	0	0	0	0	0	2	0	0	0	0	0	0	4	0	50	3	0	10	0	6	0	4	0	0	0	0	2
Gavilinnella	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	11	0	3	0	4	0	1	
Total Calcareous Specimens	3	0	0	0	0	0	0	0	0	0	0	0	1	0	50	4	0	0	0	0	40	0	7	7	6	1	6	
Total Agglutinated Specimens	311	306	236	0	0	0	0	3	0	2	2	2	2	0	0	0	1	0	0	0	42	0	2	0	0	0	0	
Total Number of Benthics	314	306	236	0	0	0	2	3	0	2	2	2	3	4	0	50	5	0	10	0	82	0	9	7	6	1	6	
Total Number of Planktics	22	2	2	0	22	0	3	8	13	25	5	313	33	5	267	86	0	8	26	210	0	98	11	323	94	106		
Total Number of Specimens	336	308	238	0	22	0	5	11	13	27	7	316	37	5	317	91	0	18	26	292	0	107	18	329	95	112		
% Data																												
<b>Planktic Morphotypes</b>																												
Biserial	100.0	100.0	100.0	0.0	0.0	22.7	0.0	100.0	87.5	100.0	28.0	100.0	62.6	90.9	100.0	94.8	75.6	0.0	100.0	100.0	100.0	0.0	100.0	54.5	40.9	59.6	50.9	
Triserial	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Trochospiral	0.0	0.0	0.0	0.0	77.3	0.0	0.0	0.0	12.5	0.0	72.0	0.0	37.4	9.1	0.0	4.9	24.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	45.5	59.1	40.4	
Planispiral	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Keeled	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
% Planktics	6.5	0.6	0.8	0.0	0.0	100.0	0.0	60.0	72.7	100.0	92.6	71.4	99.1	89.2	100.0	84.2	94.5	0.0	44.4	100.0	71.9	0.0	91.6	61.1	98.2	98.9	94.6	
<b>Benthic Morphotypes</b>																												
Calcareous Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	28.0	0.0	0.0	100.0	33.3	100.0	50.0	
Neobulimina	0.6	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	60.0	60.0	0.0	100.0	0.0	7.3	0.0	44.4	0.0	0.0	0.0	33.3	
Gavilinnella	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	33.3	0.0	20.0	0.0	20.0	0.0	0.0	0.0	13.4	0.0	33.3	0.0	66.7	0.0	16.7	
Total Calcareous Specimens	1.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	33.3	100.0	0.0	100.0	80.0	0.0	100.0	0.0	48.8	0.0	77.8	100.0	100.0	100.0		
Total Agglutinated Specimens	99.0	100.0	100.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0	100.0	100.0	66.7	0.0	0.0	0.0	20.0	0.0	0.0	0.0	51.2	0.0	22.2	0.0	0.0	0.0	0.0	









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