Shorter Contributions to Paleontology and Stratigraphy

Edited by WILLIAM J. SANDO

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By BRUCE R. WARDLAW, ROBERT A. DAVIS, DAVID M. ROHR, and RICHARD E. GRANT

Leonardian and Wordian units in the northern Del Norte Mountains represent deposition in a fan delta and distal tidal flat complex.

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Leonardian-Wordian (Permian) Deposition in the Northern Del Norte Mountains, West Texas

By Bruce R. Wardlaw,¹ Robert A. Davis,² David M. Rohr,³ and Richard E. Grant⁴

Abstract

The upper part of the Cathedral Mountain Formation, the Road Canyon Formation, and the first sandstone member of the Word Formation of West Texas represent deposition in a fan delta complex that successively consisted of distal fan delta lobe plain, distal delta front, and prodelta, carbonate shelf, and lower delta plain.

The Willis Ranch Member and the second sandstone member of the Word Formation and the Altuda Formation represent deposition in a distal tidal flat complex reflecting cutoff, abandonment, and migration of the active fan delta.

Conodont biostratigraphy supports correlation of the Altuda Formation with the Appel Ranch Member of the Word Formation or younger units in the Glass Mountains.

INTRODUCTION

The middle Permian deposits of the northern Del Norte Mountains of West Texas represent the southernmost and westernmost preserved sedimentary rocks deposited on a narrow shelf that includes the Glass Mountain regional standard sections for the Wolfcampian, Leonardian, and Wordian. The narrow shelf existed between the Marathon folded belt to the south and basinal deposits of the Hovey channel and Sheffield channel to the west and north, respectively (fig. 1). The Marathon folded belt probably was an emergent area and a source for the abundant clastic rocks within the Permian section (King, 1931). Clastic deposition is more prevalent in the Del Norte Mountains than it is in the Glass Mountains, where significant carbonate deposits occur within a clastic sequence (fig. 2). The deposition of clastic rocks has been variously interpreted as basal (Cys and Mazzullo, 1978; Ross, 1986) or shelfal (King, 1931; Flores and others, 1977, 1981). The clastic rocks of the northern Del Norte Mountains were deposited in shallow marine shelf, tidal flat, and fluvial deltaic settings. Periodic marine carbonate incursions, related to local relative rises in sea level, represent southward migration of shelf deposition over deltaic marine and fluvial clastic sediments.

The upper Cathedral Mountain, Road Canyon, Word, and Altuda Formations are described, and their distribution in the east-central portion of the Bird Mountain 7.5-min quadrangle in Brewster County, Texas, is shown (fig. 3). The upper Cathedral Mountain Formation represents shallow-water marine deltaic deposition including quiet-water fossil plant and high-energy channel conglomeratic deposition. The Road Canyon Formation was deposited on a shallow-water marine shelf, dominated by carbonates. The Word Formation represents shallow-water to supratidal deposition of sheet sands marked by sparse channels and overflow deposits preserved as pebble beds. Sand deposition was interrupted by very shallow water marine shelf deposition of the Willis Ranch Member, which concluded with intertidal to supratidal deposition of stromatolitic lime mudstones. The Altuda Limestone represents tidal flat and marine tidal channel deposition.

The Road Canyon Formation and the Willis Ranch Member of the Word Formation are represented by transgressive marine shelfal facies over shallow water to supratidal sandstone and conglomerate facies. The Altuda Limestone, on the other hand, is not as laterally extensive as the Road Canyon or Willis Ranch and appears as a lateral facies of carbonate-clastic deposition to the general sandstone and siltstone deposition of the upper part of the Word.

STRATIGRAPHIC UNITS

The upper Cathedral Mountain, Road Canyon, Word, Altuda, and Capitan Formations crop out in the east-central part of the Bird Mountain 7.5-min quadrangle, forming a crescent-shaped amphitheater capped by the Capitan Limestone (fig. 3). Four sections (fig. 3) were measured. Lithic units (1-18) were described and assigned to the various formations and members. Measured sections I and II (fig. 4) consist of the Cathedral Mountain Formation (units 1-4). Measured section IV (fig. 4) consists of the upper part of the Cathedral Mountain, Road Canyon, and Word Formations (units 5-13). The Altuda Formation was measured and collected for conodonts, but, because it was substantially

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Figure 1. Location of the northern Del Norte Mountains, the Glass Mountains, and important paleogeographic features of the Permian of West Texas (modified from Flawn and others, 1961; Ross, 1986).

the same as section III, it was not included in this report. Measured section III consists of the uppermost Cathedral Mountain, Road Canyon, Word, and Altuda Formations (units 5–18). The Capitan Limestone in this area is a massive cliff-forming unit composed largely of carbonate collapse breccias and virtually devoid of fossils. Its deposition is not dealt with in this text.

Cathedral Mountain Formation

Unit 1: Interbedded Coarse Siltstone, Fine Sandstone, and Carbonates

The lower part of the unit (section I, fig. 4), near intrusive rocks of Smith Peak, consists of interbedded recrystallized carbonates and coarse siltstone to fine sandstone, siliceous cement, and laminar and wavy bedding. Most primary features of the carbonates have been destroyed; only some fossil molds remain. Epidote is the dominant secondary mineral. The carbonates become less recrystallized upward where some skeletal grains are identifiable.

Above the recrystallized part of the unit are two clastic sequences that generally coarsen upward and terminate in carbonates. Clastics consist of coarse siltstone and siliceous cement grading upward to fine sandstone and of scattered discontinuous beds of sandy skeletal wackestone. The clastics display laminar and wavy bedding and bioturbation; horizontal burrows are present in the upper part. The upper part of the lower sequence is sandstone and calcareous cement and is terminated by a sandy pelletal skeletal lime mudstone overlain by an intraclastic pelletal skeletal wackestone to packstone that displays discontinuous channeling, lag deposits, graded beds, and trough crossbedding. The upper sequence is sandstone and siliceous cement that ends in a laterally discontinuous massive bed of sandy intraclastic wackestone.

In section II (fig. 4), the sandstone and carbonate intervals are almost entirely sandy intraclastic skeletal wackestone to packstone. Discontinuous graded beds and local crossbedding occur in the lower sequence. Sandy skeletal wackestone to packstone characterized by discontinuous graded beds is in the upper sequence. Siltstone in the upper sequence has siliceous cement near the bottom and calcareous cement near the top.
Unit 2: Fine Sandstone, Coarse Siltstone, and Discontinuous Carbonate Beds

Section I is represented by very fine to fine, immature, hematitic sandstone, siliceous cement, and quartz and chert grains. All sandstones but the lowest bed contain fossil leaves and horizontal burrows along bedding planes. The lowest sandstone bed contains large horizontal burrows filled with lime mud and exhibits low-angle crossbedding. Section II is represented by coarse siltstone and siliceous and calcareous cement, composed mostly of quartz but containing some chert grains and sedimentary rock fragments. Wavy bedding is common, and horizontal burrows are present in the upper parts of some beds. The carbonates are discontinuous beds of two general types in both sections: (1) thin to medium beds of sandy, intraclastic, skeletal lime mudstone containing pelletal intraclasts and (2) medium to massive beds of sandy, skeletal wackestone to packstone that display graded bedding in thicker beds and are laterally discontinuous. Sand grains are quartz and chert; some beds contain pelletal intraclasts.

Unit 3: Skeletal Carbonate

Unit 3 is generally massive-bedded, sandy, intraclastic, skeletal wackestone to packstone and minor pelletal grainstone. intraclasts are indeterminate sedimentary rock fragments and pelletal lime mudstone. Sand grains are predominantly quartz, but some are chert and feldspar. The beds contain abundant fusulinids and display some graded bedding, low-angle crossbedding, and channels that cut into one another (fig. 5A). This unit is fairly continuous over the map area but shows considerable local pinching and swelling (fig. 5B).

Unit 4: Interbedded Very Fine to Fine Sandstone and Carbonates

Sandstones are immature and hematitic and contain siliceous and calcareous cement and mostly quartz and chert grains. Some beds show increasing sedimentary rock fragments in the upper part of the unit. Beds display both parallel and wavy bedding planes. The bases of some beds contain rip-up clasts and pebbles of novaculite and silicified wood. Carbonates are discontinuous in the lower part but fairly continuous in the upper part; they are generally massive and consist of sandy, intraclastic, skeletal wackestone to grainstone and minor skeletal lime mudstone. Beds commonly display graded bedding and crossbedding. Intraclasts are common and include clastic rocks and pelletal lime mudstone. Sand grains are mostly quartz. Packstones and grainstones contain abundant fusulinids. Chert replacement of fossils is common.
Figure 3. East-central portion of the Bird Mountain 7.5-min quadrangle showing section locations (mapping by R.A. Davis, compilation by B.R. Wardlaw).
Figure 4. Measured sections I and II, units 1 through 4, and explanation of lithic symbols.
A

B

Figure 5. Channel deposits in the Cathedral Mountain Formation. A, Multiple sets of opposite-dipping, truncated, channel crossbedded wackestone and packstone interpreted as tidal channels. Bioturbation is uncommon in these beds. Cathedral Mountain Formation, section II, unit 3. B, Tidal channel deposit of crossbedded packstones cutting into siltstone. Abundant abraded marine bioclasts are present. Cathedral Mountain Formation, section II, unit 3.

Unit 5: Interbedded Mudstone, Coarse Siltstone, Fine Sandstone, and Carbonates

Unit 5 is generally poorly exposed. Sandstones and siltstones are similar to those in units below. Mudstones are common and generally sandy and commonly display contorted laminations. Carbonates are similar to those in units below but also include sandy and rare pebbly grainstone, sandy lime mudstone, wackestone, and packstone (not skeletal). One bed displays tabular crossbedded granular mudstone channeling into sandy packstone. The bed immediately above consists of a highly burrowed, very fine, immature, subarkosic sandstone and siliceous cement. The burrows are large Skolithos-type vertical burrows. The upper part of this unit is finely laminated, immature, sandy siltstones and shales and siliceous and calcareous cement.

Abundant leaf impressions are found near the top (Mamay and others, 1984). These beds contain layers of black organic shale and abundant calcispheres and are interbedded with lime mudstone containing a sparse gastropod fauna and common conodonts.

Unit 6: Sandy Conglomerate

Unit 6 is sandy conglomerate interbedded with fine sandstone lenses (fig. 6A). Conglomerate is composed mostly of chert grains, pebbles, and cobbles; carbonate clasts containing silicified fossils are present, as are uncommon logs of silicified wood and rare clasts of other rock fragments. Sandstone is very fine to fine and submature and contains calcareous and siliceous cement. Grains are mostly quartz and chert and include some sedimentary rock fragments. Beds commonly display graded bedding, reverse graded bedding, and rare slump structures that display recumbent folding.

Road Canyon Formation

Unit 7: Skeletal Carbonate and Minor Sandstone and Shale

The Road Canyon Formation thins dramatically from east to west in the map area (200–20 ft). Section III (fig. 7) contains a thin ledge of limestone composed of sandy grainstone at its base and grades upward to skeletal packstone and silty skeletal wackestone. Quartz and skeletal grains commonly show slight imbrication in the grainstones. Skeletal elements in the packstone and wackestone are commonly large. Section IV (fig. 7) contains a poorly exposed, thick sequence of sandy, skeletal packstone at its base. In the upper part of the sequence are sandy skeletal packstone and wackestone interbedded with limey medium sandstone containing quartz and lithic grains. Carbonates are predominantly packstone in the lower part and wackestone in the upper part. Lime mudstone is common at the base of the skeletal wackestone beds. Packstone contains rip-up clasts. The uppermost part of the formation is a poorly sorted, fine, immature calcareous sandstone grading to shale and overlain by a thick ledge of carbonate composed of lime mudstone grading to skeletal wackestone.

Word Formation

First Unnamed Sandstone Member

Unit 8: Pebby, Very Fine to Coarse Sandstone and Discontinuous Conglomerate Beds

Section III (fig. 8) is fine to medium sandstone that can be divided into two parts. The lower part is submature and contains siliceous cement at the base and calcareous cement at the top; the sandstone is hematitic and limey and
characterized by bimodal grain distribution. The upper (larger) part is immature, contains siliceous cement, and fines upward; discontinuous layers of chert pebbles are present throughout. The unit is dominated by angular quartz grains, some chert, and very sparse mica and sedimentary rock fragments. Scattered low-angle cross bedding is found in float. Section IV (fig. 8) is represented from base to top by (1) very fine, silty, immature sandstone and siliceous cement, (2) fine, immature sandstone and calcareous cement, (3) fine, submature sandstone and siliceous cement, and (4) very fine, immature sandstone and calcareous cement. Silicified wood is common as cobbles at the base. A lenticular-shaped channel deposit of submature sandy conglomerate, containing calcareous and siderite cement, and chert pebbles and cobbles is near the base. Relatively clean quartz sands are in the middle of the unit, and a coarse fining-upward sequence near the top displays scattered discontinuous pebble beds and low-angle cross bedding.

Willis Ranch Member

Unit 9: Cherty Sandy Carbonate and Minor Sandy Siltstone

Section III (fig. 8) is represented by sandy skeletal packstone and sandy, pelletal, skeletal grainstone. Cross bedding and graded bedding occur sporadically throughout this unit. Abundant fusulinids and sparse rip-up clasts of sedimentary rock occur in the middle of the unit as a channel deposit of silty fusulinid packstone in silty, cherty lime mudstone. Chert is abundant in some layers along bedding planes. Section IV is represented by sandy skeletal wackestone and one bed of sandy siltstone near the middle of the unit. Wackestone has common chert stringers and faint cross bedding throughout the unit. Fusulinids are abundant in the middle of the unit.

Unit 10: Interbedded Siltstone, Sandstone, Lime Mudstone, and Discontinuous Skeletal Carbonate Beds

In unit 10, sections III and IV are similar, both consisting of interbedded sandy siltstone, siltstone, and sandy mudstone. Section III exhibits a few beds of limey, pelletal, fine sandstone in siltstone and a thick discontinuous bed of fusulinid packstone to wackestone containing common cobble-sized lithoclasts near the base (channel lag deposit) overlain by lime mudstone. In section IV, two relatively thin, discontinuous beds of fusulinid wackestone to lime mudstone occur. The uppermost bed is overlain by laminated siltstone and contains abundant clasts and intraclasts of pelletal lime mudstone in a heavily dolomitized matrix.

Unit 11: Stromatolitic Lime Mudstone

The thin-bedded lime mudstone that comprises unit 11 exhibits microscopic algal filaments (fig. 6B) and irregular algal laminations.
Figure 7. Measured sections III and IV, units 5 through 7, and explanation of lithic symbols.
SECTION IV

WILLIS RANCH
MEMBER,
WORD

FORMATIONS

UNIT 12
UNIT 11
UNIT 10
UNIT 9
UNIT 8

NEED TO CLARIFY TABLES AND FIGURES

SECTION III

UNIT 12
UNIT 11
UNIT 10
UNIT 9
UNIT 8

First Sandstone Member, Word Formation

LIMESTONE OR LIMEY
SANDSTONE OR SANDY
SILTSTONE OR SILTY
MUDSTONE AND SHALE OR MUDDY
CONGLOMERATE OR CONGLOMERATIC
TRACHYTE SILL

Figure 8. Measured sections III and IV, units 8 through 12, and explanation of lithic symbols.
Unit 12: Interbedded Sandstone, Siltstone, Mudstone, and Carbonate

Unit 12 in section III is composed of siltstone and siliceous cement, overlain by a skeletal lime mudstone containing abundant brachiopod spines; fine to medium, submature sandstone and calcareous cement; and siltstone and siliceous cement, overlain by silty skeletal lime mudstone containing lithoclasts of lime mudstone. There is abundant calcite veining in the unit. Section IV is represented by siliceous siltstone overlain by skeletal coarse sandstone containing calcareous cement, abundant brachiopod spines, and some chert.

Second Unnamed Sandstone Member

Unit 13: Very Fine to Medium Sandstone

Section III (fig. 9) contains a thin interval of fine to medium sandstone, which is immature and hematitic and contains siliceous cement. In section IV (fig. 9), the unit is considerably thicker and consists of medium, submature sandstone and siliceous cement; very fine, immature sandstone and calcareous cement; and fine and medium, mature sandstone and siliceous cement. The dominant grains in both sections are quartz; some chert and rare feldspar are also present. Ripples displaying mud drapes are common near the top of both sections, and clasts containing scattered low-angle crossbedding are found in float. Tertiary trachyte sills cut through this unit in both sections.

Altuda Formation

Unit 14: Interbedded Carbonate and Mudstone

Unit 14 is silty, intraclastic, pelletal, skeletal wackestone to lime mudstone containing intraclasts of pelletal lime mudstone. Some micritic envelopes are present around sparite-filled rounded voids. The unit becomes more skeletal and the wackestone more coarse toward the top.

Unit 15: Interbedded Carbonate and Siltstone

Skeletal, pelletal wackestone to packstone, some with intraclasts of pelletal lime mudstone and other lithic fragments, are interbedded with pelletal limey siltstone and silty lime mudstone, which are commonly composed of pellets, some of which display micritic envelopes, as in unit 14. A trachyte sill cuts the top of this unit in section III (fig. 9).

Unit 16: Mudstone and Minor Discontinuous Carbonate Beds

Poorly exposed mudstone contains small ledges of discontinuous carbonate beds near the top. The carbonate is pelletal lime mudstone and sparse skeletal, intraclastic pelletal packstone containing intraclasts of pelletal lime mudstone and other lithic fragments.

Unit 17: Interbedded Carbonate and Mudstone

Unit 17 is gradational with unit 16 and represents an increase in the number and thickness of carbonate beds. The carbonates in this unit are the same lithology as those in unit 16.

Unit 18: Interbedded Lime Mudstone and Mudstone

Finely laminated silty lime mudstone having indistinct grains exhibits scattered ripple marks. Limey mudstone is generally not laminated.

CONODONT BIOSTRATIGRAPHY

Behnken (1975) and Clark and Behnken (1979) have developed a loosely defined biostratigraphic zonation for Leonardian and Guadalupian rocks based on the succession of *Neogondolella* species in the Permian sequence of the Guadalupe Mountains of West Texas.

Guadalupe Mountains

*Neogondolella idahoensis* occurs in the Bone Spring Formation. The range of *N. serrata* begins at the base of the Cutoff Shale and continues through the Brushy Canyon Formation of the Delaware Mountain Group into the lower part of the Getaway Limestone Member of the Cherry Canyon Formation (Delaware Mountain Group). The range of *N. aserrata* begins in the uppermost bed of the Getaway Member of the Cherry Canyon Formation (B.R. Wardlaw, unpublished data, 1988) and continues into the South Wells and Manzanita Limestone Members of the Cherry Canyon Formation and the Hegler Limestone Member of the Bell Canyon Formation (Delaware Mountain Group). *N. post-serrata* (and various morphotypes not recognized in this paper, including *N. denticulata, N. babcocki*, and *N. rosenkrantzi* of Clark and Behnken, 1979) occurs in the upper part of the Hegler, Pinery, Rader, McCombs, and Lamar Limestone Members of the Bell Canyon Formation.

Glass Mountains

*Neogondolella idahoensis* occurs in the Skinner Ranch and Cathedral Mountain Formations. The changeover of *N. idahoensis* to *N. serrata* is sharp and occurs in the lower third of the Road Canyon Formation (Grant and Wardlaw, 1984). *N. serrata* is found in the upper part of the Road Canyon Formation and the China Tank and Willis Ranch Members of the Word Formation. *N. aserrata* first
occurs in the limestone lens between the Willis Ranch and Appel Ranch Members of the Word Formation and persists in the Appel Ranch Member. Conodont faunas have become very sparse in the Vidrio Limestone Member of the Word Formation but appear to contain *N. aserrata*. Conodont faunas have not been recovered from the Capitan Limestone in the eastern Glass Mountains.

**Del Norte Mountains**

*Neogondolella idahoensis* occurs in the Cathedral Mountain Formation and the lowermost beds of the Road Canyon Formation. *N. idahoensis* and *N. serrata* overlap ranges for a few feet in the basal beds of the Road Canyon. *N. serrata* is found throughout the remainder of the Road Canyon and most beds of the Willis Ranch Member of the Word Formation. The uppermost stromatolitic lime mudstone and the brachiopod spine bed of the Willis Ranch Member are devoid of conodonts. The sandstones of the upper part of the Word Formation are also devoid of conodonts and other marine fossils. *N. aserrata* first occurs in the lowest beds of the Altuda Formation and persists throughout that unit. The overlying upper massive member of the Capitan Limestone, represented mostly by collapse breccias, is nearly devoid of all fossils.

The occurrence of the faunal changeover of *N. idahoensis* to *N. serrata* within the lower part of the Road Canyon Formation in both the Glass and the Del Norte Mountains (fig. 2) strongly correlates that unit. The faunal changeover of *N. serrata* to *N. aserrata* occurs within the Word Formation between the Willis Ranch Member and the Appel Ranch Member in the Glass Mountains. In the northern Del Norte Mountains, this faunal changeover occurs within the Word Formation between the Willis Ranch Member and the overlying Altuda Formation, which correlates the Altuda Formation in the Del Norte Mountains with the Appel Ranch Member of the Word Formation or younger units in the Glass Mountains (see Rudine and others, 1988).

Wardlaw and Collinson (1984) have developed a model for Permian conodont biofacies (a series of nearshore to offshore biofacies) within the Phosphoria Formation and related rocks in the northern Rocky Mountains. Although conodont faunas from the Permian of the Del Norte Mountains (table 1) are not exactly the same, the model may still be applicable. Limestone samples from the Cathedral Mountain Formation all contain a rich fauna dominated by *Neostreptognathodus*; *Neogondolella* and scattered occurrences of *Hindeodus* and *Sweetina* are also present. These faunas are diagnostic of intermediate facies. Conodont faunas from limestones sampled in the Road Canyon Formation and the Willis Ranch Member of the Word Formation contain a rich fauna dominated by *Neogondolella*; *Xaniognathus* and commonly *Hindeodus* and scattered occurrences of *Sweetina*, *Neostreptognathodus*, and *Sweetognathus* are also present. These faunas are diagnostic of offshore facies. The lime mudstones at the base of the Altuda Formation contain a fauna that is almost entirely and abundantly *Hindeodus* but includes very rare elements of *Sweetina* and *Sweetognathus*. These faunas are diagnostic of offshore facies. The lime mudstones at the base of the Altuda Formation contain a fauna that is almost entirely and abundantly *Hindeodus* but includes very rare elements of *Sweetina* and *Sweetognathus*. These faunas are diagnostic of offshore facies.

### Table 1. Conodont faunas recovered from samples of Permian units from the northern Del Norte Mountains of West Texas

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<td>USGS 29410-PC</td>
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</tbody>
</table>

1 Conodont species are indicated by numbers, as follows:
1. *Neogondolella idahoensis* (Youngquist, Hawley, and Miller)
2. *Neogondolella serrata* (Clark and Ethington)
3. *Neogondolella aserrata* Clark and Behnken
4. *Neostreptognathodus pravi* Behnken
5. *Neostreptognathodus sulcoplicatus* (Youngquist, Hawley, and Miller)
6. *Neostreptognathodus newelli* Wardlaw and Collinson
7. *Hindeodus excavatus* (Behnken)
8. *Hindeodus* sp.
9. *Sweetina festiva* (Bender and Stoppel)
10. *Sweetina* sp.
11. *Sweetognathus iranicus* Kozur, Mostler, and Rahimi-Yazd
12. *Sweetognathus* sp.
13. *Xaniognathus abstractus* (Clark and Ethington)

2 Sample from extension of section IV into Altuda Formation, in ascending order.
Figure 9. Measured sections III and IV, units 13 through 18, and explanation of lithic symbols.
of near-shore facies. Skeletal wackestones and packstones sampled throughout the remainder of the formation yield faunas dominated by *Neogondolella*, like those recovered from the Road Canyon and Willis Ranch, and indicative of offshore facies. Only one sample was taken from a sparsely skeletal bed of the laminated lime mudstone at the top of the formation, and it contains a sparse fauna of *Neogondolella, Xaninograptus, Hindeodus*, and *Sweetina*, which indicates an offshore facies.

These generalized facies are only relative and may be strongly related to energy regimes of the depositional environment (that is, offshore corresponds to lower energy depositional environments). But it is clear that faunas from the Cathedral Mountain Formation appear to consistently indicate higher energy, nearer shore deposition than faunas from the Road Canyon, Word, and Altuda Formations, with the exception of faunas at the base of the Altuda, which also indicate nearer shore deposition.

**DEPOSITIONAL SETTING**

The clastic-dominated deposition of the Del Norte and Glass Mountains has generally been considered to be basinal (recently, Ward and others, 1986; Ross, 1986). The rocks described here for the northern Del Norte Mountains are better explained as part of a generally marine–fan delta complex. The Cathedral Mountain Formation appears to represent deposition of the fluvial (lower delta plain)-dominated fan delta. The Road Canyon Formation appears to have been the result of a major marine incursion by shelfal carbonates. The first sandstone member of the Word Formation marks the return of a distal fluvial-dominated fan delta. The remainder of the Word Formation and the Altuda Formation appear to represent deposition of a distal tidal-dominated fan delta. The nearby Marathon folded belt would have been an excellent source. This fan delta depositional model is not unlike the well-documented fan delta complexes developed along the Ouachita thrust belt (Thompson, 1982) and along the Amarillo-Wichita uplift (Dutton, 1982) in the Pennsylvanian. The probably arid climate of the Permian in West Texas (Newell and others, 1953) would support the development of a fan delta complex.

**Cathedral Mountain Formation**

Unit 1 (interbedded coarse siltstone, fine sandstone, and carbonates), unit 2 (fine sandstone, coarse siltstone, and discontinuous carbonate beds), unit 3 (skeletal carbonate), and unit 4 (interbedded very fine to fine sandstone and carbonate) represent deposition in a laterally variable marine distal fan delta lobe plain. The coarsening-upward sequences represent distal fan belt lobes, and overlying carbonates represent abandonment of the lobes. Fine sandstone, siltstone, and silty wackestones to packstones represent generally marine interlobe plain deposition characterized by variably distributed outwash sands, relatively quiet water silt deposition, and carbonate tidal channel and shallow shelf deposition.

Unit 5 (interbedded mudstone, coarse siltstone, fine sandstone, and carbonates) represents distal delta front and prodelta deposition.

Unit 6 (sandy conglomerate) represents a return of fan delta lobe deposition.

The abundant delicate leaf fossils in unit 2 and the upper part of unit 5 and the intermediate conodont biofacies in all the carbonates support the depositional interpretation.

**Road Canyon Formation**

Skeletal carbonate and minor sandstone and shale represent shallow marine shelf deposition that includes small incursions of distal delta front and prodelta deposition. The basal beds of skeletal packstone containing rip-up clasts indicate probable transgressive sedimentation over the fan delta lobe plain due to a local relative rise in sea level.

**Word Formation**

The first sandstone member, unit 8 (pebbly, very fine to coarse sandstone, and discontinuous conglomerate beds), appears to represent lower delta plain deposition, rare channel conglomerates, and common overflow and sheet flow pebble beds.

In the Willis Ranch Member, unit 9 (cherty, sandy carbonate and minor siltstone), unit 10 (interbedded siltstone, sandstone, lime mudstone, and discontinuous skeletal carbonate beds), unit 11 (stromatolitic lime mudstone), and unit 12 (interbedded sandstone, siltstone, mudstone, and carbonate) are interpreted as an incursion of shallow shelf carbonate deposition, perhaps due to a relative rise in sea level followed by shallow tidal flat deposition accompanied by carbonate tidal channels and shallow subtidal supratidal stromatolitic lime mudstone deposition.

The second sandstone member, unit 13 (very fine to medium sandstone), represents very shallow to exposed tidal flat deposition.

**Altuda Formation**

Unit 14 (interbedded carbonate and mudstone) and unit 15 (interbedded carbonate and siltstone) represent marine tidal flat deposition that may be attributed to a slight relative rise in sea level. The units become coarser and more skeletal upward, perhaps indicative of slightly more open circulation to the tidal flat.
Unit 16 (mudstone and minor discontinuous carbonate beds) and unit 17 (interbedded carbonate and mudstone) represent shallow mud flat and carbonate tidal channel deposition. Tidal channels increase in size and abundance upwards.

Unit 18 (interbedded lime mudstone and mudstone) appears to represent shallow subtidal to supratidal tidal flat deposition.

The deposition of the Willis Ranch Member and the second sandstone member of the Word Formation and the Altuda Formation represents a complex of distal tidal flat deposition, far removed from the fan delta complex, which probably represents cutoff, abandonment, and migration of active fan delta deposition. The tidal flat is variously represented by sand, carbonate, and mud deposition in apparent shallowing-upward and deepening-upward sequences. The Willis Ranch Member and the second sandstone member of the Word Formation represent a shallowing-upward sequence dominated by carbonate at its base and sand at its top. Most of the Altuda Formation represents a generally deepening-upward sequence initiated by a possible marine incursion marked by interbedded skeletal carbonates and mudstones followed by mudstones. The mudstones are increasingly cut by carbonate tidal channels toward the top. The uppermost part of the Altuda Formation represents a shallowing-upward sequence of laminated lime mudstones and mudstones.

REFERENCES CITED


Chapter B

Variation and Ontogeny of Calycoceras (Proeucalycoceras) canitaurinum (Haas, 1949) from the Upper Cretaceous (Cenomanian) of the Western Interior of the United States

By WILLIAM A. COBBAN and W. JAMES KENNEDY

Description and illustrations of an important upper Cenomanian index ammonite from the Western Interior of the United States

U.S. GEOLOGICAL SURVEY BULLETIN 1881

Shorter Contributions to Paleontology and Stratigraphy
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   Family ACANTHOCERATIDAE de Grossouvre  B4
      Subfamily ACANTHOCERATINAE de Grossouvre  B4
         Genus Calycoceras Hyatt  B4
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Variation and Ontogeny of Calycoceras (Proeucaleycoceras) canitaurinum (Haas, 1949) from the Upper Cretaceous (Cenomanian) of the Western Interior of the United States

By William A. Cobban and W. James Kennedy

Abstract

Mantelliceras canitaurinum Haas, 1949 was originally described from the basal part of the Cody Shale near Greybull, Wyo. The species, which belongs to the genus Calycoceras Hyatt, 1900, subgenus Proeucalycoceras Thomel, 1972, shows considerable variation. This upper Cenomanian index fossil is known from north-central Montana south to southwestern New Mexico and possibly to Trans-Pecos Texas.

INTRODUCTION

Calycoceras (Proeucaleycoceras) canitaurinum (Haas, 1949) is a large, ornate ammonite that was first described as Mantelliceras canitaurinum from the basal part of the Cody Shale near Greybull, Wyo. (Haas, 1949, p. 9, pls. 1–3; pl. 4, figs. 1, 2, 4; text figs. 1–4), where it was associated with Metoicoceras praecox (Haas, 1949) and Dunveganoceras pondi Haas, 1949. The last-named species is widely used as the index fossil for the lowest zone of the upper Cenomanian in the northern part of the Western Interior in north-central and south-central Wyoming, along the flanks of the Black Hills in southwestern South Dakota and northeastern Wyoming, and, less commonly, in eastern Colorado and central Kansas. The species has not been found farther south. In contrast, C. (P.) canitaurinum has a much wider geographic distribution (text fig. 1) that extends from north-central Montana to New Mexico and possibly to Trans-Pecos Texas. In the southern area, where Dunveganoceras pondi is absent, C. (P.) canitaurinum serves as the zonal index fossil for the interval (Cobban, 1984, fig. 2). Haas’s type specimens, which consist of fragmentary adults up to 290 mm in diameter, lack the early whorls. We here describe abundant new collections that illustrate the ontogeny, intraspecific variation, and dimorphism within the species.

The fossils described in this report are kept in the U.S. National Museum of Natural History (USNM) in Washington, D.C. All specimens have USNM catalog numbers. Plaster casts of a few of the specimens are at the Federal Center in Denver, Colo. We thank R.E. Burkholder (retired from the U.S. Geological Survey) for assistance with the photography, and Kennedy acknowledges the assistance of the staff of the Geological Collections, Oxford University Museum and the Department of Earth Sciences, Oxford, U.K., and the financial support of the Natural Environment Research Council (U.K.), the Royal Society, and the Astor Fund (Oxford).

LOCALITIES OF COLLECTIONS

Localities at which Calycoceras (Proeucaleycoceras) canitaurinum have been collected in the Western Interior are shown in figure 1. The U.S. Geological Survey (USGS) Mesozoic locality number, name(s) of collectors, year of collection, locality, and stratigraphic assignment are as follows (prefix D indicates Denver Mesozoic locality numbers; all others are Washington, D.C., Mesozoic locality numbers):

<table>
<thead>
<tr>
<th>Locality Number</th>
<th>Collector(s)</th>
<th>Year</th>
<th>Locality</th>
<th>Stratigraphic Assignment</th>
</tr>
</thead>
<tbody>
<tr>
<td>D1155</td>
<td>W.A. Cobban</td>
<td>1956</td>
<td>Northern side of Black Coulee southwest of Carter in the S1/2 NE1/4 sec. 17, T. 23 N., R. 6 E., Chouteau County, Montana. Marias River Shale, from a gray septarian limestone concretion 7.6 m below top of Floweree Member.</td>
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<tr>
<td>21368</td>
<td>W.A. Cobban</td>
<td>1947</td>
<td>North of Woody Creek in the NE1/4 SE1/4 sec. 20, T. 3 S., R. 32 E., Big Horn County, Montana. Cody Shale, from septarian limestone concretions in shale unit 29.5 to 34.0 m above base.</td>
<td></td>
</tr>
<tr>
<td>21850</td>
<td>J.B. Reeside, Jr., and D.A. Andrews</td>
<td>1938</td>
<td>East of Herren Gulch in SW1/4 SE1/4 sec. 9, T. 53 N., R. 92 W., Big Horn County, Wyoming. Cody Shale, from silty concretions 24.4 m above base.</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Part of the Western Interior of the United States showing localities where Calycoceras (Proeucalyccoceras) canitaurinum (Haas) has been collected. Numbers are U.S. Geological Survey Mesozoic localities.
E.A. Merewether, 1975. NE¼ NW¼ sec. 12, T. 48 N., R. 83 W., Johnson County, Wyoming. Frontier Formation, from large, brown sandstone concretions 4 to 6 m below top.


E.A. Merewether, 1974; E.A. Merewether and W.A. Cobban, 1984. Emigrant Gap in the SE½ NW¼ sec. 32, T. 34 N., R. 81 W., Natrona County, Wyoming. Frontier Formation, from concretions about 2.7 m below a 2.7-m-thick bed of bentonite.

D.A. Merewether, 1973. SW¼ SW¼ sec. 32, T. 30 N., R. 82 W., Natrona County, Wyoming. Frontier Formation, about 9 m above a 3-m-thick bed of bentonite in Belle Fourche Member.


W.A. Cobban, 1957. E½ SE½ sec. 27, T. 21 N., R. 86 W., Carbon County, Wyoming. Frontier Formation, from brown-weathering limestone concretions in a shale unit in the upper part 13.7 to 18.3 m below a 0.4-m-thick bed of micaceous bentonite.


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R.E. Burkholder and W.A. Cobban, 1961. NE\(^{1/4}\) NW\(^{1/4}\) sec. 23, T. 19 N., R. 1 W., Sandoval County, New Mexico. Dakota Sandstone, from large sandstone concretions at top of Twowells Tongue.

C.H. Dane and E.R. Landis, 1967. Highway 44 about 3.4 km south of Holy Ghost Spring, Sandoval County, New Mexico. Dakota Sandstone, from Twowells Tongue.

C.H. Dane and E.R. Landis, 1967. About 0.7 km south-southeast of Holy Ghost Spring, Sandoval County, New Mexico. Mancos Shale, from 4.5 m below top of Whitewater Arroyo Tongue.

W.A. Cobban, 1966. Just northwest of Armijo Lake, Sandoval County, New Mexico. Dakota Sandstone, from basal part of Twowells Tongue.

W.A. Cobban, 1966. Bottom of arroyo below (east of) Paguate-Seboyeta road in the NW\(^{1/4}\) NE\(^{1/4}\) sec 29, T. 11 N., R. 5 W., Valencia County, New Mexico. Mancos Shale, from glauconitic, calcareous sandstone concretions 14 to 15.5 m below top of Whitewater Arroyo Tongue.

W.A. Cobban, 1967. At road bend just southwest of McCartys in the SE\(^{1/4}\) SW\(^{1/4}\) sec. 27, T. 10 N., R. 8 W., Valencia County, New Mexico. Mancos Shale, from a sandy concretion a few feet below the top of the Whitewater Arroyo Tongue.

W.A. Cobban, 1969. Mount Powell in the Ev\(^{1/2}\) NW\(^{1/4}\) sec. 8, T. 14 N., R. 13 W., McKinley County, New Mexico. Mancos Shale, from a 0.6-m-thick bed of fine-grained sandstone 11.5 m below top of Whitewater Arroyo Tongue.

W.A. Cobban, 1970. West of Whitewater Arroyo in the NE\(^{1/4}\) sec. 17, T. 12 N., R. 19 W., McKinley County, New Mexico. Mancos Shale, from a limestone concretion 8.2 m above base of Whitewater Arroyo Tongue.

W.A. Cobban, 1970. West of Whitewater Arroyo in the NE\(^{1/4}\) sec. 17, T. 12 N., R. 19 W., McKinley County, New Mexico. Mancos Shale, from a limestone concretion 10 m above base of Whitewater Arroyo Shale Tongue.

W.A. Cobban, 1973. State Route 32 in the NW\(^{1/4}\) sec. 18, T. 9 N., R. 17 W., McKinley County, New Mexico. Mancos Shale, from Whitewater Arroyo Tongue.

W.A. Cobban, 1967. NW\(^{1/4}\) sec. 15, T. 4 N., R. 20 W., Catron County, New Mexico. Mancos Shale, from a concretionary limestone bed in Whitewater Arroyo Tongue.

E.R. Landis and W.A. Cobban, 1967. SE\(^{1/4}\) sec. 33, T. 3 N., R. 5 W., Socorro County, New Mexico. Mancos Shale, from a thin bed of sandstone 24 m below top of Whitewater Arroyo Tongue.

S.C. Hook, J.R. Wright, R.R. Cobban, and W.A. Cobban, 1977. Cane Spring Canyon in the NW\(^{1/4}\) SE\(^{1/4}\) sec. 8, T. 17 S., R. 15 W., Grant County, New Mexico. Colorado Formation, from siltstone 3 m above base.


S.C. Hook, E.R. Landis, and W.A. Cobban, 1976. NW\(^{1/4}\) NW\(^{1/4}\) sec. 18, T. 21 S., R. 8 W., Luna County, New Mexico. Colorado Formation, from a basal 1.5-m-thick sandstone bed.

S.C. Hook, J.R. Wright, D.E. Tabet, and J.R. Wright, 1977. NW\(^{1/4}\) NW\(^{1/4}\) sec. 18, T. 21 S., R. 8 W., Luna County, New Mexico. Colorado Formation, from silty limestone 1.8 m above base.

S.C. Hook and W.A. Cobban, 1977. NW\(^{1/4}\) NW\(^{1/4}\) sec. 18, T. 21 S., R. 8 W., Luna County, New Mexico. Colorado Formation, from limestone concretions 3.4 m above base.

CONVENTIONS

Dimensions of specimens are given in millimeters and are indicated as follows: D, diameter; Wb, whorl breadth; Wh, whorl height; Wb:Wh, ratio of whorl breadth to height; and U, umbilical diameter. Numbers in parentheses are percentages of the diameters. The suture terminology of Wedekind (1916) as described by Kullmann and Wiedmann (1970) is followed, where E is the external lobe, L is the lateral lobe, U is the umbilical lobe, and I is the internal lobe.

SYSTEMATIC PALEONTOLOGY

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894
Family ACANTHOCERATIDAE de Grossouvre, 1894
Subfamily ACANTHOCERATINAE de Grossouvre, 1894
Genus Calycoceras Hyatt, 1900
(Synonym: Metacalyoceras Spath, 1926)

Type species.—By designation under the Plenary Powers (ICZN Opinion no. 557) *Ammonites navicularis* Mantell, 1822, p. 198, pl. 22, fig. 5 (ICZN Specific Name no. 1633).
Subgenus Proeucalycoceras Thomel, 1972

Type species.—By original designation Calycoceras (Eucalycoceras) besairei Collignon, 1937 (p. 37, pl. 3, figs. 1–4; pl. 8, fig. 5), from the Cenomanian of Madagascar.

Diagnosis.—The subgenus includes medium- to large-sized dimorphic species that have compressed to depressed whorls. Juveniles have dense, sometimes flat-topped ribs, alternately long and short, displaying umbilical, inner and outer ventrolateral and siphonal tubercles. Ribs dominate in compressed individuals, whereas tubercles are more important in depressed ones; siphonal tubercles may be lost at an early ontogenetic stage. Ornament changes abruptly on the last part of the phragmocone and early part of the adult body chamber, where there are moderate to very strong, distant, well-rounded ribs that cross the venter transversely. Umbilical bullae are present on the long ribs, ventrolateral tubercles are weak or absent, and the whorl section is rounded to subquadrate.

Genus Calycoceras (Proeucalycoceras) canitaurinum (Haas, 1949)

Plate 1. figures 1–12; plate 2. figures 1–12; plate 3. figures 1–7; plate 4. figures 1, 2; text figure 2.

1949. Mantelliceras canitaurinum Haas, p. 9, pls. 1–3; pl. 4, figs. 1, 2, 4; text figs. 1–4.
1977b. Calycoceras? canitaurinum (Haas). Cobban, fig. 5i.

Types.—Holotype, here designated, is AMNH 26413:1, the original of Haas (1949, pl. 1, figs. 1, 2); the holotype and a number of paratypes are all from the lower part of the Cody Shale about 9.7 km east and 11.3 km north of Greybull, Wyo., in the north-central part of T. 53 N., R. 92 W., in the upper Cenomanian Dunveganoceras pondi zone.

Material.—About 120 specimens from 47 localities in the Western Interior were examined. Sixteen specimens (USNM 422686–422700) from four localities (USGS Mesozoic localities 21818, 21850, D7913, and D11753) in Wyoming are described in this report.

Dimensions.—Dimensions of 11 specimens are as follows:

<table>
<thead>
<tr>
<th>USNM no.</th>
<th>D (mm)</th>
<th>Wb (mm)</th>
<th>Wh (mm)</th>
<th>Wb/Wh</th>
<th>U (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>422686</td>
<td>24.9(100)</td>
<td>16.7(67.1)</td>
<td>11.0(44.2)</td>
<td>1.51</td>
<td>5.8(23.3)</td>
</tr>
<tr>
<td>422687</td>
<td>29.5(100)</td>
<td>18.7(53.7)</td>
<td>14.0(47.5)</td>
<td>1.36</td>
<td>27.0(23.6)</td>
</tr>
<tr>
<td>422688</td>
<td>34.8(100)</td>
<td>17.5(50.3)</td>
<td>18.7(53.7)</td>
<td>.94</td>
<td>6.8(19.5)</td>
</tr>
<tr>
<td>422689</td>
<td>50.3(100)</td>
<td>23.3(66.3)</td>
<td>27.3(54.3)</td>
<td>.85</td>
<td>9.7(19.3)</td>
</tr>
<tr>
<td>422690</td>
<td>51.0(100)</td>
<td>26.4(51.8)</td>
<td>24.0(47.1)</td>
<td>1.1 - (-)</td>
<td></td>
</tr>
<tr>
<td>422691</td>
<td>60.8(100)</td>
<td>32.0(56.2)</td>
<td>27.5(45.2)</td>
<td>1.16</td>
<td>14.3(23.5)</td>
</tr>
<tr>
<td>422692</td>
<td>64.3(100)</td>
<td>29.2(45.4)</td>
<td>31.3(48.7)</td>
<td>.93</td>
<td>10.7(16.6)</td>
</tr>
<tr>
<td>422693</td>
<td>84.3(100)</td>
<td>42.3(50.2)</td>
<td>38.3(44.5)</td>
<td>1.12</td>
<td>19.2(28.8)</td>
</tr>
<tr>
<td>422694</td>
<td>96.0(100)</td>
<td>45.3(47.4)</td>
<td>46.5(48.4)</td>
<td>.98</td>
<td>23.3(24.3)</td>
</tr>
<tr>
<td>422695</td>
<td>100.3(100)</td>
<td>74.5(74.2)</td>
<td>41.9(41.1)</td>
<td>1.78</td>
<td>30.0(29.9)</td>
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<tr>
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<td>110.5(100)</td>
<td>75.5(68.3)</td>
<td>52.3(47.3)</td>
<td>1.44</td>
<td>30.6(27.7)</td>
</tr>
<tr>
<td>107.3(100)</td>
<td>66.5(62.0)</td>
<td>48.8(45.5)</td>
<td>1.36</td>
<td>30.6(28.5)</td>
<td></td>
</tr>
</tbody>
</table>

1 c. costal diameter; ic, intercostal diameter.
2 - Measurements not possible.

Description.—Large; specimens interpreted as macroconchs are up to 300 mm in diameter and are incomplete. Specimens interpreted as microconchs are rarer and have diameters up to 150 mm at the end of the phragmocone. The earliest growth stages seen are at diameters of 25 to 50 mm (pl. 1, figs. 1–6); these growth stages show a wide range of morphological variation from compressed with weak ornament to depressed with strong ornament. This variability continues through middle growth and extends through most of the phragmocone whorls (pl. 1, figs. 10–12; pl. 3, figs. 1–3).

In compressed juveniles, such as USNM 422688 (pl. 1, figs. 1–3), coiling is moderately involute, and U = 19.5 percent of the diameter. The umbilicus is shallow and displays an outwardly inclined umbilical wall and a broadly rounded umbilical shoulder. The ratio of costal whorl breadth to height is 0.94, the greatest breadth being at the umbilical bullae. Perched on the umbilical shoulder are 11 to 12 bullae per whorl that give rise to blunt prospirradiate ribs, singly or in pairs; the adapertural rib of any given pair is weaker than the adapical one. One and rarely two shorter ribs intercalate between the bullate ones, generally arise below midflank, and sometimes tenuously link to the umbilical shoulder. Hypotype USNM 422687 has 26 ribs per whorl at a diameter of 34 mm. USNM 422690 has 34 at a diameter of 50 mm, and USNM 422692 has an estimated 40 at a diameter of 66 mm. At small sizes, the ribs develop a small inner ventrolateral tubercle linked by a thickened rib to a feebly clavate outer ventrolateral one. A strong rib passes straight across the flat, broad venter and supports a feebly clavate siphonal tubercle that is slightly weaker than the outer ventrolateral tubercles (pl. 1, figs. 3, 4). Siphonal tubercles disappear at a diameter of 37 mm in USNM 422690, 41 mm in USNM 422692, and 47 mm in USNM 422689. Inner ventrolateral tubercles disappear at an equally early stage (43 mm in USNM 422690 and lesser.

Variation and Ontogeny of Calycoceras (Proeucalycoceras) canitaurinum 85
diameters in other specimens). When the inner ventrolateral tubercles are lost, the whorl sides become more flattened; the ribs broaden and flatten and become wider than the interspaces on both flank and venter from diameters of as little as 45 mm in USNM 422689 and as much as 85 mm in USNM 422694. At this stage, these compressed specimens have a very distinctive appearance. As size increases, the ribs become markedly flexuous, broadened, and crowded, and flattening is especially obvious on the outer flank and ventrolateral shoulder. Thirty-six ribs per whorl are present in USNM 422694 at a diameter of 105 mm and 40 to 42 in USNM 422692 at the same diameter. The ventrolateral tubercles decline and disappear, leaving a flattened venter crossed by flattened bandlike ribs that are much wider than the interspaces (pl. 2, figs. 9, 10); this feature is diagnostic in middle growth. Toward the end of the phragmocone, these ribbonlike flat-topped ribs are replaced by narrower, rounder ribs, separated by wider interspaces on the venter. A feebly clavate ventrolateral horn appears that bounds a flattened to slightly concave venter. On the flanks, the ribs coarsen markedly, to a density of 28 per whorl and 13 on the last half whorl of the phragmocone of USNM 422697 (pl. 4). The ribs become coarse, distant, and prorsiradiate and regularly alternate long and short. Each long rib has a strong umbilical bulla, and a midlateral bulla develops with growth. Neither is present on the shorter ribs.

A series of passage forms links this extreme of variation to the depressed, coarsely ribbed specimens like those shown in plate 2 (figs. 11, 12), plate 3 (figs. 1–3), and text figure 2, which are characterized by very depressed whorl sections. Ratios of whorl breadth to height are 1.51 in USNM 422686 at a diameter of 24.9 mm, 1.36 in USNM 422687 at 29.5 mm, 1.78 in USNM 422695 at 100.3 mm, and 1.44 in USNM 422696 at 110.5 mm. Coiling is evolute, U varying between 23.3 and 30.8 percent of diameter in the above specimens. The inner ventrolateral tubercles of the preceding whorl are housed in notches in the umbilical wall of the succeeding one. In USNM 422686, 28 ribs per whorl correspond to 12 sharp umbilical tubercles from which primary ribs arise singly or in pairs and develop strong conical inner ventrolateral tubercles and feebly clavate, weaker outer ventrolateral and siphonal rows linked by a strong transverse rib. Some nonbullate primaries are also present and have a full complement of ventrolateral and siphonal tubercles, as may some of the shorter intercalated ribs, although others may lack the inner ventrolaterals.
As diameter increases, this coarse ornament persists. The siphonal tubercles are lost at a diameter of as little as 45 mm, although the ribs may be elevated at midventer beyond this diameter. The ribs are strong, narrow, and rectiradiate to rursiradiate and regularly alternate long and short. Strong umbilical bullae may migrate out to an inner flank position, pronounced flare and then a bulla develop at midflank, and as diameter increases, this coarse ornament persists. The ribs are separated by a median groove, and poorly differentiated inner and outer ventrolateral tubercles persist to a diameter of 115 mm in USNM 422695 (pl. 3, figs. 1–3) but merge progressively into the ribs from a diameter of 65 mm in USNM 422696 (pl. 2, figs. 11, 12). Even these coarsely ornamented specimens pass through a stage of broad, flat-topped, ribbonlike ventral ribs, such as USNM 422700, where the adapical and adapertural edges of the ribs are separated by a median groove, and poorly differentiated riblets loop across the venter on the surface of the main rib.

On mature body chambers, the ribbing coarsens markedly, as few as 12 ribs being present on the last half whorl. The ribs are strong, blunt, distant, and alternately long and short. Long ribs begin on the umbilical wall and rise into subspinose umbilical bullae that migrate out to a low flank position toward the adult aperture. Each rib supports a lateral bulla and short ventrolateral horn. The shorter ribs generally lack the lateral bulla. The venter is concave in costal section at this stage. All ribs flatten on crossing the venter and may show feeble division into a pair of riblets that loop between the horns. The umbilical and lateral bullae appear to decline toward the adult aperture, but none of our specimens are complete.

The suture line, which has been well illustrated by Haas (1949, figs. 1–4), is moderately incised; E is narrow, E/L is broad and asymmetrically bifid, and L is narrow.

Discussion.—The adult whorls of C. (P.) canitauri­num, which have coarse, alternately long and short ribs, are immediately distinguishable from all other Western Interior acanthoceratid species.

Juveniles of some variants show a remarkable similarity to certain C. (Newboldiceras) Thomel (1972), but early loss of siphonal tubercles in C. (P.) canitaurinum distinguishes it from C. (N.) newboldi newboldi (Kossmat, 1897, p. 5 (112), pl. 1 (12), figs. 2, 3; pl. 3 (14), fig. 2), and C. (N.) newboldi spinosum (Kossmat, 1897, p. 7 (114), pl. 2 (13), figs. 2, 3; pl. 3 (14), fig. 1). C. (N.) plane­costatum (Kossmat, 1897, p. 9 (116), pl. 2 (13), fig. 1) nuclei may be very close to those of certain C. (P.) canitaurinum (for example, pl. 1, figs. 6–8, 10–12), but the rounded flanks and rounded, flexuous ribs of plane­costatum separate the two.

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Collignon, M., 1937, Ammonites cénomaniens du sud-ouest de Madagascar; Annales Géologiques de Madagascar, no. 8, p. 29–72, pls. 1–11.


Variation and Ontogeny of Calycoceras (Proeucalycoceras) canitaurinum
PLATES 1–4
PLATE 1

Calycoceras (Proeucalycoceras) canitaurinum (Haas) (p. B5).

[All figures natural size]

Figures 1–3. Hypotype USNM 422688, from the upper part of the Frontier Formation at USGS Mesozoic locality D11753 (text fig. 1).

4, 5, 9. Hypotype USNM 422690, from the basal part of the Cody Shale at USGS Mesozoic locality 21850 (text fig. 1).

6–8. Hypotype USNM 422692, from near the top of the Frontier Formation at USGS Mesozoic locality 21818 (text fig. 1).

10–12. Hypotype USNM 422693, from near the top of the Frontier Formation at USGS Mesozoic locality 21818 (text fig. 1).
PLATE 2

*Caly coceras (Proeucalycoceras) canitaurinum* (Haas) (p. B5).

[All figures natural size]

Figures 1–3. Hypotype USNM 422687, from the upper part of the Frontier Formation at USGS Mesozoic locality D11753 (text fig. 1).

4–6. Hypotype USNM 422686, from the upper part of the Frontier Formation at USGS Mesozoic locality D11753 (text fig. 1).

7, 8. Hypotype USNM 422691, from the upper part of the Frontier Formation at USGS Mesozoic locality D7913 (text fig. 1). See text figure 2 for whorl section.

9, 10. Hypotype USNM 422698, from near the top of the Frontier Formation at USGS Mesozoic locality D11753 (text fig. 1).

11, 12. Hypotype USNM 422696, from near the top of the Frontier Formation at USGS Mesozoic locality D11753 (text fig. 1).
PLATE 3
Calycoceras (Proeucalycoceras) canitaurinum (Haas) (p. B5)

[All figures natural size]

Figures 1–3. Hypotype USNM 422695, from near the top of the Frontier Formation at USGS Mesozoic locality 21818 (text fig. 1).
4, 5. Hypotype USNM 422689, from near the top of the Frontier Formation at USGS Mesozoic locality D11753 (text fig. 1).
6, 7. Hypotype USNM 422699, from near the top of the Frontier Formation at USGS Mesozoic locality D11753 (text fig. 1).
PLATE 4
*Calycoceras (Proeucalycoceras) canitaurinum* (Haas) (p. B5).
[Both figures natural size]

Figures 1, 2. Hypotype USNM 422697, from the basal part of the Cody Shale at USGS Mesozoic locality 21850 (text fig. 1).
Chapter C

Observations on the Cenomanian (Upper Cretaceous) Ammonite Calycoceras (Calycoceras) obrieni Young, 1957 from Arizona and New Mexico

By WILLIAM A. COBBAN and W. JAMES KENNEDY

Description of an upper Cenomanian marker ammonite from the southern part of the Western Interior of the United States

U.S. GEOLOGICAL SURVEY BULLETIN 1881

Shorter Contributions to Paleontology and Stratigraphy
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[Plates follow References cited]
1–5. Calycoceras (Calycoceras) obrieni Young

FIGURE
1. Columnar section of the upper part of the Twowells Tongue of the Dakota Sandstone exposed in the eastern side of Cottonwood Canyon, Apache County, Arizona, showing U.S. Geological Survey Mesozoic fossil locality numbers and the more diagnostic molluscan fossils C2
Observations on the Cenomanian (Upper Cretaceous) Ammonite *Calycoceras (Calycoceras) obrieni* Young, 1957 from Arizona and New Mexico

*By* William A. Cobban and W. James Kennedy

**Abstract**

*Calycoceras (Calycoceras) obrieni* Young, 1957 is revised on the basis of new collections from the upper Cenomanian *Metoicoceras mosbyense* zone of Arizona and New Mexico, and differences between it and *C. (C.) naviculare* (Mantell, 1822) are described.

**INTRODUCTION**

*Calycoceras obrieni* Young, 1957 (p. 1171, pl. 150, figs. 1-4; text figs. If, h) is a large, densely ribbed ammonite originally described on the basis of a single badly preserved specimen from the lower part of what Keith Young termed the “Mesaverde Formation” in eastern Apache County, Arizona. Subsequent authors followed Matsumoto (1959, p. 81; Kennedy, 1971, p. 73) in regarding *C. obrieni* as a synonym of *C. (C.) naviculare* (Mantell, 1822), an important upper Cenomanian marker fossil in many parts of the world. We have redescribed *Calycoceras obrieni* on the basis of new, well-preserved specimens that show it to be a valid species, if closely allied to *C. (C.) naviculare*, of which it may be the ancestor.

The fossils described in this report are kept in the U.S. National Museum of Natural History (USNM) in Washington, D.C. and the Texas Memorial Museum (TMM), Austin. All specimens have USNM catalogue numbers. Plaster casts of a few of the specimens are at the Federal Center, Denver, Colo. We thank R.E. Burkholder, retired from the U.S. Geological Survey (USGS), for taking the photographs. Kennedy acknowledges the assistance of the staff of the Geological Collections, Oxford University Museum and the Department of Earth Sciences, Oxford, U.K., and the financial support of the Natural Environment Research Council (U.K.), the Royal Society, and the Astor Fund (Oxford).

**AGE AND OCCURRENCE OF CALYCOCERAS (CALYCOCERAS) OBRIENI**

The holotype of *C. obrieni* and other fossils described by Young were collected by R.K. Deford and others in 1955 in the E½ secs. 3 and 10, T. 10 N., R. 31 E., eastern Apache County, Arizona, from 21 to 27 m above the base of what was then termed the “Mesaverde Formation.” Young regarded the formation as either upper Cenomanian or lower Turonian and certainly close to the boundary of the two stages. He recorded *Metoicoceras defordi* Young, 1957, *Calycoceras obrieni* Young, 1957, *Dunveganoceras* (?) sp. A, and *Dunveganoceras* (?) n.sp. B and illustrated a specimen of *Exogyra columbella* Meek.

The sandstone unit that yielded this fauna is now referred to as the Twowells Tongue of the Dakota Sandstone, and the generalized stratigraphic relationships of the unit have been discussed by Landis and others (1973). Some 27 m of the Twowells Tongue are exposed in the Cottonwood Canyon area that yielded the type material. The lower 18 m are unfossiliferous, but the upper part yielded a series of faunas, as text figure 1 summarizes. *Metoicoceras mosbyense* Cobban, 1953 (of which *M. defordi* Young, 1957 is a synonym) ranges throughout most of the interval and co-occurs with *C. (C.) obrieni*, firmly establishing it as *mosbyense* zone. The highest ammonite fauna, from concretions above the *Pycnodonte newberryi* coquina, is poorly preserved but includes *Pseudaspidoceras* cf. *flexuosum* Powell, 1963 and *Mytiloides* sp.; this assemblage is early Turonian. Reexamination of Young’s original material plus new collections shows that *Dunveganoceras* (?) n.sp. B of Young is a fragmentary *Mammites*, probably of the group of *M. powelli* Kennedy, Wright, and Hancock, 1987; we believe it to be derived from the highest fossil horizon and to be early Turonian, not a contemporary of *C. obrieni*.

**REPOSITORIES OF SPECIMENS**

The following abbreviations are used to indicate the repositories of specimens cited in the text: TMM, Texas Memorial Museum, Austin; USNM, National Museum of Natural History, Washington, D.C.

**CONVENTIONS**

Dimensions of specimens are given in millimeters and are indicated as follows: *D*, diameter; *Wb*, whorl
Figure 1. Upper part of the Twowells Tongue of the Dakota Sandstone exposed in the eastern side of Cottonwood Canyon in the NE\(\text{4 SE}\text{4 sec. 3, T. 10 N., R. 31 E., Apache County, Arizona, showing U.S. Geological Survey Mesozoic fossil locality numbers and the more diagnostic molluscan fossils.}

C2 Shorter Contributions to Paleontology and Stratigraphy
breadth; \( Wh \), whorl height; \( Wb:Wh \), ratio of whorl breadth to whorl height; and \( U \), umbilical diameter. Numbers in parentheses are percentages of the diameters.

**SYSTEMATIC PALEONTOLOGY**

**Family ACANTHOCERATIDAE de Grossouvre, 1894**

**Subfamily ACANTHOCERATINAE de Grossouvre, 1894**

**Genus and Subgenus Calycoceras Hyatt, 1900**

*Type species.*—ICZN Opinion 557, 1959, name no. 1633; *Ammonites navicularis* Mantell, 1822, p. 198, pl. 22, fig. 5.

**Calycoceras (Calycoceras) obrieni** Young, 1957

Plates 1–5

1957. *Calycoceras obrieni* Young. p. 1171, pl. 150, figs. 1–4; text figs. 1f, h.


1971. *Calycoceras obrieni* Young. Kennedy, p. 73


1981. *Calycoceras obrieni* Young. Wright and Kennedy, p. 36.

*Type.*—Holotype by monotypy is TMM 18469 from the Twowells Tongue of the Dakota Sandstone in the upper Cenomanian *Metoicoceras mosbyense* zone of Cottonwood Canyon, sec. 3, T. 10 N., R. 31 E., Apache County, Arizona.

*Material.*—Three topotypes (including hypotypes USNM 422680–422681) collected by W.A. Cobban at USGS Mesozoic locality D6173 in the NE\(\frac{1}{4}\) SE\(\frac{1}{4}\) sec. 3, T. 10 N., R. 31 E., Apache County, Arizona; one hypotype (USNM 422679) collected by Cobban at USGS Mesozoic locality D12163 in the SE\(\frac{1}{4}\) SE\(\frac{1}{4}\) sec. 28, T. 1 N., R. 21 W., Catron County, New Mexico; and two hypotypes (USNM 422678 and 422663) collected by Cobban at USGS Mesozoic locality D12070 in the SE\(\frac{3}{4}\) SW\(\frac{1}{4}\) sec. 30, T. 10 N., R. 30 E., Apache County, Arizona.

*Dimensions.*—Dimensions of five of the six specimens described herein are as follows:

<table>
<thead>
<tr>
<th>USNM no.</th>
<th>(D) (mm)</th>
<th>(Wb(%))</th>
<th>(Wh(%))</th>
<th>(Wb:Wh)</th>
<th>(U) (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>422678</td>
<td>114.0 (100)</td>
<td>64.2 (56.3)</td>
<td>43.8 (38.4)</td>
<td>1.47</td>
<td>38.0 (33.3)</td>
</tr>
<tr>
<td></td>
<td>108.0 (100)</td>
<td>54.2 (50.2)</td>
<td>41.7 (38.6)</td>
<td>1.30</td>
<td>37.8 (35.0)</td>
</tr>
<tr>
<td>422679</td>
<td>90.0 (100)</td>
<td>57.0 (63)</td>
<td>37.0 (41.1)</td>
<td>1.54</td>
<td>26.7 (29.7)</td>
</tr>
<tr>
<td></td>
<td>157.0 (100)</td>
<td>104.0 (66.2)</td>
<td>65 (41.4)</td>
<td>1.6</td>
<td>42.0 (26.8)</td>
</tr>
<tr>
<td></td>
<td>147.0 (100)</td>
<td>82.5 (55.9)</td>
<td>57 (38.6)</td>
<td>1.45</td>
<td>42.0 (28.5)</td>
</tr>
</tbody>
</table>

1. \(c\), costal diameter; \(ic\), intercostal diameter.
2. \(-\), measurements not possible.

**Description.**—USNM 422679 shows the early phragmocone whorls and replaced shell preserved at a diameter of 72 mm (pl. 1, figs. 4, 5). Coiling is evolute; 33 percent of the previous whorl is covered, the inner ventrolateral tubercles of the preceding whorl being housed in shallow notches in the umbilical wall of the succeeding one. The umbilicus is deep, comprises 29 percent of the diameter, and has a flattened wall. The whorl section is depressed reniform in intercostal section, the greatest breadth occurring just outside the umbilicus, and the flanks and venter are broadly and evenly rounded. There are 13 rectiradiate to feebly rursiradiate primary ribs per whorl visible in the umbilicus and 15 per whorl at a diameter of 72 mm. These ribs arise at the umbilical seam and strengthen across the umbilical wall, where they are rounded and separated by wide interspaces. The ribs strengthen markedly across the umbilical shoulder into strong umbilical bullae, which form the point of greatest width of the whorl in costal section. A strong, narrow, high rib connects to a smaller, sharp, inner ventrolateral bulla, the rib profile being markedly concave in profile between the bullae. A lower rib passes straight across the venter to the corresponding inner ventrolateral bulla on the opposite flank without diminution in strength or development of outer ventrolateral or siphonal tubercles at the smallest diameter visible, estimated to be 33 mm. These strong bullate primaries are separated by two to four nontuberculate ribs. Some extend down to the umbilical seam but are much weaker than the primaries; others arise at levels from inner to outer flank, and some are feebly linked to the bullate primaries. These incipient secondary and intercalated ribs strengthen across the ventrolateral shoulder, and all ribs are equally developed across the venter, to give a total rib density of 40 to 42 per whorl at a diameter of 63 mm.

Between diameters of 42 and 63 mm (this interval is concealed in the specimen), the venter flattens, and feebly outer ventrolateral bullae appear, initially little more than an angulation in the rib profile. The ribs broaden and coarsen markedly from this diameter and become markedly rursiradiate. USNM 422680 is a somewhat distorted internal mold 100 mm in diameter (pl. 1, figs. 1–3). It is less depressed than USNM 422679 but shows a comparable ornament and ontogenetic development and has 17 bullate primaries and a total of 38 ribs per whorl.

USNM 422681 continues the ontogeny (pl. 3). It is 167 mm in maximum costal diameter, has just over half a whorl of body chamber preserved, and is an internal mold. There are 27 ribs on the outer whorl. Twelve ribs arise at the umbilical seam and develop into umbilical bullae that strengthen markedly and migrate outward as size increases. These ribs give rise to very coarse, rursiradiate ribs that are high and flared across the flanks. The latter ribs bear well-differentiated outer ventrolateral bullae that are connected across the venter by a broad, coarse rib that is slightly sunken between the ventrolateral tubercles when
viewed in profile. At the beginning of the outer whorl, these strong bullate primaries are separated by two intercalated ribs; the adapical ribs are short, whereas the adapertural ones are long and extend in some cases to the umbilical seam, although they are not bullate. In the last 120° of body chamber, only a single intercalated rib is present, arising on the outer flank and having a ventral development comparable to that of the primaries.

USNM 422682 is a complete adult displaying a preserved shell; the maximum costal diameter is 196 mm (pls. 4, 5). Ornament is the same as that of USNM 422681, but the flares on the primary ribs on the flank are very pronounced and yield a costal whorl breadth to height ratio of up to 1.6. The ribs sharpen and narrow markedly, and the umbilical bulla weakens on the last primary rib before the aperture.

USNM 422678 and 422683 (pl. 2, figs. 1–6) are from the Twowells Tongue 17 km southwest of the type locality of C. (C.) obrieni in the SW¼ SE¼ SW¼ sec. 30, T. 10 N., R. 30 E., in Apache County, Arizona. Both appear to represent a slender form of C. (C.) obrieni. USNM 422678 is 114 mm in maximum costal diameter, 240° of the last whorl being body chamber. The coiling is evolute; U is 33.3 percent of the costal diameter and 35.0 percent of the intercostal diameter, and the umbilical wall is rounded. The whorl section is depressed reniform in intercostal section, and the whorl breadth to height ratio is 1.30, the greatest breadth occurring just outside the umbilical shoulder. The costal ratio is 1.47, the greatest breadth being at the umbilical bullae. At the smallest diameter visible in the umbilicus of the specimen, 14 to 15 primary ribs arise at the umbilical seam, where they are broad, strong, rounded, and rursiradiate. At the smallest diameter, there is a strong umbilical bulla and a slightly weaker inner ventrolateral umbilicus. At the last visible diameter, 14 to 15 primary ribs arise at the umbilical seam, strengthen across the umbilical wall, and develop into prominent umbilical bullae, which give rise to pairs of narrow, sharp, rursiradiate ribs separated by single intercalated ribs that arise below midflank. Well-differentiated outer ventrolateral bullae are present to a diameter of 85 mm, connected across the venter by a broad, transverse rib. The venter remains flattened beyond 85 mm, but the ventrolateral tubercles efface, although this effacement may, in fact, reflect wear on the surface of the specimen. USNM 422683 is wholly septate and slightly crushed, the maximum preserved diameter being 91 mm. Nineteen ribs are present on the last half whorl; they are fewer and coarser than those in USNM 422678, are long and short, and do not arise in pairs from bullae, so that the specimen is intermediate in ribbing strength and character between USNM 422682 and USNM 422678.

**Discussion.**—C. (C.) obrieni has been treated as a synonym of C. (C.) naviculare (Mantell, 1822), as the introduction noted. On the basis of the new material described here, the two species can be distinguished as follows. Taking descriptions of Western Interior C. (C.) naviculare by Cobban (1971) and those of European material by Kennedy (1971) and Wright and Kennedy (1981) as the basis, the inner whorls of C. (C.) obrieni generally have a narrower venter and show a more gradual increase in whorl breadth. Intercostal section is similar in middle and later growth, but large specimens have much coarser ribs that are expandable into marked lateral flanges (pls. 3–6). Outer ventrolateral tuberculation or angulation is more marked, and there is commonly a significant depression in the ribs over the venter.

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PLATE 1
-Calycoceras (Calycoceras) obrieni Young (p. C3).
[All figures natural size]


4. 5. Hypotype USNM 422679, from the Twowells Tongue at USGS Mesozoic locality D12163.
PLATE 2
*Calycoceras (Calycoceras) obrieni* Young (p. C3).

[All figures natural size]

Figures 1–3. Hypotype USNM 422683, from the Twowells Tongue of the Dakota Sandstone at USGS Mesozoic locality D12070. Figure 2 is a Latex peel of the inner dorsum area.

4–6. Hypotype USNM 422678, from the Twowells Tongue of the Dakota Sandstone at USGS Mesozoic locality D12070.
PLATE 3
*Calycoceras (Calycoceras) obrieni* Young (p. C3).

[Both figures natural size]

Figures 1, 2. Hypotype USNM 422681, from the Twowells Tongue of the Dakota Sandstone at USGS Mesozoic locality D6173.
Hypotype USNM 422682, from the Two wells Tongue of the Dakota Sandstone at USGS Mesozoic locality D6173. See plate 5 for end views.
CALYCOCELAS
PLATE 5
_Calycoceras (Calycoceras) obrieni_ Young (p. C3).

[Figure natural size]

Hypotype USNM 422682, from the Twowells Tongue of the Dakota Sandstone at USGS Mesozoic locality D6173. See plate 4 for side view.
Revision of the *Nucula percrassa* Conrad, 1858 Group in the Upper Cretaceous of the Gulf and Mid-Atlantic Coastal Plains: An Example of Bias in the Nomenclature

By G. LYNN WINGARD and NORMAN F. SOHL

U.S. GEOLOGICAL SURVEY BULLETIN 1881

Shorter Contributions to Paleontology and Stratigraphy
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Revision of the *Nucula percrassa* Conrad, 1858 Group in the Upper Cretaceous of the Gulf and Mid-Atlantic Coastal Plains: An Example of Bias in the Nomenclature

By G. Lynn Wingard and Norman F. Sohl

**Abstract**

A discriminant analysis of *Nucula percrassa* Conrad, *N. slackiana* Gabb, *N. tippahensis* Harbison, and *N. sp.* was conducted to resolve questions about their taxonomic, geographic, and stratigraphic relationships. The specimens analyzed were from lower Campanian through upper Maastrichtian units of the Gulf and Mid-Atlantic Coastal Plains. The results indicate that there are no genetically based morphologic features that can distinguish between *N. percrassa*, *N. slackiana*, and *N. tippahensis*; therefore, these three names are synonymized within the single concept *N. percrassa* Conrad, 1858 as here revised. An insufficient number of specimens prevented *N. cibolensis* Stephenson and *N. chattfieldensis* Stephenson (upper Campanian and Maastrichtian, Texas) from being included in the statistical analysis, but the available specimens show no significant morphological differences from *N. percrassa* as defined here. *N. cibolensis* and *N. chattfieldensis* were consequently synonymized with *N. percrassa*. The fourth group, *N. sp.* (previously regarded as a juvenile), was determined during the analysis to be a separate species, named *N. severnensis* n.sp.

The methods by which paleontologists define species and select type specimens change as knowledge increases. This study illustrates instances of nomenclatural biases based on assumed stratigraphic or geographic isolation of populations or on typological differences. The existence of such biases can have profound effects on the calculation of rates of evolution and extinction. For the Nuculidae, the bias was toward shorter species durations and increased species diversity. This study indicates the importance of establishing fossil species by the objective examination of preserved morphologic differences. Until consistent, reproducible taxonomies are constructed, paleontologists should proceed cautiously with inductive conclusions about the evolution and extinction of organisms.

**INTRODUCTION**

*Nucula* has been known in marine Cretaceous rocks of North America ever since Morton (1833, p. 292) recognized specifically indeterminate molds in what is now the Merchantville Formation (lower Campanian) in the vicinity of Bordentown, N.J., as belonging to this genus. By 1893, Boyle (1893, p. 200–203) listed 24 described North American species that were primarily from the Upper Cretaceous of the Western Interior and the Atlantic and Gulf Coastal Plains (see app. 1 for a complete listing); 29 additional Cretaceous species were described subsequently. There has been no overall synthesis of these Cretaceous species, nor have there been any redescriptions or analyses of most of them since their original descriptions. *N. truncata* Gabb, 1864 (non Nilsson, 1827) was renamed *Acila demessa* by Finlay (1926, p. 522), and *N. perequalis* Conrad, 1860 is placed by us in the Nuculanidae (see discussion in the next section). All other species originally placed in *Nucula* are still assigned to that genus and to the family Nuculidae.

In a study of late Maastrichtian Mollusca of the Atlantic and Gulf Coastal Plains, Sohl and Koch (1983) realized that confusion exists as to the number of species of *Nucula* that are present in the fauna and the characters that previous workers used to distinguish the species. The species were described at times when correlations of the units in which they are found were less well known than they are now, and we have determined that some species names are artifacts of a provincial nomenclature. The present study utilizes the many new collections made throughout the Coastal Plains and applies techniques of morphometric analysis to solve taxonomic questions.

Our survey of the literature on fossil and living marine bivalves convinced us of the great morphologic similarity between extant species of *Nucula* and those of many fossil deposits of Cretaceous and Tertiary ages. Therefore, this study may also serve as an example of analytical techniques that can be applied to other groups of mollusks that show very conservative character state changes over long periods of time.

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Coastal Plain Upper Cretaceous Nuculidae

Species assigned to the Nuculidae have been described from Gulf and Atlantic Coastal Plain formations (see app. 1) ranging in age from Cenomanian through the Maastrichtian. Geographically, they range from occurrences on the Banquereau Banks off Nova Scotia to Mexico. All species have been assigned to Nucula, except for Acila banquereauensis Stephenson, 1936 and A. (Truncacita) chicotana Stephenson, 1952. It is doubtful that all these Late Cretaceous species should be included in Nucula ss. As Allen and Hannah (1986, p. 225) stated, "From the earliest writings to the present, malacologists have experienced great difficulty in separating clearly and defining adequately the proto branch taxa..." We believe that a number of clear distinctions can be made among the Cretaceous Coastal Plain species that have been lumped under Nucula (Nucula). For example, representatives of all three major groups proposed by Schenk (1934) are present: (1) forms having a crenulate ventral margin, (2) forms having a smooth ventral margin, and (3) forms having a divaricate ornamentation. Schenk recognized six genera of nuculids as subdivisions of these three major groupings. Five additional proposed taxa were viewed as being of questionable rank or position. Subsequently, two other schemes of nuculid classification have appeared. Keen (1969) recognized 10 genera within the family, whereas Allen and Hannah (1986) accepted only 3. The disparity in numbers between these two classifications exists because Allen and Hannah did not treat the eight genera and subgenera that are known only from the fossil record. In addition, they incorrectly ascribed Keen’s classification to Newell in their references. Despite these shortcomings, the diagnoses that Allen and Hannah provided are more useful than those of Keen because they contrast the same characters between taxa. Keen’s diagnoses suffer from a lack of detail and a lack of uniformity; she failed to contrast the same features between all taxa.

Despite these failings, most of the adequately founded and described Late Cretaceous nuculids of the Coastal Plains can be placed in existing genera or subgenera. The most common group of species are those allied to Nucula percrassa Conrad, 1858, which consists of forms exhibiting a subovate to subtrigonal valve outline, a crenulate inner ventral margin, an oblique ligament, and a flat-lying radial sculpture (pl. 1, figs. 1–10). The sum of characters indicates placement of these species in Nucula (Nucula). The species described below may all be assigned to this subgenus.

A second grouping is characterized by Nucula amica Gardner, 1916 (pl. 5, figs. 4, 7, 9) and is united in having a subtrigonal valve outline, a crenulate inner ventral margin, an internal ligament, a short chondrophore, and a strongly defined comarginal lirae; fainter raised radial elements cross the comarginal lirae and lend the shell surface a subcancellate appearance. This group is assignable to Nucula on the basis of shape and hinge characters but finds no parallel in ornament among the subgenera of the genus.

The third grouping is typified by species such as Nucula cuneifrons Conrad, 1860 (pl. 5, figs. 1, 5, 6, 8) that are trigonally subovate in valve outline and display a noncrenulate ventral margin and fine, closely spaced comarginal ribs. This group is similar to N. (Leionucula) f. (Leionucula) Quenstedt, 1930 in possessing an oblique resilifer but differs in possessing distinct raised comarginal ribs (pl. 5, fig. 8). Quenstedt (1930, p. 112), in his diagnosis of the subgenus, stated that the shells are characteristically smooth. Schenk (1934, p. 34), in his description of the type species of Leionucula (N. albensis d’Orbigny, 1844), stated that, “although there are concentric growth stages, the shell is without definite ribs.” If such a definition is adhered to, another assignment is needed for N. cuneifrons. The strong comarginal elements of N. cuneifrons are similar to the ornament found on Nucula castor d’Orbigny, 1850, the type species of Nuculoma Cossmann, 1907. In fact, Allen and Hannah (1986, p. 229) considered Leionucula a synonym of Nuculoma; they described the outer layer of shell as “smooth, glossy, [and] without radial elements.” As the illustrations of the type species Nucula castor provided by Cossmann (1907, pl. 2, figs. 14–15) and Schenk (1934, pl. 4, fig. 5) indicate, the outer shell surface bears close spaced collabral threads. Although the hinge structures of the two are similar, Cossmann emphasized that Nuculoma is “Lithodomous shaped” and thus almost subquadrate, as opposed to the decidedly subtrigonal shape of Leionucula. In sum, the group of species allied to Nucula cuneifrons shows some features that are common to both these taxa but more that are akin to Leionucula.

The fourth species group encompasses those species assigned by Stephenson (1936, 1952) to Acila and characterized by divaricate sculpture. This group of nuculids is the rarest in the Coastal Plains.

One species, Nucula perequalis Conrad, 1860, and its junior objective synonym, N. eufaulensis Gabber, 1860, stand alone in character. Shells of this species are rare and poorly known. Stephenson (1941, pl. 8, figs. 7–9) has presented illustrations and described the species but has omitted several features that we believe cast doubt on current assignment of the species. We have examined two well-preserved topotypes and find that they lack nacreous shell layers and possess a shallow pallial sinus. Such characters suggest that this species is better placed among the Nuculanacea. Of the four groups accepted as nuculids, it is the N. percrassa group that is the most common and persistent in the Cretaceous deposits of the Coastal Plains and will be the subject of the following discussions.
Mode of Occurrence and Abundance of Cretaceous Coastal Plain Nuculids

The four groups of nuculids defined above all occur most commonly in the Upper Cretaceous of the Coastal Plains in micaceous, clayey, fine sands deposited on the inner shelf in shallow marine waters of normal salinity. They occur only rarely in lagoonal clays, in coarse sands, and in deeper water, middle to outer shelf chalky deposits. Their preservation in the inner shelf deposits is excellent. Aragonitic shell material is still present, including the lustrous mother-of-pearl inner nacreous shell layers. Preservation as phosphatic internal molds is moderately common in the basal reworked beds of the transgressive phases of the Coastal Plain depositional cycles. Such molds, when well preserved (pl. 7, figs. 7, 9), replicate muscle scar patterns especially well.

Nuculids only rarely form a major element of Coastal Plain bivalve associations. Some measure of their frequency of occurrence and individual abundance can be gauged from Sohl and Koch’s (1983) study of the late Maastrichtian fauna of the Haustator bilira Assemblage Zone. During that study, the fauna from 642 localities within this zone included specimens that must be considered among the giants of the genus. The largest specimen measured is 45 mm in length and comes from the Ripley Formation of the Chattahoochee River Valley near Eufaula, Ala. An examination of extant nuculids in the collections of the Division of Mollusks of the U.S. National Museum of Natural History (USNM NH) turns up only one specimen, N. mirabilis Adams and Reeve, 1850, from the Sea of Japan, that reached such a size (44 mm) (USNM NH Division of Mollusks no. 204519). A specimen of N. iphigenia Dall, 1896 from the Gulf of Panama (USNM NH Division of Mollusks no. 122896) was 35 mm long. The majority of extant species ranged between 6 and 25 mm in length. The largest recorded nuculid that we are aware of was cited by Schenk (1934, footnote p. 46) as a specimen of Acila (Acila) divaricata (Hinds), 1843, housed in the collections of the University of Berlin, that attained a length of 49 mm. Schenk also provided seven tables of measurements of fossil and living species indicating that most species fall within the length ranges that we found in our survey. A comparison of Schenk’s tables with the measurements of N. (N.) percrassia provided in table 2 indicates that this Cretaceous species must be classed among the largest of all known nuculid species.

Previous Work on the Nucula percrassia Lineage

Nucula percrassia Conrad, 1858 and Leda slackiana Gabb, 1860 have been a particular source of confusion and controversy since their original descriptions (compare pl. 1, table 1 are representative of the intermixed mud and fine sand facies in which aragonitic shells are preserved and molluscan diversity is high. The unconsolidated sediment can be washed and sieved and the smallest species recovered. In coarse sand or chalk facies, nuculids are commonly absent or usually constitute only a fraction of a percent of all bivalve specimens.

Another facet of the Nucula (N.) percrassia lineage on the Coastal Plains is shell size. In comparison with other species of Nucula, both extant and fossil, this species includes specimens that must be considered among the giants of the genus. The largest specimen measured is 45 mm in length and comes from the Ripley Formation of the Chattahoochee River Valley near Eufaula, Ala. An examination of extant nuculids in the collections of the Division of Mollusks of the U.S. National Museum of Natural History (USNM NH) turns up only one specimen, N. mirabilis Adams and Reeve, 1850, from the Sea of Japan, that reached such a size (44 mm) (USNM NH Division of Mollusks no. 204519). A specimen of N. iphigenia Dall, 1896 from the Gulf of Panama (USNM NH Division of Mollusks no. 122896) was 35 mm long. The majority of extant species ranged between 6 and 25 mm in length. The largest recorded nuculid that we are aware of was cited by Schenk (1934, footnote p. 46) as a specimen of Acila (Acila) divaricata (Hinds), 1843, housed in the collections of the University of Berlin, that attained a length of 49 mm. Schenk also provided seven tables of measurements of fossil and living species indicating that most species fall within the length ranges that we found in our survey. A comparison of Schenk’s tables with the measurements of N. (N.) percrassia provided in table 2 indicates that this Cretaceous species must be classed among the largest of all known nuculid species.

Previous Work on the Nucula percrassia Lineage

Nucula percrassia Conrad, 1858 and Leda slackiana Gabb, 1860 have been a particular source of confusion and controversy since their original descriptions (compare pl. 1, Table 1. Occurrence of Nucula (N.) percrassia at selected localities of the Haustator bilira Assemblage Zone (Maastrichtian) of the Coastal Plain

<table>
<thead>
<tr>
<th>Locality</th>
<th>No. of bivalve genera/species</th>
<th>Total no. of bivalve specimens</th>
<th>No. of specimens of N. percrassia</th>
<th>N. percrassia specimens, in percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Owl Creek Formation, Miss.</td>
<td>66/78</td>
<td>2,005</td>
<td>186</td>
<td>9</td>
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<tr>
<td>USGS 707, 25423, loc. 19.</td>
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<td>Providence Sand, Ga.</td>
<td>48/76</td>
<td>4,215</td>
<td>148</td>
<td>3.5</td>
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<td>USGS 6412, 25935, loc. 22.</td>
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<tr>
<td>Severn Formation, Md.</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>USGS 28858, loc. 25</td>
<td>36/41</td>
<td>2,120</td>
<td>167</td>
<td>8</td>
</tr>
<tr>
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<td>259</td>
<td>9</td>
</tr>
<tr>
<td>USGS 32775, loc. 23</td>
<td>53/68</td>
<td>3,052</td>
<td>200</td>
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</tr>
</tbody>
</table>

Revision of the Nucula percrassia Conrad, 1858 Group
Table 2. Summary statistics for the *Nucula* (*N.*) *percassa* group

[The three left-hand columns show data for species as previously defined; these categories were tested in the discriminant analysis portion of this paper. The two right-hand columns represent species as defined in this paper. Note the proximity of the mean, median, and mode values, which is indicative of a normal distribution]

<table>
<thead>
<tr>
<th></th>
<th>Previous usage</th>
<th>This paper</th>
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<tr>
<td></td>
<td><em>N. percassa</em></td>
<td><em>N. slackiana</em></td>
</tr>
<tr>
<td></td>
<td>Conrad</td>
<td>Gabb of Gardner</td>
</tr>
<tr>
<td>Height, in millimeters</td>
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<td></td>
</tr>
<tr>
<td>Number of cases</td>
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<td>83</td>
</tr>
<tr>
<td>Mean</td>
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</tr>
<tr>
<td>Median</td>
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<td>20.00</td>
</tr>
<tr>
<td>Mode</td>
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<td>20.00</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>3.94</td>
<td>2.51</td>
</tr>
<tr>
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<tr>
<td>Minimum value</td>
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<td>10.00</td>
</tr>
<tr>
<td>Maximum value</td>
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<td>23.50</td>
</tr>
<tr>
<td>Length, in millimeters</td>
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<td></td>
</tr>
<tr>
<td>Number of cases</td>
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<td>81</td>
</tr>
<tr>
<td>Mean</td>
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<tr>
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<td>67</td>
</tr>
<tr>
<td>Mean</td>
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<tr>
<td>Mode</td>
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<tr>
<td>Standard deviation</td>
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<td>6.44</td>
</tr>
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<tr>
<td>Minimum value</td>
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<td>94.00</td>
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<tr>
<td>Maximum value</td>
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<td>Anterior angle, in degrees</td>
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<tr>
<td>Number of cases</td>
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<td>Mode</td>
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<tr>
<td>Standard deviation</td>
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<td>Range</td>
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<td>Mean</td>
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<td>Mode</td>
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<td>Standard deviation</td>
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<td>6.40</td>
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<td>Range</td>
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<td>28.00</td>
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<td>Minimum value</td>
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</tr>
<tr>
<td>Maximum value</td>
<td>92.00</td>
<td>96.00</td>
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</tbody>
</table>
juvenile form, but the analysis presented herein indicates N. slackiana ed have thus been established. A form appears to be significant stratigraphically (see pl. 4 in the literature on the Upper Cretaceous beds of "Crosswicks," N.J. By 1876, Gabb (1876, p. 318) began to question his own identification and stated "...but from its size and shape I have little doubt that it will prove identical with percrassa."

Gardner (1916, p. 511) took the opposite position in her study of the Cretaceous deposits of Maryland and stated that Nucula slackiana is not Nucula percrassa. She believed that the two species represented geographically restricted species, distinguished on characteristics of height, convexity of umbo, and ventral margin. Stephenson (1955) agreed with her conclusions. Richards (1958) reviewed the literature on N. percressa and N. slackiana and concluded that a more careful study needed to be done to determine whether the two forms are conspecific. Differences between the height-length ratios of N. percrassa and N. slackiana might not be enough to consider the two forms a distinct species, according to Speden (1970). He believed that a statistical study might show whether they are conspecific, subspecies, or distinct species.

Harbison (1945) contributed to the taxonomic splitting of the percrassa lineage when she named Nucula tippahensis from Maastrichtian-age deposits of the Ripley Formation in Mississippi (pl. 1, figs. 7–10; pl. 2, figs. 7–8, 10–11). She stated that a "new specific name is used, as the form appears to be significant stratigraphically" (see pl. 4 for stratigraphic comparison). Three species names—two conceived in part on the basis of being geographic isolates and the third on the basis of being stratigraphically restricted—have thus been established.

Occurring in deposits with either Nucula percrassa or N. slackiana is a small, trigonal, previously unnamed species of Nucula, similar in form to N. amica Gardner (1916, p. 514) but differing in its lack of strong comarginal ribs (compare pl. 5, figs. 2, 11, to pl. 5, figs. 4, 7, 9). The near absence of immature forms of N. percrassa and N. slackiana raises the possibility that this Nucula sp. is a juvenile form, but the analysis presented herein indicates that it is a separate species, which we name N. severnensis n.sp.

The purpose of this study is to clarify the taxonomic, geographic, and stratigraphic relationships of the above-mentioned species of Nucula Lamarck for the time interval from early Campanian through Maastrichtian. The morphologic characteristics used to differentiate the taxa by the original authors were applied in discriminant analyses to compare specimens grouped by taxonomic assignment, geographic locality, and stratigraphic position.

Acknowledgments

We express our gratitude to John Pojeta (U.S. Geological Survey, Washington, D.C.), Carl Koch (Old Dominion University, Norfolk, Va.), and Martin Buzas (Smithsonian Institution, Washington, D.C.) for their thorough reviews of the manuscript and for their numerous suggestions for its improvement. Philip Wirtz (George Washington University, Washington, D.C.) provided extensive instruction and assistance in the analytical portion of this paper. The comments and suggestions made in the early phases of this study by Anthony Coates and Diane Lipscomb (also of George Washington University) are appreciated. Thanks are also due to Robin Espenschade (U.S. Geological Survey volunteer) for her help in the compilation of appendix 1.

MATERIALS AND METHODS

Four hundred and eighty-three specimens were selected randomly from U.S. Geological Survey and USNM NH collections containing well-preserved Nucula spp. (text figs. 1, 2, 3; app. 2). Specimens were measured for length, height, hinge angle, anterior angle, and posterior angle. To facilitate the angular measurements and to circumvent the problems caused by using calipers to measure height and length on rounded specimens, reproductions were made by placing the specimens on a Litton Royfax copier. The illustration obtained allowed a grid to be constructed around the specimen and precise measurements to be taken, according to the method illustrated in text figure 4. When specimens were too small to copy, a camera lucida was used to trace the specimens, and the same measurements were taken. The methods used to measure specimens worked only on preserved shells; thus, the possibility of using internal molds, including topotypes of N. slackiana from New Jersey, was eliminated.

For this analysis, four taxonomic categories were tested: (1) Nucula percrassa Conrad, (2) N. slackiana Gabb of Gardner, (3) N. tippahensis, and (4) N. sp., later identified as N. severnensis n.sp. Identifications of N. percrassa and N. slackiana are made by following the convention in use since 1916 (Gardner, 1916); specimens from the Upper Cretaceous of the eastern Gulf Coast were placed in N. percrassa, whereas specimens from the Upper Cretaceous of the mid-Atlantic Coastal Plain were designated N. slackiana. In addition, Nucula from Pleasant Ridge Lake, Miss., and the surrounding area in Maastrichtian beds of the Ripley Formation were assigned to N. tippahensis, and small, thin, trigonal specimens were placed in N. sp. The data were analyzed by means of the discriminant analysis program contained within the Statistical Package for the Social Sciences (SPSS Inc., 1983), on the George Washington University IBM-4341.
DISCRIMINANT ANALYSIS

The first discriminant analysis compared the morphologic characteristics of three “species” of *Nucula* occurring in the upper Maastrichtian: *N. percrassa*, *N. slackiana*, and *N. severnensis* n.sp. The overlap of points between *N. percrassa* and *N. slackiana* plotted along the first and second canonical discriminant axes is illustrated in text figure 5 and could have been predicted by examining the univariate statistics presented in table 2 or by visually examining the specimens. Despite this overlap, *N. percrassa* is correctly classified in the statistical sense by its morphologic characteristics 78.2 percent of the time and *N. slackiana* 89.2 percent of the time (table 3). The Maryland samples containing specimens of *N. slackiana* were collected from the same formation and within several miles of each other (text figs. 3, 6), whereas the specimens of *N. percrassa* were collected from four States (text figs. 1, 2) and were distributed across a 430-km (300-mi) spread. The higher percentage of correctly classified (again, in the statistical sense) *N. slackiana* is therefore predictable. Relatively high classification values for *N. percrassa* and *N. slackiana* do not eliminate the possibility that the two forms represent only one species. The relatively high confidence level of 90 percent statistically correct classification was selected because the discriminant analysis program is designed to maximize the differences between groups; consequently, any degree of overlap between groups is significant. In addition, the classification phase is performed with the same specimens from which the groups
were originally discriminated. These two factors combine to make groups appear more discrete than they actually are. (For a complete description of discriminant analysis, see the discussion by Davis (1973, p. 442-456, fig. 7.3).) On the basis of the overlap of characters illustrated in text figure 5, of visual inspection of the specimens, and of classification values of less than the 90-percent confidence level, we concluded that *N. percrassa* Conrad and *N. slackiana* Gardner represent end members of the same species.

*Nucula severnensis* n.sp. forms a fairly discrete group on the plot of the canonical discriminant functions (text fig. 5), particularly along function 1, which accounts for 72.59 percent of the variance among the three groups. During the classification phase, 60 out of 61 specimens of *N. severnensis* n.sp. (98.4 percent) were correctly identified in the statistical sense (table 3). A morphological examination of immature specimens of *N. percrassa* eliminated the possibility that *N. severnensis* n.sp. was a juvenile *N. percrassa* (compare pl. 3, figs. 1–10, with pl. 3, figs. 11–19). *N. severnensis* was therefore identified as a new species within the Upper Cretaceous of Maryland and the Gulf Coast, and it was not included in any further analyses.

A plot on the first and second canonical discriminant functions of the data for *N. percrassa* and *N. slackiana*, grouped by State from the uppermost Maastrichtian collections (level 5 on text fig. 6), illustrates a clustering of centroids and an overlap of all regions (text fig. 7). Accurate predictions of the collection locality, based on observations of the shell morphology, can be made only 66.39 percent of the time (table 4). The Maryland specimens again form the most discrete group because of the geographic proximity of the collections, 84.1 percent being correctly classified statistically. Surprisingly, the distribution of points along canonical discriminant function 1 (accounting for 91.18 percent of the variance) and the classification results revealed a coupling of Maryland with Alabama and Mississippi with Georgia. Since the Alabama and Georgia samples were collected from opposite banks of the same river (text fig. 2), it was expected that the analysis would indicate a high degree of similarity between these samples. These results further substantiate the contention that *N. slackiana* specimens collected in Maryland are...
members of the same species as the Gulf Coast specimens assigned to *Nucula percrassa*. No justification exists for identifying a specimen as *N. percrassa* solely because it is found in Alabama or as *N. slackiana* because it is found in Maryland.

An analysis of the Maryland specimens versus the gulf specimens was performed to determine if a morphological gradient exists between the regions. Text figure 8 illustrates the gradation from one group to the other and the presence of the centroids in the region of superposition. Despite the statistically correct classification of 87.39 percent of the specimens (table 5), the analysis lends support to the idea of a continuous morphological gradient of specimens.

To document whether splitting was occurring on a stratigraphic basis, the Gulf Coast Upper Cretaceous stratigraphic column was divided into five groups (text fig. 6). The morphologic characteristics of *Nucula* at each level were compared. Gradational changes in the mean values of the morphologic characters are not discernible moving up the stratigraphic column (table 6), nor do the plots along the canonical discriminant functions 1 and 2 reveal a linear pattern (text fig. 9). Instead, the centroids are clustered, and the territories are at least partially superimposed. Visual inspection of the specimens does not reveal any distinctive differences (pl. 4). During the classification phase of the analysis, only 46.04 percent of the specimens were grouped correctly in the statistical sense (table 7). These results indicate a period of nearly 15 Ma in which virtually no recognizable morphologic change occurred in the species *N. percrassa*.

The data from stratigraphic level 3 come entirely from specimens assigned to *Nucula tippahensis*. Other than the larger-than-average size (see height and length values in tables 2 and 6) of the specimens from level 3, *N. tippahensis* does not stand out as a distinct identifiable species either in the plot (text fig. 9) or in the classification results (table 7). Harbison (1945) named *N. tippahensis* on the basis of characteristics that differentiated it from toptype specimens of *N. percrassa*. An analysis comparing toptype *N. percrassa* to toptype *N. tippahensis* was performed. Even though totopotypes of *N. percrassa* are morphologic end members of the *percrassa* population, a plot of *N. tippahensis* along canonical discriminant function 1 overlaps that of *N. percrassa* (text fig. 10). Classification results revealed that 88.60 percent of the specimens would be correctly identified in the statistical sense (table 8). The partial superposition of this plot, the lack of distinctive characters in comparison with the entire Late Cretaceous suite as a whole, classification values below the 90th percentile, and

### Table 3. Classification results for discriminant analysis of data grouped into three “species” of *Nucula* occurring within the upper Maastrichtian (level 5, text fig. 6)

<table>
<thead>
<tr>
<th>Actual group</th>
<th>Total number of cases</th>
<th>Predicted group membership,(^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>N. percrassa</em></td>
</tr>
<tr>
<td><em>N. percrassa</em></td>
<td>156</td>
<td>122 (78.2)</td>
</tr>
<tr>
<td><em>N. slackiana</em></td>
<td>83</td>
<td>7 (8.4)</td>
</tr>
<tr>
<td><em>N. severnensis</em></td>
<td>61</td>
<td>0 (0.0)</td>
</tr>
</tbody>
</table>

\(^1\) Percentage of “grouped” cases correctly classified: 85.33 percent.
Harbison's (1945, p. 78) own description of Owl Creek *N. percrassa* as "senile," imply that specimens identified as *N. tippahensis* are actually members of the *N. percrassa* population. It is possible that topotypes of *N. percrassa* from the Owl Creek Formation represent a certain stage in the ontogeny of the species or possibly ecophenotypes.

Since height and length were the primary discriminating variables in our analysis, one concern of this investigation was that specimens were actually being classified by growth stage. The emphasis placed on height and length in the original species descriptions of *Nucula percrassa*, *N. slackiana*, and *N. tippahensis* should have caused earlier authors to be concerned that they were actually identifying different phases in an ontogenetic sequence. Division by age group was not a problem in this investigation, however, as evidenced by the lack of mixing between groups in the analysis of State, regional, and stratigraphic data. If such a separation were occurring, the juveniles from all the groups would be mixed together and would form a plot isolated from that of the adults.

**IMPLICATIONS FOR PALEONTOLOGISTS**

Several points of evolutionary significance emerge from this analysis of *Nucula percrassa*. First, a period of 15 Ma of evolutionary stasis has occurred for *N. percrassa*. Accordingly, the species has only limited biostratigraphic utility. In addition, the taxonomic splitting of the *N. percrassa* lineage demonstrates the problems that can arise when previously published species lists are used in calculating evolutionary rates.

*Revision of the Nucula percrassa Conrad, 1858 Group* D9
Stratigraphic or geographic separation of populations often influences paleontologists to assume the presence of a new species, despite a lack of change in the preserved morphology of the separated groups. A type of circular reasoning can develop when a paleontologist makes such assumptions about evolutionary change. To determine when or if a new species has evolved in a lineage, an author might apply a previously calculated average rate of evolution for that group. Later, this author’s data may be included in a recalculation of the average rate for that group of organisms, or they may be used to further substantiate the accuracy of this rate. The original rate used by the author may not have been accurate in the first place, especially if it had been based on previously published species lists. For example, if rates of evolution were calculated for the Late Cretaceous Nuculidae by using the published record, the results would be biased toward a shortened duration for species; in addition, species diversity for the Nuculidae would be too high. Methods of defining species that are based on assumptions can introduce a nomenclatural bias.

Figure 7. Discriminant analysis of the data grouped by collection locality: 1, Mississippi (58 specimens in the analytical phase, 109 in the classification phase); 2, Georgia (27 specimens in the analytical phase, 37 in the classification phase); 3, Alabama (4 specimens in the analytical phase, 10 in the classification phase); 4, Maryland (66 specimens in the analytical phase, 82 in the classification phase). Canonical discriminant function 1 accounts for 91.18 percent of the variance and function 2 for 8.27 percent. The standardized discriminant function coefficients are as follows: height, 1.72698; length, −1.30692; hinge angle, −0.46599; anterior angle, −0.01744; posterior angle, 0.15842. Asterisks mark the centroids.

Figure 8. Discriminant analysis of the data grouped by region: 1, Gulf Coast region (89 specimens included in the analytical phase, 156 in the classification phase); 2, Maryland (66 specimens in the analytical phase, 82 in the classification phase). Canonical discriminant function 1 accounts for 100 percent of the variance. The standardized discriminant function coefficients are as follows: height, 1.72698; length, −1.30692; hinge angle, −0.46599; anterior angle, −0.01744; posterior angle, 0.15842. Asterisks mark the centroids.

Figure 9. Discriminant analysis of the data grouped by stratigraphic position; 1 represents the oldest stratigraphic level, and 5 represents the youngest (see text fig. 6 for exact position of levels). The number of specimens included in the analytical and classification phases are 32 for level 1, 25 for level 2, 40 for level 3, and 25 for level 4. For level 5, 89 specimens were included in the analytical phase and 156 in the classification phase. Canonical discriminant function 1 accounts for 65.97 percent of the variance and function 2 for 30.01 percent. The standardized canonical coefficients are as follows. Function 1: height, 1.62370; length, −1.00906; hinge angle, −0.48111; anterior angle, 0.03953; posterior angle, −0.04751. Function 2: height, 0.17464; length, 0.55760; hinge angle, 0.70151; anterior angle, −0.08734; posterior angle, 0.33718. Asterisks mark the centroids.
into our understanding of evolutionary processes and ultimately will obscure information on the rates of morphologic change with time.

Two basic paleontological concepts are at the heart of the problems raised here: (1) the definition of species and (2) the selection of type specimens. The question of how to define species has been debated at great length (Lovtrup, 1979; McAlester, 1962; Weller, 1961; Wiley, 1978), but, for paleontologists, usually only the preserved hard parts of specimens are available for recognizing and defining species. The discrimination of a new fossil species should be based solely on preserved morphologic differences and should take into account a reasonable amount of intraspecific variation. Measurement of morphologic differences is an objective and testable data base available to paleontologists. The species description should include the statistical conclusions about the mode and tempo of evolution.

Statistical programs currently available to paleontologists offer a means of analyzing morphologic variability and may assist in the recognition of new species. Previous work needs to be critically reexamined in light of new ideas and methods. Until consistent, reproducible taxonomies are constructed, we should proceed cautiously with our inductive conclusions about the mode and tempo of evolution.

**SYSTEMATIC PALEONTOLOGY**

Class BIVALVIA Linne, 1758

Subclass PALEOTAXODONTA Korobkov, 1954

Order NUCULOIDA Dall, 1889

Family NUCULIDAE Gray, 1824

Genus Nucula Lamarck, 1799

Subgenus Nucula (Nucula) Lamarck, 1799

*Type species.*—Arca nucleus Linne, 1758, by monotypy.

*Discussion.*—The presence of crenulations on the inner ventral margin and the presence of well-developed external radial ribs suggest placement of both *Nucula percassa* and *N. severnensis* in the subgenus *N. (Nucula)* rather than in other subgenera that occur in the Cretaceous. These species lack the highly oblique resilifer and smooth external surface of *N. (Leionucula)* Quenstedt, 1930 and the strong, raised radial ribs of *N. (Pectinucula)* Quenstedt, 1930.

In addition to the presence of the diagnostic crenulations and external radial ribs, the muscle scar pattern is similar to that displayed on the specimen of the type

1 nom. transl. et correct. Newell, 1965 (ex suborder Nuculacea, Dall, 1889.)
species *Arca nucleus* Linne, 1758, as figured by Schenk (1934, pl. 5, figs. 1, 1a). Muscle scar patterns are exceptionally well displayed on the valve interiors of specimens of *Nucula percassa*. The clarity of these impressions is enhanced because of both the large size and the especially thick shell of the species. They are less deeply impressed and clear on the interiors of the smaller and thinner shelled valves of *N. severnensis*. Text figure 11 illustrates the general placement of these muscle scars on the interior of the shell and the descriptive terms applied. Plate 7 shows representative specimens illustrating the variation in shape and number of scars of certain types.

The anterior and posterior adductor muscle scars are the largest and most deeply impressed. As text figure 11 indicates, the areas of attachment of both quick and catch muscles can commonly be distinguished on the surface of the adductor scars. The specimens shown on plate 1 (figs. 1, 5, 8) and plate 7 (figs. 2, 5, 6) show the separation reasonably well. The area covered by the catch muscle (smooth) is greater than that occupied by the quick muscle (striated) that lies toward the shell interior.

Muscles that control the movement of the foot are distributed over the dorsal surface of the valve interior. All such scars lie dorsal to a line connecting the center points of the adductor scars. The paired anterior protractor muscle scars are situated immediately ventral to the hinge plate and posterior to the posterior-dorsal margin of the anterior adductor muscle (text fig. 11; pl. 7, figs. 7, 9, 11). In both *Nucula percassa* and *N. severnensis*, the anterior protractor muscle scars are elongate, the anterior end being expanded into a ventrally extended hooklike insertion area (pl. 7, figs. 8, 9, 11).

The anterior pedal retractor muscle scars consist of a gently curvilinear series of circular to oval scars extending over the upper part of the shell interior between the posterior end of the anterior adductor and the ventral-median muscle scar (text fig. 11; pl. 7, figs. 2, 4, 5, 11). In *Nucula percassa*, the number of such scars ranges between three (pl. 1, fig. 1) and six (pl. 1, fig. 9). The number may vary between different valves of the same individual, as an articulated specimen (pl. 7, figs. 8, 10, 11) shows. On this individual, the right valve (pl. 7, fig. 10) possesses four anterior pedal retractor muscle scars and the left valve five (pl. 7, fig. 11). *N. severnensis* most commonly has only one round to dorsal-ventrally elongated scar (pl. 7, fig. 3), but,

### Table 7. Classification results for discriminant analysis of data grouped by stratigraphic level
(Level 1 is the oldest, and level 5 is the youngest. Exact position of each level shown in text fig. 6. Discriminant analysis plot shown in text fig. 9)

<table>
<thead>
<tr>
<th>Actual group</th>
<th>Total number of cases</th>
<th>Level 1</th>
<th>Level 2</th>
<th>Level 3</th>
<th>Level 4</th>
<th>Level 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level 1</td>
<td>32</td>
<td>20 (62.5)</td>
<td>3 (9.4)</td>
<td>6 (18.8)</td>
<td>0 (0.0)</td>
<td>3 (9.4)</td>
</tr>
<tr>
<td>Level 2</td>
<td>25</td>
<td>14 (4.0)</td>
<td>13 (52.0)</td>
<td>2 (8.0)</td>
<td>3 (12.0)</td>
<td>6 (24.0)</td>
</tr>
<tr>
<td>Level 3</td>
<td>40</td>
<td>4 (10.0)</td>
<td>2 (5.2)</td>
<td>20 (50.0)</td>
<td>11 (27.5)</td>
<td>3 (7.5)</td>
</tr>
<tr>
<td>Level 4</td>
<td>25</td>
<td>2 (8.0)</td>
<td>4 (16.0)</td>
<td>7 (28.0)</td>
<td>9 (36.0)</td>
<td>3 (12.0)</td>
</tr>
<tr>
<td>Level 5</td>
<td>156</td>
<td>17 (10.9)</td>
<td>38 (24.4)</td>
<td>16 (10.3)</td>
<td>19 (12.2)</td>
<td>66 (42.3)</td>
</tr>
</tbody>
</table>

1 Percentage of "grouped" cases correctly classified: 46.04 percent.

### Table 8. Classification results for discriminant analysis of data on topotypes of *Nucula percassa* and *Nucula tippahensis*

[Discriminant analysis plot shown in text fig. 10]

<table>
<thead>
<tr>
<th>Actual group</th>
<th>Total number of cases</th>
<th>Predicted group membership,(^1) (%) of cases</th>
<th>Nucula percassa</th>
<th>Nucula tippahensis</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nucula percassa</em> ...</td>
<td>74</td>
<td>66 (89.2)</td>
<td>8 (10.8)</td>
<td></td>
</tr>
<tr>
<td><em>Nucula tippahensis</em></td>
<td>40</td>
<td>5 (12.5)</td>
<td>35 (87.5)</td>
<td></td>
</tr>
</tbody>
</table>

1 Percentage of "grouped" cases correctly classified: 88.60 percent.
rarely, a second generally rounded scar may occur (text fig. 11). The scar or scars lie close to a line drawn from the center of the anterior adductor to the ventral-median scar, but the anterior scar is closer to the anterior adductor than to the ventral-median scar, and the second scar is at a midpoint on that line.

The next set of muscles appearing in a posterior direction are the dorsal-median (=median muscle scar of Schenk, 1934) and ventral-median muscles. Both occur well above, or dorsal to, a line connecting the center of the adductor scars. The ventral-median scar (text fig. 11) (=central muscle scar of Schenk, 1934) is generally circular, less pronounced, and smaller than the dorsal-median scar (pl. 1, figs. 5, 8, 9; pl. 4, figs. 2, 3, 6; pl. 7, figs. 4, 5, 6). The dorsal-median scar ranges in shape from nearly circular (pl. 1, fig. 4; pl. 4, fig. 6) to dorsal-ventrally elongate (pl. 1, fig. 9; pl. 4, figs. 2, 3; pl. 7, figs. 5, 11). The function of the dorsal-median and ventral-median muscles is conjectural. Heath (1937, p. 14) stated that the greater number of muscle strands of the dorsal muscle extend into the pedal tissue; the ventral muscle strands form part of the posterior part of the visceral sac wall, a few fibers being attached “superficially to the upper portions of the foot.” Driscoll (1964, p. 63) suggested that these muscles may, by contraction, reinforce the action of the pedal retractors or that they may simply form a firm attachment of the pericardial region of the shell.

There is another cluster of small muscle scars within the umbonal cavity (PE, text fig. 11). These scars are best seen on internal molds, where they form prominences on the surface of the umbonal region (pl. 7, figs. 7, 9). In Nucula percrassa, these scars number from two to five and are aligned in a track from the base of the resilifer trending anteriorly and ventrally toward the dorsal-median muscle scar. The two dorsalmost scars are the strongest, the strength of the others decreasing away from the umbo. When only two scars are present, they represent the dorsalmost pair. The number of scars may vary between the valves of the same individual; for example, five scars are present on the left valve and four on the right valve of the

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**Figure 11.** Musculature of the Nucula percrassa group. AA, anterior adductor (shaded area is quick muscle, white area is catch muscle); AP, anterior protractor; AR, anterior pedal retractors; DM, dorsal-median muscle; PA, posterior adductor (shaded area is quick muscle, white area is catch muscle); PE, pedal elevator muscle; PL, pallial line; PR, posterior pedal retractor; VM, ventral-median muscle. A, Outline of right valve interior of N. severensis (USNM 423847) illustrated on plate 7, figure 3. B, Left valve interior of N. percrassa (USNM 423832) illustrated on plate 7, figure 2. C, Dorsal view of internal mold of N. percrassa (USNM 423833) illustrated on plate 7, figure 9.
internal mold shown as figure 9 on plate 7. In *N. severnensis*, equivalent scars have been seen only on the largest individuals, where they consist of two closely spaced scars in the dorsalmost part of the umbonal cavity slightly anterior to the base of the resilifer. Their trend is dorsal-ventral; they do not form an anteriorly inclined track, as they do in *N. percrassa*. Heath (1937, p. 14) stated that “several authors have described muscles in *Anodonta*, *Cardium*, etc., which are termed *levator peidis*, ‘Fussheber,’ or merely ‘Heber.’ These are attached to the shell in the neighborhood of the umbo, but we have no detailed information as to their distribution.... In the case of the protobranchs they may reinforce the pedal retractors.” Pojeta (1987, p. 406, figs. 14.98D, E) has provided clear illustrations of similarly placed muscle scars, termed pedal elevators, in the genus *Astarte* that serve to raise the foot into the shell.

A final set of pedal muscles, the posterior pedal retractors, are located on the posterior dorsal slope, immediately ventral of the posterior hinge teeth and near the anterior dorsal margin of the posterior adductor (text fig. 11C). On both *Nucula percrassa* and *N. severnensis*, the scars are shallowly impressed and narrowly elongate, following a track parallel to the margin of the hinge plate (pl. 7, figs. 7, 8, 10, 11).

Earlier in this paper, it was stated that four species groups of nuculids could be distinguished in the Cretaceous deposits of the Gulf and Atlantic Coastal Plains. These groupings were distinguished on the basis of obvious characters of external ornament and the presence of crenulations on the ventral margin. All are, however, linked by characters of the family Nuculidae, including general features of dentition, possession of an internal ligament, and a nacreous inner shell layer. They are also allied in having a corresponding pattern of muscle impressions on the interior of the valves. In the groups of which *Nucula amica* and *N. cuneifrons* are representative, muscle scar patterns are more difficult to delineate than they are in the *N. percrassa* group, mainly because the shells are smaller and thinner. Specimens have been seen, however, in which both anterior and posterior pedal retractors are discernible, anterior pedal retractors and dorsal-median scars are present, and all are in the same relative placement on the respective valves, as they are in the *N. percrassa* group. Thus, although the base plan is repetitive, the shape and number of scars may vary.

Although little emphasis has been placed on the conchological character of muscle scar patterns by neontologists or paleontologists dealing with Mesozoic or Tertiary nuculids, those dealing with Paleozoic members of the superfamily have, in recent years, emphasized their character and placement. Although the prime driving force for this interest has been the interpretation of proper shell orientation, it also leads to interpretation of functional morphology and phylogenetic speculation.

Driscoll (1964) pointed out that a group of Mississippian protobranchs that he studied possessed muscle scar patterns analogous to those present in many living forms but markedly different, especially in number, from those present on Ordovician species. He suggested a trend toward reduction of the number of muscle scars from the early to the late Paleozoic, the arrangement of those scars centering on a modern mode by at least the Mississippian. Further examples of Ordovician paleotaxodonts having multiple muscle scars have been presented by Bradshaw (1970). In all these Ordovician bivalves, it is somewhat difficult to directly ascribe the presumed pedal muscle to individual scars of more recent forms. Both Bailey (1983) and Bradshaw (1974) have described Devonian nuculids. The figures presented by Bailey (1983, fig. 30) of the musculature attachment in *Nuculoidea deceptiformis* Bailey, 1983 show an arrangement that fundamentally parallels that of the Cretaceous species described here, lacking only the pedal elevator group.

As the preceding paragraph has made obvious, the general relative arrangement of the pedal muscle attachment was arrived at early in nuculid evolution, but much remains to be investigated. For example, Heath (1937, pl. V, fig. 39) indicated that, in *Acila divaricata*, the anterior pedal protractors and anterior pedal retractors are clustered together. This grouping is certainly different from that of *Nucula percrassa* (text fig. 11), in which the retractors are well separated, as they are in the Devonian forms mentioned above. Because *Acila* appears after the origin of these other groups, one might question whether this clustering may reflect some phylogenetic trend or is only of functional significance. The presence of such differences among the later nuculids does indicate that further work is needed to understand the range of differences among living and fossil nuculids. A study of muscle scar patterns may provide criteria pertinent to developing a stable taxonomic arrangement of the Nuculacea.

**Nucula percrassa** Conrad, 1858

Plate 1, figures 1–10; plate 2, figures 1–11; plate 3, figures 1–10; plate 4, figures 1–10; plate 5, figures 3, 10; plate 6, figures 1, 2, 4–16; plate 7, figures 1, 2, 4–11.


**Leda slackiana** Gabb, 1860, p. 397, pl. 69, fig. 36. *Nuculanacea slackiana* Conrad, 1868, p. 725.
Diagnosis. — Elongate, subelliptical shell; beak lying at posterior one-third of shell; posterior-dorsal margin straight and steeply angled; posterior margin truncate; anterior-dorsal margin straight and gently inclined; closely spaced radial striations and comarginal growth lines; hinge angle wide (average value 116°).

Description. — Shell equivale and variably convex; degree of convexity increases with age; elongate, subelliptical, and inequilateral in outline, beak lying posterior to midlength; opisthogyrate. Lunule long, proportionally narrow, and poorly defined; escutcheon broad, rather short, distinctly outlined. Posterior-dorsal margin straight and inclined steeply away from beak; posterior ridge present and more sharply defined at younger growth stages; posterior margin truncate. Anterior-dorsal margin straight to very slightly convex and inclined gently away from beak; anterior margin elongate and smoothly curved. Ventral margin usually gently curved and crenulate; occasionally a posterior flattening causes an increased convexity of shell surface that accentuates toward posterior end. Surface ornamentation consists of closely spaced, radial, incised striations over anterior two-thirds of shell, becoming raised fine ridges over posterior third, and comarginal growth lines that become more prominent ventrally. Interior shell material is nacreous. Chevron-shaped taxodont dentition; anterior series shows a dramatic increase in size and height of teeth along the anterior-dorsal margin, becoming smaller and shorter as anterior-ventral margin is approached; posterior series shows a slight increase in size and a dramatic increase in height of teeth posteriorly but decreases toward the posterior-ventral margin; 23 to 31 teeth are present in anterior series and 8 to 12 in posterior series. Hinge angle formed by intersection of anterior and posterior series is wide (average 116°); anterior hinge plate convex toward valve interior immediately anterior to beak, then proceeds in a nearly straight line toward anterior-ventral margin; posterior hinge plate is straight to slightly concave toward valve interior. Resilifer lies below anterior series of teeth and in line with posterior series, forming a distinct spoon-shaped pit that extends into valve interior past hinge plate; on left valve, resilifer rises up from pit, above posterior row of teeth, to form a toothlike process in line with posterior series; correspondingly, a slight recess is found on right valve. Isomyarian adductor muscle scars vary from shallow to deep impressions, depending somewhat on growth stage. Pallial line is usually distinct and parallels ventral margin of shell, often making a sharp bend at posterior end of shell. Pedal retractor and protractor muscle scars are commonly visible above midline of inner valve surface; anterior adductor muscle scar is commonly most prominent. Prodissoconch resembles adult form.

Discussion. — As herein defined, Nucula percrassa is a morphologically variable species. The objective range of variability is discussed in the statistical analysis portion of this study and can be seen by examining table 2. The observable range of variability of overall shape and hinge angle is well exemplified by a comparison of figures 1 and 5 on plate 1. These two specimens typify the morphologic end members, figure 1 being the extreme of proportional elongation relative to height and also having a hinge angle greater than that of the specimen represented by figure 5. Intermediate morphologies are illustrated on plate 1 (figs. 1, 9), plate 3 (figs. 2, 3, 6), and plate 4 (figs. 4, 5, 8, 9). Variation in the prominence of the umbonal area, flattening, or subsinusing of the posterior-ventral margin can be seen by comparing the figures on plate 2 and plate 6. The specimens shown on plate 1 (figs. 1, 2), plate 2 (fig. 5), and plate 6 (figs. 9, 10) especially show the character cited in the original description by Conrad (1858, p. 327) as “basal margin rounded, slightly contracted anteriorly [posteriorly].” Flattening of the outline of the ventral margin is especially well seen in some specimens among populations from the Owl Creek Formation of Mississippi but is occasionally also seen on other specimens, particularly those from the Coon Creek Tongue of the Ripley Formation of Tennessee (pl. 2, fig. 8). Similar inbending of the ventral margin has also been noted in other species of Nucula, often accompanied by extreme thickening of the shell material, and has been judged to be a gerontic feature (Stephenson, 1941, p. 73).

A number of other species that have been described from the Cretaceous rocks of the Coastal Plain appear to be related to Nucula percrassa. N. cibolensis Stephenson, 1941 is from the Kemp Clay (late Maastrichtian) and is, according to the author, differentiated from N. percrassa in being larger and proportionally shorter, having more rounded posterior and anterior margins, and lacking a faint posterior radiating sulcus. N. chatfieldensis Stephenson (1941, p. 73) is described from somewhat compressed specimens from the Nacatoch Sand (Maastrichtian) of Texas. It was distinguished on the basis of being less elongate than N. percrassa and coming from a stratigraphic position lower than that of the type locality. Internal shell features and hinge character are poorly known for both these Texas species, but both appear to fall within the range of morphologic variability of N. percrassa, as it is conceived herein.

Nucula stantoni Stephenson, 1923, described from the Black Creek Formation (Campanian) at Snow Hill, N.C., is also a member of the N. percrassa lineage. It was differentiated from N. percrassa primarily because it is
more trigonal in outline and smaller in size, both characters that need to be tested with a suite of specimens larger than what is currently available. *N. prepercrassa* Stephenson, 1956 was described from the lower part of the Eutaw Formation on Ochillee Creek in Chattahoochee County, Georgia. The rocks at this locality are of lower to middle Santonian age (Sohl and Smith, 1980, p. 398). Stephenson (1956, p. 234) noted the similarity to *N. percussa* but stated that it differed "in that the shell is much thinner, the hinge is narrower, the chondrophore is larger and projects farther inward...." Too few specimens of this species exist to determine how consistent these differences are, but there is no doubt that both are closely related members of the same lineage.

One additional species probably related to *Nucula percussa* has been described by Stephenson (1947) and named *N. nulla*. All known specimens were recovered from well cores at a depth between 2,750 and 2,750 ft in the Avent No. 1 well in Grenada County, Mississippi. Stratigraphically, they come from beds of probable early Campanian age. All known specimens are small (less than 5 mm in length) and have a crenulate ventral margin. The internal features are unknown save for the dentition, which is of *Nucula* type. Comparison with *N. severnensis* is discussed in the description of that species. In sum, the relationship to other described species is unsure, and specimens may represent only immature members of a described species.


**Stratigraphic range.**—Middle lower Campanian through Maastrichtian.

**Types.**—Holotype *Nucula percussa*, Academy of Natural Sciences of Philadelphia (ANSN); hypotypes USNM 32713, 128084, 128085, and 423803–423837. Holotype *N. slackiana*, ANSP; hypotypes USMN 131858. Holotype *N. tippahensis*, USNM 103751.

**Nucula severnensis n.sp.**

Plate 3, figures 11–19; plate 5, figures 2, 11; plate 6, figure 3; plate 7, figure 3.

**Diagnosis.**—Subtrigonal shell, posterior margin inclined steeply away from beak. Faint radial striations and comarginal growth lines ornament surface. Hinge angle approximates a right angle.

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**Description.**—Shell is equivalve, slightly to moderately convex, and subtrigonal in outline; beak lies posterior to middle; opisthogyrate. Lunule elongate narrow and indistinctly margined; escutcheon proportionally broad, distinct. Posterior-dorsal margin is inclined steeply away from beak; margin is straight to slightly convex outward; posterior ridge may be sharp and well defined; posterior margin is truncate. Anterior-dorsal margin is slightly curved and inclined away from the beak at a more gentle angle than posterior margin; anterior margin truncate. Ventral margin is gently curved and crenulate. Surface ornamentation consists of comarginal growth lines and faint incised radial striations commonly becoming raised lines on posterior quarter. Interior shell material is nacreous. Chevron-shaped taxodont dentition; anterior teeth increase in size and height anteriorly, becoming smaller and shorter as anterior-ventral margin is approached; posterior series shows a slight increase in size of teeth and an increase in height toward middle of posterior hinge plate, decreasing toward ventral margin; 22 to 29 teeth occur in anterior series; 10 to 12 teeth are present in posterior series. Hinge angle formed by intersection of anterior and posterior series of teeth approximates a right angle (average = 93°); anterior hinge plate is convex in toward valve interior, following curvature of anterior-dorsal margin; posterior hinge plate is straight to slightly concave toward valve interior. Resilifer lies below anterior series of teeth and in line with posterior series and forms a triangular-shaped, basally flattened pit that extends somewhat into valve interior past hinge plate; on left valve, resilifer rises up from recess, above posterior series of teeth to form a toothlike process in line with posterior series; in an analogous position on right valve is a small recess. Isomyarian adductor muscle scars usually form shallow depressions. Pallial line faint and somewhat obscured by radial striations visible on interior of shell surface. Pedal muscles usually distinctly impressed. Prodissconch resem­bles adult form.

**Discussion.**—The primary difference between *Nucula percussa* and *N. severnensis* is shape: *N. percussa* is subelliptical, whereas *N. severnensis* is subtrigonal (compare pl. 3, figs. 1–10, with pl. 3, figs. 11–19). This difference in shape is even more pronounced when internal molds of the two species are compared (pl. 7, figs. 1–6). An examination of the mean values for the hinge angles of the two species in table 2 provides a less subjective way of expressing this difference in shape. The average value of the hinge angle in *N. percussa* is 116°, giving the species its subelliptical appearance. The subtrigonal shape of *N. severnensis* is produced by an average value of 93° for the hinge angle. The hinge angle is the primary discriminating variable in the discriminant analysis comparing *N. percussa* to *N. severnensis* (text fig. 5); the standardized canonical discriminant function coefficient is 0.67 for function 1, which accounts for about 73 percent of the variance between the species. Length, the second most
important discriminating variable in the analysis of the two species (standardized canonical discriminant function coefficient is 0.61), is intuitively tied to the value of the hinge angle; the wider the angle, the greater the length. An additional component of the difference in shape between *N. percrassa* and *N. severnensis* is the anterior margin. In *N. percrassa*, it is elongate and smoothly curved, an average value for the angle of the anterior-ventral margin being 55° (table 2), whereas, in *N. severnensis*, the anterior margin is truncate, an average value for the angle of the anterior-ventral margin being 62° (table 2). The angle of the anterior-ventral margin is the third most important discriminating variable along function 1 in the discriminant analysis of the species (standardized canonical discriminant function coefficient is −0.13).

Additional variations between *Nucula percrassa* and *N. severnensis* can be seen along the hinge plate. In *N. percrassa*, the anterior series of teeth bends slightly toward the interior of the valve in the region of the umbo and then continues in a nearly straight line toward the anterior margin (pl. 4, figs. 2, 3, 7). The anterior series of teeth in *N. severnensis* gradually curves toward the interior of the shell as it approaches the anterior margin, following the curvature of the anterior-dorsal margin (pl. 3, figs. 12, 13, 15, 18). The resilifer of *N. percrassa* is spoon shaped and extends proportionally farther past the hinge plate than the triangular-shaped, basally flattened resilifer of *N. severnensis* (compare pl. 3, fig. 7, pl. 4, fig. 3, and pl. 7, fig. 8, with pl. 3, figs. 12, 15, 18).

*Nucula Waltonensis* Stephenson (1941, p. 74), from the Nacatoch Sand of Texas, is somewhat similar to *N. severnensis* in its trigonal outline and fine, faint, comarginal ribbing. Because features of the hinge and interior are unknown, close comparison of the two is impossible, given the available specimens. The holotype (USNM 76295), a small (6.8 mm long, 5 mm high) bivalved specimen, differs from *N. severnensis* in having a more concave posterior-dorsal margin and a more rounded esculcheon margin. In these characters, it appears morphologically closer to *N. stantoni* Stephenson, 1923, from the Black Creek Formation of North Carolina, than to *N. severnensis*.

**Occurrences.**—Alabama: Providence Sand, loc. 20.
Georgia: Ripley Formation, loc. 14; Providence Sand, locs. 21, 22.
Maryland: Severn Formation, locs. 23–25.

**Stratigraphic range.**—Middle through upper Maastrichtian.

**Types.**—Holotype, USNM 423838. Paratypes, USNM 423839–423847 (shown); USNM 423848–423853 (not shown).

### SUMMARY AND CONCLUSIONS

A discriminant analysis of the *Nucula percrassa* lineage has clarified the taxonomic, geographic, and stratigraphic relationships within the group. Morphologic characters deemed important by the original authors of the species were used as the discriminating variables in the analysis to test the validity of the authors' assumptions. The results indicate that *N. percrassa* Conrad, *N. slackiana* Gabb, and *N. tippahensis* Harbison are all members of the same species. Consequently, we suggest that the names *N. slackiana* Gabb and *N. tippahensis* Harbison be treated as synonyms of *N. percrassa* Conrad. Occurring with *N. percrassa* in beds of Maastrichtian age from Maryland and the Gulf Coast is *N. severnensis* n.sp., named and described within this paper. This species had previously been surmised to be a juvenile *N. percrassa* or *N. slackiana*. Discriminant analysis was thus shown to be a very simple, graphic means of testing previously defined species; we hope that this technique will be utilized in similar studies in the future.

The results of this study raise issues relevant for all paleontologists, especially our methods of defining species and selecting type specimens. Because morphologic similarities between individuals and populations are the only testable data available to paleontologists, identifications of new species should be based solely on morphologic divergence. Prior assumptions of stratigraphic or geographic isolation are not valid criteria for distinguishing species. Ideally, a holotype representing the median of a population should be selected, and paratypes should represent the full suite of morphologic divergence, especially end members. The statistical range of variation seen within a population should be included in the species description. Only by reaching a consensus on these issues can we develop a consistent, reproducible data base.

The continued use of the published species record to extrapolate conclusions about evolutionary processes and rates could bias our calculations and conceal important facts about the real processes of biological change. The published record of the Nuculidae contains a bias toward shortened species durations and too much diversity. No doubt, future studies will reveal similar evidence regarding the reliability of the published record for other groups of organisms. Meanwhile, we should proceed cautiously with our inductive conclusions about evolutionary processes.

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## APPENDIX 1. NUCULID SPECIES FROM THE UPPER CRETACEOUS OF NORTH AMERICA

<table>
<thead>
<tr>
<th>Species name</th>
<th>Formation (if known)</th>
<th>Locality</th>
<th>Author(s)</th>
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Meek, F.B., 1858, Transactions of the Albany Institute, v. 4, p. 39.
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APPENDIX 2. DESCRIPTION OF COLLECTION LOCALITIES

The following locality descriptions are organized in stratigraphic order within each formation. Each description includes the U.S. Geological Survey (USGS) Mesozoic collection number(s), followed in parentheses by the collector and the date of collection.

CAMPANIAN

Coffee Sand

Locality 1. USGS Mesozoic collection 9501 (L.W. Stephenson, 1915). Ten kilometers (6 mi) east of Booneville on road to Hare’s old mill site (on Big Brown Creek) in Prentiss County, Mississippi. Well-preserved fossils were collected from the lower 1.5 m (5 ft) of a 13.7-m (45-ft) section; Stephenson and Monroe (1940, p. 159) described the sediment as a dark-gray, compact, finely micaceous, glauconitic sand. These beds are in the lower part of the Coffee Sand.

Locality 2. USGS Mesozoic collections 17254 (W.H. Monroe, 1936), 17809 (L.W. Stephenson and W.H. Monroe, 1938), 25483 (L.W. Stephenson and N.F. Sohl, 1955), and 26338 (N.F. Sohl and H.I. Saunders, 1956). Roadcut on north-facing slope of Mantachie Creek Valley, 3.2 km (2 mi) due west of Ratliff in Lee County, Mississippi, SI/2, sec. 9, T. 8 S., R. 7 E. Abundant fossils are found in the first meter of a 10.7-m (35-ft) section of massive, dark-colored, micaceous, glauconitic, clayey sand. These beds lie in the middle of the lower Coffee Sand, stratigraphically above locality 1.

Blufftown Formation

Locality 3. USGS Mesozoic collections 6405 (L.W. Stephenson, 1909) and 26033 (N.F. Sohl and H.I. Saunders, 1955). Type locality of the Blufftown Formation. Bluffs on the left bank of the Chattahoochee River at Blufftown, 45.6 km (28.5 mi) above Eufaula landing, and 50 km (31.25 mi) below Columbus in Stewart County, Georgia (Julia quadrangle, 84°57’45” N., 32°11’ W.). Stephenson (Veatch and Stephenson, 1911, p. 135) described the lower 3 m (10 ft) of the section as a “gray, calcareous, finely arenaceous, fossiliferous clay”; overlying this lower layer is 13.7 m (45 ft) of a “gray, calcareous, glauconitic sand” with concretionary layers. Fossils listed were recovered from the lower 13.7 m (45 ft). The remaining 45.7 m (150 ft) of section consists of a “gray, calcareous, marine sand,” overlain by a weathered, unconsolidated sand.

MAASTRICHTIAN

Ripley Formation, Coon Creek Tongue

Locality 4. USGS Mesozoic collections 10198 (B. Wade, 1917) and 25406 (N.F. Sohl, 1950-53). Type locality of the Coon Creek Tongue of the Ripley Formation. The old Dave Week’s place, on Coon Creek, 5.6 km (3.5 mi) south of Enville, 12 km (7.5 mi) north of Adamsville, and 198 m (660 ft) east of the main Henderson-Adamsville road, in the northeastern part of McNairy County, Tennessee. Wade (1926, p. 9-10) described the 9.1-m (30-ft) section along the banks of Coon Creek as consisting of a dark bluish-green and gray, clayey, glauconitic, micaceous, medium fine sand; concretionary masses may form locally.

Locality 5. USGS Mesozoic collections 18078 (L.C. Conant, A. Brown, and W.H. Monroe, 1939), 18616 (L.W. Stephenson and W.H. Monroe, 1941), and 25411 (N.F. Sohl, 1950-52). Scraped area along the northern side of the dam at Pleasant Ridge Lake in Union County, Mississippi, NW1/4 NE1/4 NE1/4 sec. 11, T. 6 S., R. 4 E. Collections were made from the lower 3 m (10 ft) of the section, which consists of a blue-gray, silty, calcareous, micaceous, glauconitic, very fossiliferous sand and a layer of crab-bearing concretions near its base. The overlying layer is a dark-gray, silty, micaceous, iron-stained clay interbedded with a medium-grained sand.

Locality 6. USGS Mesozoic collection 711 (T.W. Stanton, 1889). Bed of Hall Branch of Talla­hatche River on the old C.R. Hall farm, near Molino in Union County, Mississippi, sec. 5, T. 6 S., R. 4 E. Stanton described, in his field notes, the 396-m (0.25-mi) exposure along the creek bed as “an almost continuous exposure of dark clay marl, 10 or 15 feet [3-4.6 m] thick.”
Locality 7. USGS Mesozoic collection 25410 (N.F. Sohl, 1950-1952). Roadcut in east-facing slope of Hall Branch, 1.4 km (0.9 mi) west of Molino in Union County, Mississippi. SW¼ NE¼ sec. 8, T. 6 S., R. 4 E. This locality is 0.8 km (0.5 mi) north of locality 6. The sample was collected from the lowest bed of the Coon Creek exposed at this outcrop—a blue-gray, silty, micaceous, calcareous, glauconitic, fossiliferous sand. This bed most likely correlates with the bed sampled at locality 6, but an exact determination is impossible. The lower bed is overlain by 4.2 m (14 ft) of Coon Creek interbedded sands and clays, capped by 48 m (16 ft) of the McNairy Sand.

Locality 8. USGS Mesozoic collection 6873 (L.W. Stephenson, 1910). Lee’s old mill site, roadcut on northeast-facing slope of Tallahatchie River valley. 3.2 km (2 mi) north-northeast of Keownville, on the road to Molino in Union County, Mississippi. NW¼ NE¼ sec. 17, T. 6 S., R. 4 E. Five beds of the upper portion of the Coon Creek Tongue crop out at this locality (see Sohl, 1960, p. 30-31, locs. 14, 15, and 16, for complete section). The first 10.4 m (34.5 ft) of the section consists of a micaceous sand, interbedded with clay and alternating between fossiliferous and noncalcareous beds, overlain in turn by a thin (0.2 m) layer of blue-black, sandy, laminated, micaceous, carbonaceous clay. Nine meters (30 ft) of McNairy Sand rests on top of the Coon Creek beds. An incomplete section was exposed in 1910, but the sample that Stephenson collected then probably came from bed 4, a blue-black, massive, silty, micaceous, glauconitic, fossiliferous sand. This unit is stratigraphically higher than the beds described at localities 6 and 7.

Locality 9. USGS Mesozoic collection 25409 (N.F. Sohl, 1950-52). Locality description same as that for locality 8. This sample was also collected from bed 4.

Locality 10. USGS Mesozoic collection 25407 (N.F. Sohl, 1950-52). Roadcut on northeast-facing slope of Hall Creek, a tributary of the Tallahatchie River, 4.6 km (2.9 mi) (airline) southwest of Dumas in Tippah County, Mississippi, center S½ NW¼ sec. 34, T. 5 S., R. 4 E. The sample was collected from the lowermost unit of the 11-m (37-ft) section, which is a blue-gray, medium-grained, silty, clayey, micaceous, glauconitic, highly fossiliferous sand containing many large fossil concretions. Four additional Coon Creek beds overlie unit 1 and consist of alternating sands and clays (see Sohl, 1960, p. 28, loc. 6, for the complete section). The section is topped with a layer of McNairy Sand.

Ripley Formation, upper marine sands

Locality 11. USGS Mesozoic collection 708 (T.W. Stanton, 1889). Bullock’s old overshot mill, 3.2 km (2 mi) south of Dumas in Tippah County, Mississippi, sec. 36, T. 5 S., R. 4 E. Stanton, in his field notes, stated that fossils were collected from “8 or 10 feet [2.4-3.0 m] of dark marl” at water level. Although the outcrop was overgrown by 1910 when L.W. Stephenson visited the site, he placed the collection in the Coon Creek Tongue (Stephenson and Monroe, 1940, p. 188). Sohl argues that the matrix and fauna present could just as easily be placed in the upper part of the Ripley; the presence of the outcrop “20 or 30 feet” [6.1-9.1 m] below a ferruginous limestone layer, most likely the Keownville Limestone Member of the Ripley, suggests this possibility (Sohl, 1960, p. 28, loc. 5).

Locality 12. USGS Mesozoic collection 26339 (N.F. Sohl and H.I. Saunders, 1956). Roadcut on secondary road on the north-facing slope of the South Branch of Wilhite Creek, 3.7 km (2.3 mi) southeast of Keownville in Union County, Mississippi, SE¼ NW¼ sec. 33, T. 6 S., R. 4 E. Fossils occur in a gray, micaceous, glauconitic, clayey fine sand about 2 m thick and located 63.5 cm (25 in) below the Chiwapa Sandstone Member of the Ripley.

Locality 13. USGS Mesozoic collection 857 (T.W. Stanton, 1891). Chattahoochee River, between Eufaula and Barbour Creek, 3.2 km (2 mi) below Eufaula landing in Barbour County, Alabama. The collector provided no additional information. Before construction of the Walter F. George Dam at Fort Gaines, Ga., there were numerous exposures of fossiliferous, dark-gray, clayey sand of the Ripley Formation along the Chattahoochee River bluffs in this area. Which of these exposures is represented by Stanton’s collection is unsure, but, presumably, it would have come from beds less than 1 m below locality 14.

Chattahoochee River, left bank about 3.2 km (2 mi) below the Central of Georgia railroad crossing in Quitman County, Georgia. Collections were made from a 3-m section of dark-gray, sparsely glauconitic, micaceous, clayey fine sand.

Localities 15-19

Localities 15-19: USGS Mesozoic localities 25991 (N.F. Sohl and H.I. Saunders, 1955). Bluffs of Chattahoochee River, left side about 396 m (0.25 mi) above the mouth of Barbour Creek at water level and 6.4 km (4.0 mi) south of Eufaula in Quitman County, Georgia. Collected from a 2.5-m section consisting of blue-black, very micaceous, glauconitic, clayey fine sand.

Owl Creek Formation

Localities 16-19: USGS Mesozoic collections 25424 (N.F. Sohl, 1951–53). Head of ravine, underpass, and roadcut just north of road fork 1.2 km (0.75 mi) south of Dumas in Tippah County, Mississippi, center of eastern edge of SE ¼ sec. 24, T. 5 S., R. 4 E. The 2.4-m (8-ft) exposure of the Owl Creek at this section overlies 49.8 m (166 ft) of the Ripley and is overlain by 1.8 m (6 ft) of the Prairie Bluff(?). Chalk (see Sohl, 1960, p. 29–30, loc. 47, for complete section). The Owl Creek at this locality is a blue-gray, silty, micaceous, glauconitic, calcareous, fossiliferous sand.

Localities 17-18: USGS Mesozoic collection 713 (T.W. Stanton, 1889). Exposures in Walnut Creek bed, Braddock’s farm, on south-facing slope of Walnut Creek valley 6 km (3.75 mi) east-southeast of Falkner in Tippah County, Mississippi, NE ¼ SE ¼ SE ¼ sec. 16, R. 3 S.; T. 4 E. Two and one-half meters (8 ft) of the Ripley is overlain by 7.65 m (25.5 ft) of the Owl Creek; 7.2 m (24 ft) of the Clayton Formation tops the section. The sample was collected from the 2.7-m-thick (9-ft-thick) lower bed of the Owl Creek, which Stephenson (Stephenson and Monroe, 1940, p. 233) described as a blue-gray, calcareous, argillaceous, very fine sand containing abundant fossil shells.

Localities 19-22: USGS Mesozoic collections 25422 (N.F. Sohl and H.I. Saunders, 1955). Bluffs on right bank of Owl Creek, 4 km (2.5 mi) northeast of Ripley in Tippah County, Mississippi. Sec. 27, T. 2 S., R. 4 E. Sample was collected from a 6-m (20-ft) layer of blue-gray, silty, micaceous, glauconitic, very fossiliferous sand of the Owl Creek, overlain by about 9 m (30 ft) of the Clayton (Paleocene).

Providence Sand

Localities 20-22: USGS Mesozoic collections 25921 (N.F. Sohl and H.I. Saunders, 1955). Bluffs of White Oak Creek at bridge of Barbour County Route 47 and Alabama State Route 95 at the Barbour-Henry County line in Alabama, SE ¼ SW ¼ sec. 8, T. 9 N., R. 29 E. Collected from about 2 m of blue-black, coarse, sparsely glauconitic, clayey, fine-to medium-grained sand exposed in stream bed and banks.

Localities 20-21: USGS Mesozoic collection 855 (T.W. Stanton, 1891). Chattahoochee River at mouth of Pataula Creek in Georgia. Stanton described the outcrop in his field notes as “25 or 30 feet [7.6–9.1 m] of blue sandy clay interrupted midway by 4 feet [1.2 m] of coarse gray sandstone.”

Localities 22: USGS Mesozoic collections 6412 (L.W. Stephenson, 1909) and 25935 (N.F. Sohl and H.I. Saunders, 1955). One and four-tenths kilometers (0.9 mi) above the mouth of Pataula Creek at the “Narrows,” right bank 180 m (200 yd) below the waterfalls, Clay County, Georgia. Stephenson (Veatch and Stephenson, 1911, p. 184) described the section as 6.9 m (23 ft) of “dark greenish gray, massive, micaceous, argillaceous, marine sand with indurated ledges” 0.3 to 1.8 m (1–6 ft) apart, overlain by 3.6 m (12 ft) of “brownish, weathered, argillaceous, marine sand.”
Severn Formation

Locality 23. USGS Mesozoic collection 32775 (N.F. Sohl, 1971). Excavations for Landover Mall shopping center near intersection of Maryland Route 202, Interstate 95, and Brightseat Road in Prince Georges County, Maryland. Collection is from the upper part of a 4-m (13.2-ft) section of dark gray, micaceous, fine sand.

Locality 24. USGS Mesozoic collection 32772 (N.F. Sohl and E.G. Kauffmann, 1961–62). Exposures in small drainage ditch on the Wilson Dairy Farm south of Sheriff Road (Gardner's (1916) Brightseat locality) in Prince Georges County, Maryland. Collection is from the upper part of a 6-m-thick (19.8-ft-thick) section of gray, very micaceous, clayey, fine sand.

Locality 25. USGS Mesozoic collection 28858 (N.F. Sohl, W.O. Ross, H.I. Saunders, and E.L. Yochelson, 1960). Excavations immediately west of bridge of Interstate 95 and just north of Central Avenue, within cloverleaf approach and exit, in Prince Georges County, Maryland. Sample is from the medial part of a 3.5-m (11.6-ft) section of gray, micaceous, clayey fine sand.
PLATES 1–7
Type specimens of species of *Nucula*

Figures 1–10. *Nucula percrassa* Conrad; all specimens ×2.

1, 2. Interior and exterior views of left valve of topotype figured by Stephenson (1955, pl. 15, figs. 4–7), from the Owl Creek Formation at locality 19. USGS 707. USNM 128084. Note position of insertion of anterior pedal protractor muscle (AP).

3–6. Gardner’s hypotype of *N. slackiana*, from the Severn Formation, 1.6 km (1 mi) west of Friendly in Prince Georges County, Maryland. USNM 131858.

3, 4. Exterior and interior views of right valve. Note well-developed dorsal median (DM) and ventral-median (VM) muscle scars.

5, 6. Interior and exterior views of left valve. Note the division of the anterior adductor into quick (Q) and catch (C) muscles.

7, 8. Exterior and interior views of right valve of Harbison’s holotype of *N. tippahensis*, from the Coon Creek Tongue of the Ripley Formation at locality 5. USNM 103751.

9, 10. Interior and exterior views of left valve of a topotype of *N. tippahensis* Harbison, from the Coon Creek Tongue of the Ripley Formation at locality 5. USGS 25411. USNM 423803. Note the large number of anterior pedal retractor muscle scars (AR).
Comparison of external morphologies of *Nucula percrassa* Conrad

Figures 1–11. *Nucula percrassa* Conrad; all specimens ×2.

1, 2, 4. Specimens of *N. percrassa* classified as *N. slackiana* Gabb of Gardner for the discriminant analysis, from the Severn Formation at locality 25. USGS 28858.

1. Exterior view of right valve. USNM 423804.

2. Exterior view of right valve. USNM 423805.

4. Exterior view of left valve. USNM 423806.

3, 5, 6, 9. Specimens of *N. percrassa* Conrad, classified as *N. percrassa* for the discriminant analysis.


5. Exterior view of right valve of a topotype, from the Owl Creek Formation at locality 19. USGS 707. USNM 20688.


9. Exterior view of left valve, from the Coon Creek Tongue of the Ripley Formation at locality 4. USNM 32713. Figured by Wade (1926, pl. 8, fig. 1).

7, 8, 10, 11. Specimens of *N. percrassa*, classified as *N. tippahensis* Harbison for the discriminant analysis.

7. Exterior view of left valve, from the Coon Creek Tongue of the Ripley Formation at locality 9. USGS 25409. USNM 423809.

8. Exterior view of right valve, from the Coon Creek Tongue of the Ripley Formation at locality 10. USGS 25407. USNM 423810.

10. Exterior view of left valve of a topotype, from the Coon Creek Tongue of the Ripley Formation at locality 5. USGS 25411. USNM 423811.

11. Exterior view of right valve, from the Coon Creek Tongue of the Ripley Formation at locality 10. USGS 25407. USNM 423812. Note strong radial ribs exposed by exfoliation of outer shell layers.
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PLATE 3
Comparison between upper Maastrichtian specimens of *Nucula percrassa* Conrad
and *Nucula severnensis* Wingard and Sohl, n.sp. (stratigraphic level 5, text fig. 6) at various growth stages

Figures 1–10. *Nucula percrassa* Conrad; all specimens ×3.
1. Exterior view of left valve, from the Severn Formation at locality 23. USGS 32775. USNM 423813.
2, 3. Exterior and interior views of right valve, from the Providence Sand at locality 20. USGS 25921. USNM 423814.
4, 5. Interior and exterior views of left valve, from the Severn Formation at locality 24. USGS 32772. USNM 423815.
6, 7. Exterior and interior views of left valve, from the Owl Creek Formation at locality 16. USGS 25424. USNM 423816.
8. Exterior view of left valve, from the Owl Creek Formation at locality 18. USGS 25422. USNM 423817.
9. Exterior view of right valve of a topotype, from the Owl Creek Formation at locality 19. USGS 6464. USNM 423818.
10. Interior view of right valve, from the Providence Sand at locality 22. USGS 25935. USNM 423819.

11, 12. Exterior and interior views of right valve of the holotype, from the Severn Formation at locality 25. USGS 28858. USNM 423838.
13. Interior view of right valve of a paratype, from the Severn Formation at locality 23. USGS 32775. USNM 423839.
14. Exterior view of left valve of a paratype, from the Severn Formation at locality 23. USGS 32775. USNM 423840.
15, 16. Interior and exterior views of left valve of a paratype, from the Providence Sand at locality 22. USGS 25935. USNM 423841.
17. Exterior view of right valve of a paratype, from the Providence Sand at locality 22. USGS 25935. USNM 423842.
18, 19. Interior and exterior views of right valve of a paratype, from the Providence Sand at locality 20. USGS 25921. USNM 423843.
PLATE 4
Comparison of *Nucula percrassa* Conrad arranged in descending stratigraphic order

Figures 1–10. *Nucula percrassa* Conrad; all specimens ×2. (Text fig. 6 shows stratigraphic levels and exact positions of samples.)

1. Exterior view of left valve of a topotype, from the Owl Creek Formation at locality 19, stratigraphic level 5. USGS 707. USNM 20688.
2. Interior view of right valve, from the Providence Sand at locality 22, stratigraphic level 5. USGS 25935. USNM 423820.
3. Interior and exterior views of right valve, from the Ripley Formation at locality 11, stratigraphic level 4. USGS 708. USNM 423821.
4. Exterior and interior views of right valve classified as *Nucula tippahensis* Harbison for the discriminant analysis, from the Coon Creek Tongue of the Ripley Formation at locality 10, stratigraphic level 3. USGS 25407. USNM 423822. Resilifer is broken.
5. Interior and exterior views of right valve, from the Coon Creek Tongue of the Ripley Formation at locality 4, stratigraphic level 2. USGS 25406. USNM 423823.
6. Exterior view of right valve, from the Blufftown Formation at locality 3, stratigraphic level 1. USGS 26033. USNM 423824.
7. Exterior view of right valve from the Coffee Sand at locality 2, stratigraphic level 1. USGS 17254. USNM 423825.
NUCULA
PLATE 5
Comparison of four species of Upper Cretaceous Nucula

Figures 1, 5, 6, 8. Nucula cuneifrons Conrad.
1. Interior view of right valve (×1.5), from the Coon Creek Tongue of the Ripley Formation at locality 6. USGS 711. USNM 423854. Note oblique inclination of resilifer.
5. Exterior view of left valve, scanning electron microscope (SEM) (×25), from the Providence Sand at Ft. Gaines in Clay County, Georgia. USGS 32250. USNM 423855.
6. Interior view of left valve (×3), from the Severn Formation at locality 25. USGS 28858. USNM 423856.

2, 11. N. severnensis Wingard and Sohl, n.sp., specimens from the Ripley Formation at Mercer’s Mill, Tobannee Creek in Quitman County, Georgia. USGS 27878.
2. Interior view of left valve of a paratype, SEM (×40). USNM 423844.

3, 10. N. percrassa Conrad, specimens from the Ripley Formation at Mercer’s Mill, Tobannee Creek in Quitman County, Georgia. USGS 27878.
10. Interior view of left valve, SEM (×44). USNM 423827.

4. Exterior view of right valve (×4), from the Severn Formation at locality 25. USGS 28858. USNM 423858.
7. Exterior view of left valve, SEM (×20), from the Severn Formation at locality 25. USGS 28858. USNM 423859. Note strong collabral ribs on umbonal region, in contrast to figures 3, 5, and 11.
9. Interior view of right valve, SEM ×32, from the Ripley Formation at Mercer’s Mill, Tobannee Creek in Quitman County, Georgia. USGS 27878. USNM 423860.
PLATE 6
Articulated specimens showing variations in shell obesity
and lunule and escutcheon morphology

Figures 1, 2, 4–16. *Nucula percrassa* Conrad; all specimens ×2.

1, 4. Dorsal hinge view of specimens classified as *N. slackiana* Gabb of Gardner for the
discriminant analysis, from the Severn Formation at locality 24. USGS 32772.
   1. USNM 423828.
   4. USNM 423829.

2. Dorsal hinge view of specimen classified as *N. tippahensis* Harbison for the
discriminant analysis, from the Coon Creek Tongue of the Ripley Formation at
locality 6. USGS 711. USNM 20843.

5, 7, 8. Topotype specimen classified as *N. percrassa* for the discriminant analysis, from
the Owl Creek Formation at locality 19. USGS 707. USNM 20688. Youthful
specimen does not exhibit shell thickening characteristic of more mature members
of the population.
   5. Dorsal hinge view.
   7. Posterior view.
   8. Anterior view.

6, 9, 10. Topotype specimen classified as *N. percrassa* for the discriminant analysis, from
the Owl Creek Formation at locality 19. USGS 707. USNM 20688. Specimen
illustrates senile characteristic of shell thickening, which produces a flattened
ventral margin.
   6. Dorsal hinge view.
   10. Anterior view.

11, 13, 14. Specimen classified as *N. percrassa* for the discriminant analysis, from the Owl
Creek Formation at locality 17. USGS 713. USNM 20802. Specimen exhibits a
lesser degree of shell thickening than the topotype specimen in figures 9, 10, and
12.
   11. Dorsal hinge view.
   13. Posterior view.

12, 15, 16. Specimen classified as *N. percrassa* for the discriminant analysis, from the
Providence Sand at locality 22. USGS 25935. USNM 423830.
   12. Dorsal hinge view.
   15. Posterior view.

3. *Nucula severnensis* Wingard and Sohl, n.sp. (×3); dorsal hinge view of a paratype, from the
Providence Sand at locality 20. USGS 25921. USNM 423846.
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PLATE 7
Adductor and pedal muscle scar systems

Figures 1, 2, 4–11. *Nucula percrassa* Conrad.

1. Latex mold (x1.5) of left valve interior of a topotype, from the Owl Creek
Formation at locality 19. USGS 25423. USNM 423831.

2. Latex mold (x2) of left valve interior of specimen, from the Coon Creek Tongue of
the Ripley Formation at locality 4. USGS 25406. USNM 423832.

4, 9. Internal mold (x2), from the Prairie Bluff Chalk at Braggs in Lowndes County,
Alabama. USGS 30669. USNM 423833.

4. View of right valve interior.


5, 6. Latex molds (x1.5) of specimens, from the Ripley Formation at locality 13. USGS
857.

5. Right valve interior. USNM 423834.

6. Left valve interior. USNM 423835.

7. Dorsal hinge view of internal mold (x2), from the Prairie Bluff Chalk at Braggs in
Lowndes County, Alabama. USGS 30668. USNM 423836.

8, 10, 11. Articulated specimen (x2), from the Coon Creek Tongue of the Ripley Formation at
locality 4. USGS 25406. USNM 423837.

8. Interior view through the ventral shell gape of hinge, resilifer, and muscle
scars.

10. Interior view through the ventral shell gape of the muscle scars of the right
valve.

11. Interior view through the ventral shell gape of the muscle scars of the left
valve.

3. *Nucula severnensis* Wingard and Sohl, n.sp. Latex mold (x2) of right valve interior of specimen,
from the Providence Sand at White Oak Creek at the Barbour-Henry County line, Alabama (near
loc. 20). USGS 25993. USNM 423847.

AA, anterior adductor; AP, anterior protractor; AR, anterior pedal retractor; C, catch portion of adductor muscle; DM,
dorsal-median muscle; PA, posterior adductor; PE, pedal elevator muscle; PR, posterior pedal retractor; Q, quick
portion of adductor muscle; VM, ventral median muscle.
NUCULA
Chapter E

HUM Lithosome: An Example of Regional Stratigraphic Synthesis in the Mississippian of the Western Interior of the United States

By WILLIAM J. SANDO

Development of a regional depositional model using the lithosome concept

U.S. GEOLOGICAL SURVEY BULLETIN 1881

Shorter Contributions to Paleontology and Stratigraphy
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PLATE
   A. Profiles A–A', B–B', and C–C' across the depositional strike of the HUM lithosome
   B. Profile D–D' along the depositional strike of the HUM lithosome

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1. Reference section of the HUM lithosome near Twelve Mile Pass, Tooele County, Utah E4
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2. Correlations and reference sections for other lithosomes shown on plate 1A and 1B E12
HUM Lithosome: An Example of Regional Stratigraphic Synthesis in the Mississippian of the Western Interior Region of the United States

By William J. Sando

Abstract

The rules governing formal stratigraphic nomenclature are justifiably committed to producing a stable classification based on geologic mapping and mappability. However, regional stratigraphic syntheses based on correlation of stratigraphic sections may conflict with the classification of rock units founded on geologic mapping. When a conflict occurs, it may be difficult to resolve without abandoning useful geologic maps or remapping the geology. The lithosome concept affords a practical solution to problems of stratigraphic nomenclature that arise from regional stratigraphic studies of Mississippian rocks in the Western Interior of the United States.

The informal term lithosome refers to a vertically and horizontally segregated body of sedimentary rock, characterized by its lithic content and inferred genetic significance, that mutually intertongues with one or more rock bodies of different lithic constitution. An analysis of the HUM lithosome in the Upper Mississippian of Utah, Idaho, and Wyoming is an example of how the lithosome concept can be used to communicate ideas about regional stratigraphic and depositional relationships.

The HUM lithosome is a large body of marine quartz sandstone and subtidal carbonate rock in the Antler foreland basin of the Western Interior. It is composed mostly of terrigenous detritus supplied by rivers that carried this sediment westward across the Madison paleokarst plain from sources in the Transcontinental arch area to the Antler basin in Late Mississippian time. The HUM has the form of an offshore delta shelf deposit similar to that of the present Nile delta, but no deltaic plain deposits are preserved. Carbonate factories that originated on local sea-floor highs and on a large positive area in Idaho and northern Utah contributed significant amounts of carbonate sediment to the HUM depositional complex.

INTRODUCTION

Formal lithostratigraphic units recognized in the Mississippian of the Western Interior region traditionally have been founded on geologic mapping. Most of the older units currently in use were originally defined and named in mining districts in order to describe local geologic history, interpreted from geologic mapping, before the advent of regional stratigraphic studies. Extensions of these units beyond their type localities commonly resulted from subsequent mapping that proceeded radially from these nomenclatural centers with limited information available to determine regional implications. Regional geologic maps (2° sheets and State maps) compiled from quadrangle maps and other local maps extended the formal nomenclature. This procedure resulted in a stable formal stratigraphic nomenclature that is deeply ingrained in the common geologic language of the area.

The benefits of this historical development of the lithostratigraphic nomenclature are obvious. The inherent stability of the nomenclature minimizes problems in communication among most geologists working in the region. The names of the units depicted on most maps are familiar to all, and most geologists need not concern themselves with new names or new combinations of old names when they want to work in a given local area.

Regional stratigraphic synthesis based on correlation of stratigraphic sections may result in recognition of rock units that do not coincide with units recognized on existing geologic maps. The requirements of geologic mapping for definition and identification of rock units tend to emphasize criteria of local rather than regional significance. The mapping geologist must deal with the entire geologic sequence of the map area, whereas the regional stratigrapher focuses on only a small fraction of that sequence. Inferred geologic history, depositional environment, and age relationships, which are prohibited by the North American Stratigraphic Code (North American Commission on Stratigraphic Nomenclature, 1983) as criteria for defining formal rock units, may be useful assets for the regional stratigrapher. Regionally significant rock units too thin to be mapped at conventional mapping scales may be obscured by inclusion in larger formal units recognized for mapping. Nomenclatural precedence established by previous mapping may effectively limit changes in stratigraphic classification based on new evidence or reinterpretation of old evidence.

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My regional stratigraphic analyses of the Western Interior Mississippian have now reached a stage of development where it has become almost impossible to communicate new regional lithostratigraphic concepts without drastically altering much of the stable formal lithostratigraphic classification recognized widely by other geologists. In most cases, the regional synthesis has resulted in the consolidation of local units into areally more extensive regional units and the consequent abandonment of some older names, some of which were proposed by myself and my colleagues in earlier studies. Occasionally, the need for new names to designate previously unrecognized units has been indicated. New concepts of geologic history and depositional environment inferred from the rocks have played a major role in the definition and recognition of the rock bodies.

The North American Stratigraphic Code (North American Commission on Stratigraphic Nomenclature. 1983: p. 850–851) has provided a solution to this dilemma by permitting the use of various kinds of informal stratigraphic units for “innovative approaches in regional stratigraphic studies.” H.E. Wheeler and V.S. Mallory (in Fischer and others, 1954; also Wheeler and Mallory, 1956), faced with the same dilemma, proposed the term “lithosome” to address the same problems that I have encountered. This paper presents a procedure for using lithosomes as informal units to describe regional stratigraphic relations in the Mississippian of the Western Interior.

Acknowledgments

Early fieldwork on the HUM sequence was done in the company of J.T. Dutro, Jr., to whom I am indebted for many contributions to the basic data in Idaho, western Wyoming, and northern Utah. I am likewise indebted to C.A. Sandberg and R.C. Gutschick for their contributions, made during joint field studies in Utah and Idaho. I thank Mackenzie Gordon, Jr., for sharing with me his data on critical stratigraphic sections in Utah. I am grateful to K.R. Moore for dedicated assistance in field and laboratory. I thank B.L. Mamet for foraminiferal zone determinations and Sandberg for conodont zone determinations. My thanks are also extended to Dutro, G.A. Izett, W.J. Perry, J.A. Pierce, F.G. Poole, N.F. Sohl, D.J. Stanley, J.I. Tracey, and B.R. Wardlaw for stimulating discussions of the concepts and for technical review of the manuscript.

LITHOSOMES

Definition

Lithosome is one of the many terms that were coined during the published discussions of stratigraphic nomenclature that preceded formulation of the American Code of Stratigraphic Nomenclature by the American Stratigraphic Commission (1961). Wheeler and Mallory (1953) called attention to the interrelations of rock units that affect definitions of formal stratigraphic units and focused on recognition of the arbitrary cutoff as a principle in defining formal units. A critique of this concept by A.G. Fischer (in Fischer and others, 1954) led Wheeler and Mallory (in Fischer and others, 1954, p. 929) to propose the term lithosome to distinguish lithic units that are “vertically-laterally” segregated (group, formation, member) as opposed to those that are laterally segregated (facies). As a followup to the 1954 debate, Wheeler and Mallory (1956) presented an expanded discussion of these two kinds of lithic unit and formally defined the term lithosome as “a lithostratigraphic body which is mutually intertongued with one or more bodies of differing lithic constitution” (Wheeler and Mallory, 1956, p. 2719).

Moore (1957, p. 1787–1789) altered Wheeler and Mallory’s original definition of lithosome to read “(1) an independent body of genetically related sedimentary deposits of any sort or, alternatively, (2) a spatially segregated part of any genetically related body of sedimentary deposits, in which this part is distinguished by some noteworthy characters or combination of characters judged important enough to merit separation.” Moore believed that lithosome is a synonym of Caster’s (1934) magnafacies, which was defined as “a major, continuous, and homogeneous belt of deposits that is distinguished by similar lithologic and paleontologic characters and that extends obliquely across time planes or through several defined chronostratigraphic units” (Bates and Jackson, 1980, p. 375). Moore’s definition of lithosome deemphasized the intertonguing character of its lateral margins and injected genetic homogeneity into the concept.

Weller (1958, p. 613) rejected Caster’s magnafacies as a useful term because he believed that it is merely a “rock-stratigraphic unit” coinciding with formation, group, or member, depending on the size of the rock body to which it is applied.” Weller (1958, p. 635–636) also rejected the term lithosome because he concluded that it would have little practical application and that it coincided essentially with the terms lithofacies and facies. L.L. Sloss (in Weller, 1958, p. 624) defined lithosome as a “body of sediment deposited under uniform physico-chemical conditions.”

The lithosome, as originally conceived by Wheeler and Mallory, offers a practical solution to the problem of distinguishing natural rock bodies that have been given different formal names (group, formation, member) in different geographic areas because of the historical development of the nomenclature. Although almost all lithostratigraphic units are inherently diachronous, Caster’s magnafacies does not seem appropriate as a general term for such rock bodies, because it refers to a facies geometry characterized by large-scale diachronity. The essential character-
istics of a lithosome embodied in Wheeler and Mallory's (1956) original definition and augmented by Moore (1957) and Sloss (in Weller, 1958) are (1) lithic identity, (2) vertical and lateral segregation, (3) genetic identity, and (4) intertonguing relationships with other bodies of differing lithic constitution. I propose a revised definition of lithosome as a vertically and horizontally segregated body of sedimentary rock, characterized by its lithic content and inferred genetic significance, which mutually intertongues with one or more bodies of differing lithic constitution. A lithosome may or may not be demonstrably diachronous as measured by its transgression of time planes based on biozones or physical means of measuring time. Mappability is not a requirement for recognition of a lithosome.

**Operational Procedure**

Communicating concepts of regional stratigraphic and depositional models by means of lithosomes is facilitated by using a system of nomenclature independent of the formal stratigraphic classification in order to avoid confusion between the two systems. However, because most lithosomes are lithologically and stratigraphically equivalent to formal stratigraphic units at some localities, recognition is enhanced by using names related to familiar formal names. In this paper, a lithosome name is derived by contracting the geographic name of the formal stratigraphic unit that is most typical of the lithosome and printing it in capital letters. The reference section for a lithosome may be the type section of a formal stratigraphic unit, or it may be a more representative locality discovered during later regional studies.

In the example described below, I have chosen the name HUM lithosome, derived from the Humbug Formation of Utah, to designate a body of quartz sandstone and carbonate rock in the Upper Mississippian of Utah, Idaho, and Wyoming. The HUM lithosome is founded on a reference section where its vertical boundaries coincide with those of the formal unit. The HUM lithosome is then projected from its reference section into other areas by analyzing detailed stratigraphic sections. Age relationships of its vertical boundaries are determined biometrically, where possible, or by lithostratigraphic correlation with sections where the boundaries are dated by fossils. Lateral boundaries are determined by regional lithostratigraphic analysis of the total time interval occupied by the lithosome throughout its lateral extent.

**HUM LITHOSOME**

**Reference Section and Definition**

The reference section for the HUM lithosome is on the south side of Topliff Hill, near Twelve Mile Pass, at the north end of the East Tintic Mountains in central Utah, where it coincides with the Humbug Formation (Tower and Smith, 1899) as mapped by Morris and Lovering (1961). A stratigraphic section measured by Mackenzie Gordon, Jr., H.M. Duncan, and H.T. Morris (fig. 1) serves as a description of the reference section. The HUM lithosome in this section is composed of approximately 200 m of fine- to medium-grained calcareous quartz sandstone interbedded with mostly subtidal and fossiliferous limestone and sandy limestone. Corals, brachiopods, and foraminifers, which are the most common fossils, indicate a zonal range of Composite Zones 17 to 18 in the zonation system of Sando (1985) (fig. 2). This zonal range places the HUM in the Upper Mississippian (middle and late Viséan of the European scale) at the reference locality.

The HUM lithosome in its reference section is overlain by the GREAB lithosome and underlain by the UNJO lithosome, units that coincide with the Great Blue Limestone and the Uncle Joe Member of the Deseret Limestone, respectively, as mapped by Morris and Lovering (1961) in the Tintic district.

**Regional Relations with Other Lithosomes**

The HUM lithosome occupies a large area in southeast Idaho, western Wyoming, and Utah (fig. 3), where it is composed of rocks currently mapped as Humbug Formation over most of Utah and includes parts of the Brazer Limestone in northern Utah; parts of the Wells Formation in northeast Utah, western Wyoming, and southeast Idaho; parts of the Little Flat and Aspen Range Formations in southeast Idaho; and a part of the Amsden Formation in western Wyoming (pl. 1A, 1B). It is bounded on the west by laterally equivalent rocks of the WOOM lithosome, which includes strata currently mapped as Woodman Formation (western Utah), Great Blue Limestone (western Utah), Chainman Shale (western Utah and eastern Nevada), and Deep Creek Formation (southeast Idaho). On the east, the HUM lithosome interfingers with the DAR lithosome, which includes strata currently mapped as Darwin Sandstone Member of the Amsden Formation (western Wyoming), Morgan Formation (northwest Colorado), and Molas Formation (southwest Utah).

Detailed descriptions and discussion of the many lithosomes that were deposited during the total time interval of HUM deposition in the study area are beyond the scope of this report. The relations of these units to formal stratigraphic units in control sections are shown on plate 1A and 1B. Table 2 provides data on the locations of the reference sections of these lithosomes and their relations to formal stratigraphic units in the reference sections.
Figure 1. Reference section (UT-104) of the HUM lithosome near Twelve Mile Pass, NE1/4 sec. 22, T. 8 S., R. 3 W., Tooele County, Utah. Fossil collections and description of stratigraphic section by Mackenzie Gordon, Jr., H.M. Duncan, and H.T. Morris; foraminiferal zone determinations by B.L. Mamet. Fossil collections are at the U.S. National Museum of Natural History, Washington, D.C. PC refers to the Permian and Carboniferous locality file.
Figure 2. Mississippian time scale and biozonations used in chronometric analysis of the HUM lithosome (from Sando, 1985). Shading denotes part of the scale not involved in this study.
Figure 3. Areal distribution of the HUM lithosome. Description of stratigraphic section control points is given in table 1. Structural features are from Gutschick and others (1980) and Craig and others (1979).
EXPLANATION

- Mississippian rocks never deposited or removed by subsequent erosion
- Mississippian rocks absent or buried beneath thick Cretaceous and Tertiary extrusive and sedimentary rocks
- HUM lithosome, including sandy carbonate facies
- WOOM lithosome
- Land during HUM time
- HUM lithosome removed by local erosion
- Lateral contact of HUM lithosome with WOOM lithosome and of sandy carbonate facies with main body of HUM dashed where inferred, sawteeth indicate interfingering
- Post-Mississippian thrust fault, dashed where inferred, sawteeth on upper plate
- Post-Mississippian lateral fault, dashed where inferred, arrows show relative movement
- Position of shore line late in HUM time, dashed where approximately located, hachures on landward side
- Major river

Figure 3. Explanation.

Chronometric Regional Geometry

Chronometric lithofacies profiles across (pl. 1A) and along (pl. 1B) the regional depositional strike and a chronometric interval map depicting the entire areal extent of the lithosome (fig. 3) define the form of the HUM lithosome in time and space. On the interval map (fig. 3), the lithosome appears as a lobate body of quartz sand and sandy carbonate that extends westward from the shoreline of the Madison paleokarst plain in southwest Wyoming, northwest Colorado, and southeast Utah (see Sando, 1988, for a description of the paleokarst) to interfinger with fine terrigenous sediment of the WOOM lithosome, which was deposited in deeper water in western Utah and southern Idaho. A large carbonate bank that competed for depositional space with the sand was present in southeast Idaho and northern Utah.

In cross-strike profiles (pl. 1A), the HUM appears to have the form of a clastic wedge that tapers to extinction westward from the ancient shoreline. Because the vertical dimension of these profiles is time, the wedge-shaped form represents variation in the time of deposition rather than in sedimentary thickness. The wedge represents the balance that existed through HUM time between westward progradation of the sediment and eastward transgression of the sea. A profile along the depositional strike (pl. 1B) shows a generally tabular body that bulges notably in central Utah opposite a major reentrant in the shoreline in eastern Utah, which probably marks the mouth of a major river system that contributed much of the terrigenous sediment in the HUM.

The base of the HUM ranges in age from the base of Composite Zone 14 (ca. 347 Ma) to the top of Composite Zone 17 (ca. 340 Ma) (pl. 1A, 1B). The oldest rocks in the lithosome occur adjacent to the shoreline reentrant in northeast Utah and in the offshore area in northeast Utah and southeast Idaho. The top of the HUM ranges in age from the top of Composite Zone 17 (ca. 340 Ma) into the Lower Pennsylvanian (Morrowan, ca. 318 Ma). However, HUM deposition was limited to Composite Zone 22 (ca. 329 Ma) or older zones over most of its areal extent, except for the area immediately adjacent to the shoreline in northeast Utah and southwest Wyoming. Thus, although the maximum time of HUM deposition was approximately 29 m.y., most of the lithosome was deposited over a time span of approximately 18 m.y.

Thickness Variation

An isopach map of the HUM lithosome (fig. 4) reveals a morphology that is generally inverse to that of the chronometric profiles. In this perspective, the HUM thickens westward from the ancient shoreline before interfinger­ing with the WOOM on the west. The area of thickest sediment is in central and northern Utah near the western edge of the lithosome and opposite the pronounced shoreline reentrant. Some distortion of the regional isopach pattern is evident in southeast Idaho and northern Utah owing to the influence of the carbonate bank in that area. Several peculiar areas of anomalously thick and thin lithosome are evident a few tens of kilometers seaward from the ancient shoreline.

Origin

The provenance of the terrigenous detritus that forms the bulk of the HUM lithosome was the Transcontinental arch, a mountainous area east of the Madison paleokarst plain (Sando, 1988). The paucity of fine terrigenous detritus and the maturity of the sediment suggest that supermature lower Paleozoic sandstones were the principal source rocks (Mallory, 1967, p. G25-G27). This material was transported to the area of deposition by rivers that flowed across the paleokarst plain in Wyoming and Colorado (Mallory, 1967; Sando, 1988). Some of these rivers have been mapped in Wyoming (Mallory, 1967; Sando, 1988), but a
### Table 1. Catalog of stratigraphic section control points for figures 3 and 4 and plate 1A and 1B

<table>
<thead>
<tr>
<th>Number</th>
<th>Name</th>
<th>Location</th>
<th>Source</th>
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<tr>
<td>CO-4</td>
<td>Hells Canyon</td>
<td>Sec. 31, T. 6 N., R. 102 W., Moffat County</td>
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<td>CO-10</td>
<td>Jones Hole</td>
<td>T. 9 N., R. 103 W., Moffat County</td>
<td>Bloom (1961)</td>
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<td>ID-7</td>
<td>Bannock Creek</td>
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<td>ID-8</td>
<td>Paul Peak</td>
<td>SNE sec. 28, T. 10 S., R. 34 E., Power County.</td>
<td>L.C. Quinn (written communication, 1981)</td>
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<td>ID-18</td>
<td>Dry Ridge</td>
<td>SENW sec. 6, T. 9 S., R. 45 E., Caribou County.</td>
<td>W.J. Sando (unpublished field notes, 1982)</td>
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<td>ID-21</td>
<td>Little Gray Ridge</td>
<td>Sec. 18, T. 5 S., R. 43 E., Caribou County.</td>
<td>W.J. Sando (unpublished field notes, 1982)</td>
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<td>ID-23</td>
<td>Fall Creek</td>
<td>SE sec. 8, T. 1 N., R. 43 E., Bonneville County.</td>
<td>W.J. Sando (unpublished field notes, 1982)</td>
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<td>ID-25</td>
<td>Sheep Creek</td>
<td>E sec. 28, T. 1 N., R. 45 E., Bonneville County.</td>
<td>Sando (1977), Sando and Dutro (1981)</td>
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<td>ID-64</td>
<td>Phillips No. 1 Unit Horseshoe Creek.</td>
<td>Sec. 28, T. 5 N., R. 44 E., Teton County.</td>
<td>Espach and Royse (1960)</td>
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Table 1. Catalog of stratigraphic section control points for figures 3 and 4 and plates 1A and 1B—Continued

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<td>Emma Canyon</td>
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<td>Sando and others (1959)</td>
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<td>UT-10.</td>
<td>Rex Peak</td>
<td>NE sec. 31, T. 11 N., R. 8 E., Rich County</td>
<td>Sando and others (1959)</td>
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<td>UT-20.</td>
<td>Little Brush Creek</td>
<td>SE sec. 24 and NE sec. 25, T. 1 S., R. 21 E., Uintah County.</td>
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<td>UT-25.</td>
<td>Duchesne River 2</td>
<td>SW sec. 17 and SW sec. 18, T. 1 N., R. 8 W., and SW sec. 1, T. 1 N., R. 9 W., Duchesne County.</td>
<td>Huddle and McCann (1947), Baker and others (1949), Sadlick (1957).</td>
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<td>UT-29.</td>
<td>Gulf Ute Federal 1</td>
<td>Sec. 12, T. 4 S., R. 22 E., Uintah County.</td>
<td>Sadlick (1957)</td>
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<td>UT-30.</td>
<td>Split Mountain</td>
<td>Secs. 9 and 10, T. 4 S., R. 24 E., Uintah County.</td>
<td>Thomas and others (1945), Sadlick (1957)</td>
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<td>UT-34.</td>
<td>Equity Mounds Govt. 1</td>
<td>Sec. 33, T. 15 S., R. 12 E., Carbon County.</td>
<td>Reid (1954), Sadlick (1957)</td>
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<td>UT-35.</td>
<td>Cities Service Govt. 1</td>
<td>Sec. 1, T. 16 S., R. 12 E., Emery County.</td>
<td>Wells (1954), Sadlick (1957)</td>
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<td>UT-44.</td>
<td>Shell Miller Creek</td>
<td>Sec. 26, T. 15 S., R. 10 E., Carbon County.</td>
<td>Turnbow (1961)</td>
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<td>UT-71.</td>
<td>Three States No. 1 Sinbad</td>
<td>Sec. 6, T. 22 S., R. 12 E., Emery County.</td>
<td>Wengerd and Matheny (1958), Wengerd and Matheny (1958), Parker and Roberts (1963)</td>
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<td>UT-72.</td>
<td>Reynolds No. 3 Cedar Mesa</td>
<td>Sec. 19, T. 19 S., R. 12 E., Emery County.</td>
<td>Wengerd and Matheny (1958), Parker and Roberts (1963)</td>
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Table 1. Catalog of stratigraphic section control points for figures 3 and 4 and plates 1A and 1B—Continued

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<td>NW sec. 34 and S sec. 28, T. 11 N., R. 2 E., Cache County.</td>
<td>Williams (1943), Parks (1951), Holland (1951), Poole and Sandberg (1977), Sandberg and Gutschick (1977).</td>
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<td>UT-115 ....Blacksmith Fork</td>
<td>Sec. 5, T. 10 N., R. 2 E., Cache County.</td>
<td>Williams (1943), Mullens and Izett (1964)</td>
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<td>UT-116 ....Logan Canyon</td>
<td>Sec. 12, T. 12 N., R. 2 E., Cache County</td>
<td>Williams (1943)</td>
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<td>UT-118 ....Old Laketown Canyon</td>
<td>Sec. 32, T. 13 N., R. 6 E., Rich County</td>
<td>Williams (1943)</td>
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<td>UT-121 ....Boulter Peak</td>
<td>Sec. 6, T. 9 S., R. 3 W., and sec. 31, T. 8 S., R. 3 W., Tooele County.</td>
<td>Chamberlain (1981).</td>
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<td>UT-144</td>
<td>Granite Mountain</td>
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<td>Webster and others (1984)</td>
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<td>UT-146</td>
<td>Lookout Hills</td>
<td>Secs. 11, 14, 19, 24, and 25, T. 8 S., R. 7 W., Tooele County.</td>
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<td>UT-155</td>
<td>Big Canyon (Grasshopper Ridge)</td>
<td>SNW sec. 33 and NSE sec. 32, T. 6 S., R. 6 W., Tooele County.</td>
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<td>Dry Canyon</td>
<td>SE sec. 27, T. 11 S., R. 1 E., Juab County.</td>
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<td>UT-160</td>
<td>Phillips Huntington Unit 1</td>
<td>Sec. 15, T. 17 S., R. 8 E., Emery County.</td>
<td>Reid (1954), Wells (1954)</td>
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<td>UT-161</td>
<td>Standard Oil California,</td>
<td>Sec. 27, T. 23 S., R. 11 E., Emery County.</td>
<td>Reid (1954), Wells (1954)</td>
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<td></td>
<td>San Rafael Unit 2.</td>
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<td>WY-1</td>
<td>Haystack Peak</td>
<td>NWNE sec. 27, T. 34 N., R. 117 W., Lincoln County.</td>
<td>Sando and others (1975), Sando (1977), Sando and Dutro (1981), Gutchick and others (1980).</td>
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<td>Covey Cutoff Trail</td>
<td>NWNE sec. 27, T. 34 N., R. 117 W., Lincoln County.</td>
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<td>WY-3</td>
<td>Moffat Trail</td>
<td>NWNE sec. 3, T. 33 N., R. 117 W., Lincoln County.</td>
<td>Sando and others (1975)</td>
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<td>WY-6</td>
<td>Chevron 1-18F</td>
<td>SW sec. 18, T. 18 N., R. 119 W., Lincoln County.</td>
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<td>WY-10</td>
<td>Darby Canyon</td>
<td>Secs 14, 15, and 23, T. 43 N., R. 118 W., Teton County.</td>
<td>Sando and Dutro (1960), Sando and others (1975).</td>
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<td>WY-11</td>
<td>Mountain Fuel Supply and Union Pacific Railroad 19, Church Buttes Unit.</td>
<td>Sec. 8, T. 16 N., R. 112 W., Uinta County</td>
<td>Verville and others (1973)</td>
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<td>WY-12</td>
<td>Mobil 22-19-G Tip Top Unit.</td>
<td>NWNW sec. 19, T. 28 N., R. 113 W., Sublette County.</td>
<td>Marzolf (1965)</td>
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<td>WY-13</td>
<td>Darwin Peak</td>
<td>S sec. 28, T. 40 N., R. 112 W., Teton County.</td>
<td>E. Blackwelder (unpublished field notes, 1911).</td>
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<td>WY-14</td>
<td>Phillips Canyon</td>
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<td>Sando and others (1975)</td>
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<td>WY-15</td>
<td>South Indian Creek</td>
<td>NE sec. 14, T. 38 N., R. 118 W., Lincoln County.</td>
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<td>WY-16</td>
<td>Glory Mountain</td>
<td>SE sec. 13, T. 41 N., R. 118b W., Teton County.</td>
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<td>WY-17</td>
<td>Martin Creek</td>
<td>Sec 28, T. 38 N., R. 116 W., Lincoln County.</td>
<td>Love (1954), Mallory (1967)</td>
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<td>WY-18</td>
<td>Shell LeRoy Unit 1</td>
<td>Sec. 32, T. 16 N., R. 117 W., Uinta County.</td>
<td>Verville and Momper (1960), Mallory (1967)</td>
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<td>WY-20</td>
<td>Flat Creek–Sheep Creek</td>
<td>Sec. 2, T. 42 N., R. 115 W., Teton County.</td>
<td>Love (1954), Mallory (1967)</td>
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Table 1. Catalog of stratigraphic section control points for figures 3 and 4 and plates 1A and 1B—Continued

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<td>Sheep Creek Canyon</td>
<td>S sec. 7, T. 33 N., R. 115 W., Lincoln County</td>
<td>W.W. Rubey (unpublished field notes, 1939)</td>
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<td>WY-24</td>
<td>Carter Unit 1</td>
<td>Sec. 10, T. 26 N., R. 115 W., Lincoln County</td>
<td>American Stratigraphic Company (1959)</td>
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Table 2. Correlations and reference sections for other lithosomes shown on plate 1A and 1B

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<th>Lithosome</th>
<th>Equivalent formal unit</th>
<th>Reference section</th>
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<tbody>
<tr>
<td>ASPER</td>
<td>Aspen Range Formation (upper three members only)</td>
<td>North Georgetown Canyon, sec. 16, T. 10 S., R. 44 E., Bear Lake County, Idaho (Sando and others, 1981).</td>
</tr>
<tr>
<td>BIGOO</td>
<td>Big Goose Member of Madison Limestone</td>
<td>Little Tongue River (U.S. Rte. 14), Limestone, sec. 27, T. 56 N., R. 87 W., Sheridan County, Wyoming (Sando, 1976b, 1982).</td>
</tr>
<tr>
<td>BULL</td>
<td>Bull Ridge Member of Madison Limestone</td>
<td>Bull Lake Creek, sec. 11, T. 2 N., Limestone, R. 4 W., Fremont County, Wyoming (Sando, 1968).</td>
</tr>
<tr>
<td>DAR</td>
<td>Darwin Sandstone Member of Amsden Formation</td>
<td>Darwin Peak, sec. 28, T. 40 N., R. 112 W., Teton County, Wyoming (Blackwelder, 1918; Sando and others, 1975).</td>
</tr>
<tr>
<td>DEL</td>
<td>Delle Phosphatic Member of Woodman Formation</td>
<td>South Lakeside Mountains, sec. 6, T. 1 N., R. 8 W., Tooele County, Utah (Sandberg and Gutschick, 1984).</td>
</tr>
<tr>
<td>DONUT</td>
<td>Doughnut Formation</td>
<td>Whiterocks Canyon, sec. 12, T. 2 N., R. 1 W., Uintah County, Utah (Kinney’s (1955) “black shale unit”).</td>
</tr>
<tr>
<td>GREAB</td>
<td>Great Blue Limestone</td>
<td>Silveropolis Hill, sec. 25, T. 5 S., R. 4 W., Tooele County, Utah (Mackenzie Gordon, Jr., written communication, 1978).</td>
</tr>
<tr>
<td>HORSE</td>
<td>Horseshoe Shale Member of Amsden Formation</td>
<td>Livingston Ranch, sec. 29, T. 43 N., R. 106 W., Fremont County, Wyoming (Sando and others, 1975).</td>
</tr>
<tr>
<td>MANCAN</td>
<td>Manning Canyon Shale</td>
<td>Soldier Canyon, sec. 33, T. 4 S., R. 4 W., Tooele County, Utah (Gilluly, 1932).</td>
</tr>
<tr>
<td>MCKAN</td>
<td>McKenzie Canyon Limestone</td>
<td>Bell Canyon, sec. 17, T. 11 S., R. 10 W., Beaverhead County, Montana (Sando and others, 1985).</td>
</tr>
<tr>
<td>MOFAT</td>
<td>Moffat Trail Limestone Member of Amsden Formation</td>
<td>Moffat Trail, sec. 3, T. 33 N., R. 117 W., Lincoln County, Wyoming (Sando and others, 1975).</td>
</tr>
<tr>
<td>MONCAN</td>
<td>Monroe Canyon Limestone</td>
<td>Little Flat Canyon, secs. 17 and 20, T. 7 S., R. 40 E., Bannock County, Idaho (Dutro and Sando, 1963).</td>
</tr>
<tr>
<td>RANCH</td>
<td>Ranchester Limestone Member of Amsden Formation</td>
<td>Amsden Creek, sec. 34, T. 57 N., R. 87 W., Sheridan County, Wyoming (Sando and others, 1975).</td>
</tr>
<tr>
<td>TET</td>
<td>Teto Member of Deseret Limestone</td>
<td>Ophir Canyon, sec. 22, T. 5 S., R. 4 W., Tooele County, Utah (Morris and Lovering, 1961; Sandberg and Gutschick, 1980; Gutschick and others, 1980).</td>
</tr>
<tr>
<td>UNJO</td>
<td>Uncle Joe Member of Deseret limestone</td>
<td>Same as TET</td>
</tr>
<tr>
<td>WEL</td>
<td>Wells Formation</td>
<td>Deer Creek, sec. 33, T. 9 S., R. 45 E., Caribou County, Idaho (Cressman, 1964).</td>
</tr>
<tr>
<td>WOOM</td>
<td>Woodman Formation (upper two members only)</td>
<td>Pool Canyon, sec. 23, T. 7 S., R. 18 W., Tooele County, Utah (Harmala, 1982).</td>
</tr>
</tbody>
</table>

Figure 4. Thickness variation of the HUM lithosome (in meters). Contour interval is 100 m except for 50- and 60-m contours indicated near the shoreline. Data sources are given in table 1 and figure 3.
HUM Lithosome: An Example of Regional Stratigraphic Synthesis
major river in Colorado, marked by the pronounced shoreline reentrant in eastern Utah and reflected in the chronometric profiles and isopach map, has not been mapped. In Wyoming, a sheet sand (DAR lithosome) that rests on the paleokarst topography resulted from postkarst reworking of the river sands during eastward transgression of the sea. Areas of anomalously thick sediment that occupy a belt about 45 km wide seaward of the shoreline are interpreted as offshore bars and islands similar to the ones seen today along the Texas Gulf Coast.

The depositional history of the HUM lithosome was characterized by sporadic, local, predominantly subtidal carbonate sedimentation over much of the depositional area. These carbonate deposits probably originated on local sea floor highs, where the growth of carbonate-secreting organisms produced small carbonate factories that were able to compete with the influx of sand. A large carbonate bank developed in southeast Idaho and northern Utah and dominated the depositional history of that area throughout most of HUM time. This area has been identified as a positive area in the earlier Mississippian rock record (Isaacscon and others, 1985) and later became emergent (Bannock uplift of Sando (1976a) and Skipp and others (1979)).

The HUM lithosome was described as a deltaic complex by Gutschick and others (1980, p. 126), Sandberg and others (1982, p. 714, fig. 17), and Sandberg and Gutschick (1984, fig. 5). The lobate offshore morphology of the HUM and its obvious relation to river sources (fig. 4) support a deltaic origin. On the other hand, the HUM includes very little clay and silt, and no evidence of deltaic plain deposits has been found; hence, the HUM lacks some important characteristics of classic modern and ancient deltas (see examples given by Morgan, 1970). It is similar to the present offshore Nile delta shelf deposits, which include a broad sand belt in water depths of 25 to 60 m and a belt of coralline algal mounds (Coleman and others, 1981), but the Nile delta also includes a broad, onshore delta plain. Because the prograding HUM lithosome was deposited during a transgression, the typical internal deltaic plain morphology may have been destroyed by reworking of surficial deposits as the sea transgressed eastward. The WOOM lithosome, which forms a belt of fine-grained terrigenous rocks seaward from the HUM, may well represent a prodeltaic deposit, as Sandberg and others (1982, p. 714, fig. 17) suggested.

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