Evolution of the calcareous nannofossil genus *Biscutum* in the middle to Upper Cretaceous North American mid-latitudes

Bobbi J. Brace and David K. Watkins

[1]*Department of Earth and Atmospheric Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588-0340, USA*
email: bobbibrace@huskers.unl.edu

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ABSTRACT: The calcareous nannofossil genus *Biscutum* is ubiquitous in mid to Upper Cretaceous pelagic sediments. *Biscutum constans* is an important paleoceanographic proxy for surface water fertility and *Biscutum* species are important components in several Upper Cretaceous zonation schemes. Species concepts within *Biscutum* have inconsistently been applied and interpreted owing to a convoluted taxonomic history, thus limiting its utility. Most work on the evolution of *Biscutum* has been conducted on high latitude sections or Lower Cretaceous or Jurassic sediments. As such, *Biscutum* evolution in mid-latitudes of the mid to Late Cretaceous is poorly understood.

This study documents the evolution of *Biscutum* during the mid to Late Cretaceous in a mid-latitude composite section from North America. Samples from the Western Interior Basin, North Atlantic Ocean and Gulf of Mexico were examined. Six new species of *Biscutum* are presented: *B. ubiquem, B. anthracenum, B. shamrockiae, B. dehiscum, B. subditivum* and *B. aura*. Review of the taxonomic history of *Biscutum constans* indicates that this species has been systematically misinterpreted. An emendation to the *Biscutum constans* species concept is provided based on the original work of Görka (1957). A diversification interval is documented in the mid Cretaceous during which five new species of *Biscutum* evolved in approximately six million years. Evidence from previous work indicates the occurrence of a second diversification interval in Campanian high latitudes. These results suggest a distinct shift in the site of evolutionary activity within *Biscutum* from the mid-latitudes in the mid Cretaceous to high latitudes in the Late Cretaceous.

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INTRODUCTION

The calcareous nannofossil genus *Biscutum* is ubiquitous in mid to Upper Cretaceous pelagic sediments. It is a member of the oldest known family of placolith coccoliths, the Biscutaceae, which first appeared at the Sinemurian-Pliensbachian boundary (Bown 1987, de Kaenel and Bergen 1993, Mattioli et al. 2004) and persisted into the Paleocene (e.g., Perch-Nielsen 1985) (approximately 190 – 66 Ma). *Biscutum* species have been used frequently as paleoceanographic proxies for surface water fertility as well as biostratigraphic zonal indicators. Unfortunately, species concepts within *Biscutum* have inconsistently been applied and interpreted owing to a convoluted taxonomic history, thus limiting its utility. For example, the names *Biscutum constans* and *B. ellipticum* have frequently been used interchangeably (Lees, Bown and Mattioli 2005, Bornemann and Mutterlose 2006).

The genus *Biscutum* has been important in both paleoceanographic and biostratigraphic work on Upper Cretaceous sections. Elevated abundances of *Biscutum constans* have been reported in several quantitative studies from a variety of settings (e.g., Roth 1981, Roth and Bowdler 1981, Roth and Krumbach 1986, Watkins 1989, Erba 1992) and have been interpreted to indicate increased surface water fertility. *Biscutum* species are also important components in several Upper Cretaceous high latitude zonation schemes. Wise (1983) used the total range of *B. coronum* Wind and Wise 1977 to define an upper Campanian/lower Maastrichtian zone in his Falkland Plateau zonation. Jakubowski (1987) used a *Biscutum constans* acme in his North Sea zonation to mark the Albian/Cenomanian bound-

ary. Pospichal and Wise (1990) used the last occurrences of *B. coronum* and *B. magnum* Wind and Wise 1977 in the upper Campanian and lower Maastrichtian, respectively, as markers in their Southern Ocean zonation scheme. In their synthesis of Southern Ocean biostratigraphy of the Upper Cretaceous, Watkins et al. (1996) also used the last occurrences of *B. coronum* and *B. magnum* to define upper Campanian and lower Maastrichtian zones. The last occurrences of *B. dissimilis* Wind and Wise 1977 and *B. coronum* in the Upper Cretaceous are subzonal markers in Burnett's (1998) UC zonation scheme.

Despite the widespread usage of *Biscutum* in geological studies of the Upper Cretaceous, the taxonomy of this group is not well documented. To date, much of the work on *Biscutum* evolution has been conducted on Jurassic to Lower Cretaceous sediments (Grün and Allemann 1975, Grün and Zweili 1980, Bown 1987, de Kaenel and Bergen 1993, Mattioli et al. 2004) or on high latitude Upper Cretaceous sections (Wise and Wind 1977, Wind 1979, Wise 1983, Jakubowski 1987, Pospichal and Wise 1990, Watkins et al. 1996).

The goal of this study is to refine the taxonomy of mid to Upper Cretaceous *Biscutum* in mid-latitudes to increase its utility as a biostratigraphic and paleoceanographic indicator. These taxonomic revisions enable investigation of the ways in which oceanographic changes during the mid to Late Cretaceous affected the mode and tempo of *Biscutum* evolution.

LOCALITIES

Samples from five localities were examined: three from the Western Interior Basin (WIB) including Washington County,
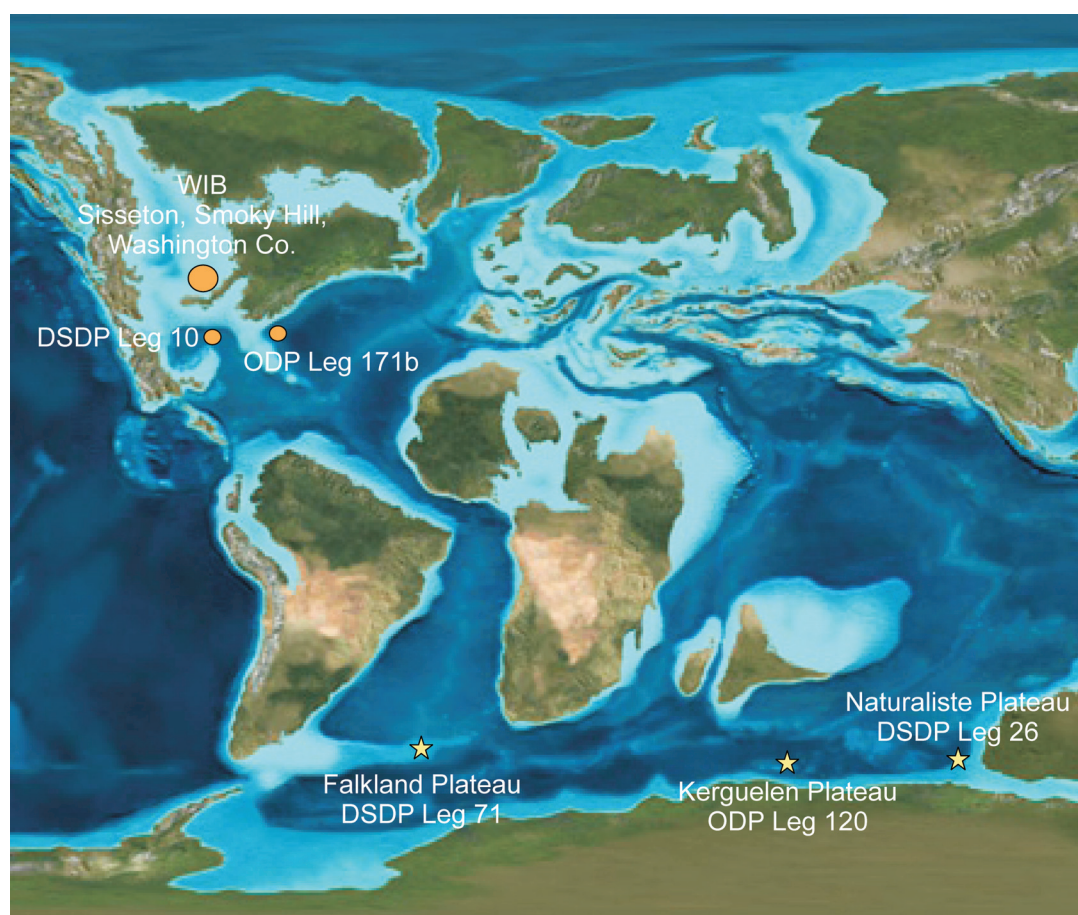
TEXT-FIGURE 1
Paleogeographic reconstruction at 90 Ma showing the location of studied localities. Circles represent mid-latitude localities. Stars represent high latitude localities. Modified from Blakey 2012.

KS; Smoky Hill type area, KS and Sisseton, SD, as well as the Gulf of Mexico (DSDP Leg 10-95) and a composite section from the North Atlantic Ocean (ODP Leg 171b-1049a/1050c/1052e) (text-figure 1). Shamrock and Watkins (2009) compiled the composite section in text-figure 2 based on good overall preservation and stratigraphic coverage. They also provided more detailed lithologic and stratigraphic descriptions of these sites. A total of 174 samples were utilized in the final analyses. Samples with low nannofossil abundances and/or poor preservation were excluded.

Clayey nannofossil ooze and chalk from Ocean Drilling Program (ODP) Leg 171b Holes 1049a, 1050c and 1052e contain exceptionally well-preserved upper Albian, Cenomanian, Turonian, upper Campanian and Maastrichtian nannofossils. Stratigraphic and lithologic descriptions of these sites are provided by the Shipboard Scientific Party et al. (1998). Chalky limestone samples of Cenomanian and lower Turonian Greenhorn Limestone from Washington County, north-central Kansas exhibit good overall preservation of nannofossils throughout. Hattin (1975) provides detailed stratigraphic and lithologic descriptions of these sections as his localities 6 and 7. Nannofossil chalk and foraminifera-nannofossil chalk to ooze from upper Coniacian, Santonian and lower Campanian samples collected during Deep Sea Drilling Program (DSDP) Leg 10 Hole 95 ex-

hibit good overall preservation. Lithologic and stratigraphic descriptions are provided in Worzel et al. (1973).

Upper Coniacian through lower Campanian very well-preserved nannofossil assemblages of Niobrara Formation chalk was sampled at Hattin's (1982) Smoky Hill type area, which spans a series of localities. Hattin (1982) provides detailed lithologic and stratigraphic descriptions of all the localities. Core samples of the Pierre Shale from Sisseton, SD were examined for coverage of mid to upper Campanian nannofossil chalk and calcareous marl/claystone sediments with variable nannofossil preservation. Samples with poor preservation were excluded from final analyses. Schultz et al. (1980) and Hanczaryk and Gallagher (2007) provide detailed descriptions of lithology and stratigraphy.

Samples from the above five localities were examined in order to reconstruct the evolution of *Biscutum* in mid-latitudes. An additional set of samples from a composite high latitude section was studied in order to confirm the absence of mid-latitude species. This high latitude composite section consisted of lower Campanian through upper Maastrichtian material from ODP Leg 120 (Kerguelen Plateau), upper Campanian samples from DSDP Leg 71 (Falkland Plateau) and Santonian through Upper Albian material from DSDP Leg 26 (Naturaliste Plateau).
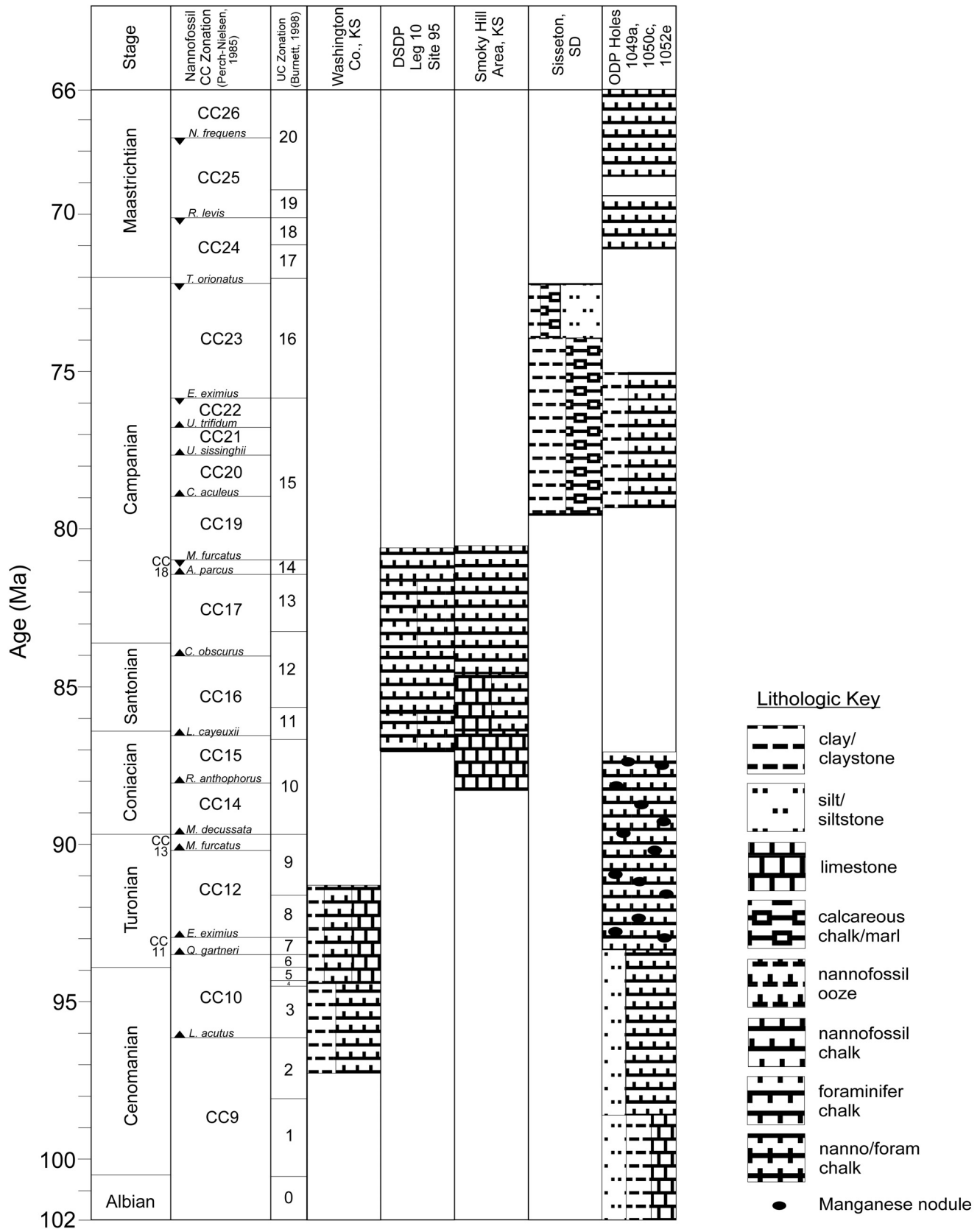
TEXT-FIGURE 2
Stratigraphic column showing mid-latitude composite section created for this study. Modified from Shamrock and Watkins (2009).
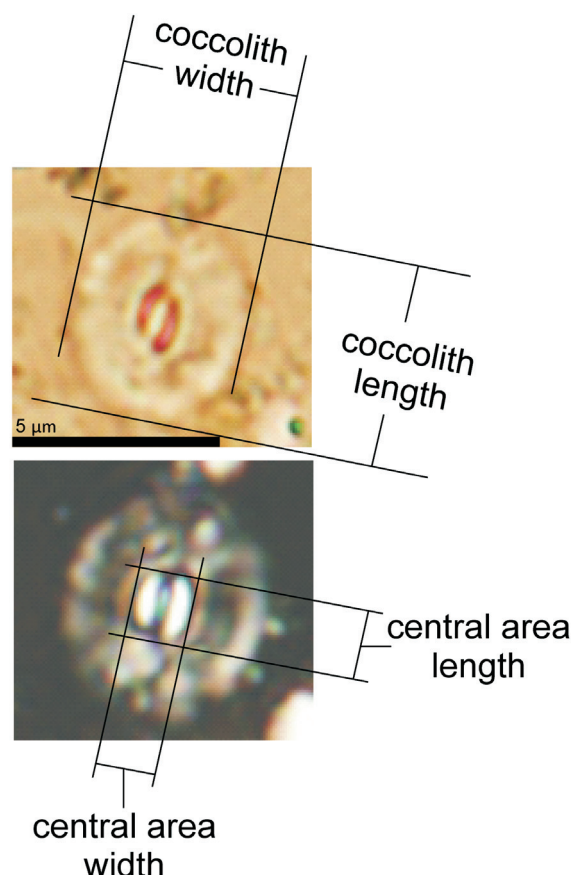
TEXT-FIGURE 3
Measured dimensions of *Biscutum* specimens. *Biscutum anthracenum* pictured. Coccolith length and width were measured from plane polarized light images (above) due to difficulties determining the extent of low birefringence distal rims in dark field. Central area length and width were measured from cross polarized light images (below).

METHODS

All samples were prepared using the double slurry method of Watkins and Bergen (2003) which has been shown to yield reproducible nannofossil abundance data at the 99.99% confidence level. Prepared slides were viewed on an Olympus BX51 light microscope at 1250x magnification using phase contrast, plane polarized light, cross polarized light and a one-quarter λ gypsum plate.

Biometric data were collected by measuring the coccolith length, width, central area length and central area width of a total of 245 specimens as shown in text-figure 3. Measured dimensions were used to calculate coccolith eccentricity, central area eccentricity and central area: total coccolith surface area. Biometric data were collected on each species occurrence and are presented in the *Systematic Paleontology* section. Specimens were photographed and subsequently analyzed using ImageJ 1.37, a JAVA-based digital image processing program with a resolution of approximately 0.20μm (Rasband 1997–2006). Specimens were initially assigned as morphotypes using qualitative criteria. Morphometric data were analyzed using the paleontological statistics program PAST (Hammer, Harper and

Ryan 2001). Geochronologic ages provided are estimates assigned according to the cyclostratigraphic model of Watkins, Cooper and Norris (2005) and age designations of Shamrock and Watkins (2009).

All figured specimens and type species have been deposited in the Micropaleontology Collection at the University of Nebraska-Lincoln. Species descriptions use terms recommended by "Guidelines for coccolith and calcareous nannofossil terminology" (Young et al. 1997). Data are archived at the World Data Center-A for Paleoclimatology http://www.ncdc.noaa.gov/paleo/data.html (Brace and Watkins 2013).

TAXONOMIC HISTORY

Review of *Biscutum* taxonomy reveals confusion at both the generic and species levels. The taxonomic history of the genus, as well as species considered in this study, is summarized below. In 1957, Görka described two species which were illustrated by simple hand drawn line drawings and later transferred into *Biscutum*. The two species, *Discolithus constans* and *Tremalithus ellipticus*, serve as the basis for much of today's confusion due to the lack of detail in Görka's original diagnoses.

Black's original 1959 diagnosis of the genus *Biscutum* was generalized and included imperforate coccoliths of more than one layer of closely appressed plates. Black (1959) did not specify whether the coccoliths should be round, elliptical or both, nor did he give any description of the central area. The generotype, *Biscutum testudinarium* Black 1959, consists of a proximal view of a broken, upper Cenomanian specimen. The incomplete nature of the holotype has caused problems in determining the diagnostic outline of *Biscutum*, as the eccentricity of the broken holotype cannot be determined with any degree of certainty. Black described the central area of *B. testudinarium* such that the elements of the proximal shield do not reach the center which is in turn occupied by "a group of granules which may possibly be expansions of the proximal ends of [elements] belonging to the [distal] disc" (Black 1959, p. 325).

Black (1972) later provided his own emendation to *Biscutum*, restricting it to Biscutaceae with broadly elliptical to nearly circular outlines and bilateral symmetry, thus separating *Biscutum* from two closely-related genera, *Bidiscus* Bukry 1969 and *Paleopontosphaera* Nöel 1965, both of which are defined as round forms.

Wise and Wind (1977) noted that, when viewed from the distal side, the interelemental sutures in the distal rim are characterized by dovetail tongue-and-groove configurations. This interlocking construction is readily apparent in SEM (scanning electron microscope) images, but not generally apparent when viewed using an optical microscope.

Krancer (1980) agreed with Black's 1972 emendation by considering *Biscutum* as containing forms which possess elliptical outlines and being separate from the otherwise morphologically similar *Bidiscus*, which he considered to contain only round forms. Krancer provided a description of the central area of the genus similar to Black's, consisting of "small openings or a granular arrangement of rhombic crystals" (Krancer 1980, p.4).

In Grün and Allemann's (1975) study of Berriasian nannoplankton, Grün designated *Paleopontosphaera* Nöel 1965 as a junior synonym of *Biscutum* due to similarities in coccosphere construction (22-28 coccoliths, ellipsoidal to nearly cylindrical

inner tube cycle

distal shield
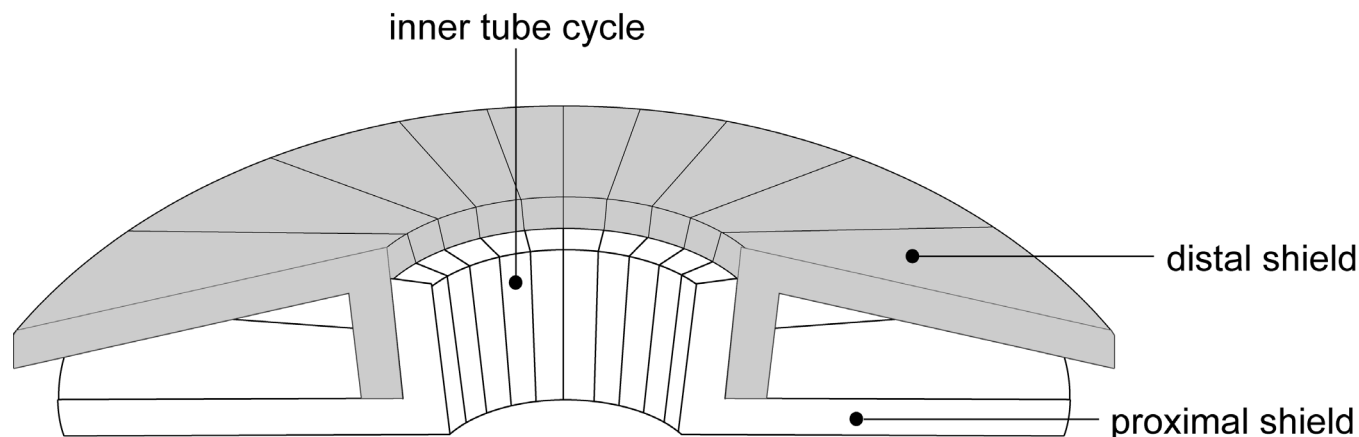
proximal shield

TEXT-FIGURE 4
Idealized profile of *Biscutum* showing proximal shield, distal shield and inner tube cycle. Gray=V-crystal units, white=R-crystal units. After Mattioli et al. (2004).

shape) in the two genera. Grün also replaced *B. testudinarium* with *B. ellipticum* as the generotype of *Biscutum* as he considered *B. ellipticum* (originally *Tremalithus ellipticus*) to be first among the synonymous species listed in Görka (1957). Grün and Zweili (1980) followed this designation.

In de Kaenel and Bergen's (1993) work on Early and Middle Jurassic coccoliths, they characterized *Biscutum* as containing both elliptical and circular forms, with *Bidiscus* as a taxonomic junior synonym. The authors emphasized rim ultrastructure due to its importance in understanding the early evolution of coccoliths. The central area is described as imperforate, but may be closed or surmounted by a cycle of elements separated from the rim. The diagnosis emphasized rim construction and allowed for variation in central area structures as well as coccolith outline. The authors indicated that important differences in the rim ultrastructures of *Paleopontosphaera* and *Biscutum* justify their separation. They described *Paleopontosphaera* as displaying a bicyclic rim extinction pattern resulting from a birefringent inner distal rim cycle of elements and considered *Biscutum* as displaying a unicyclic rim extinction pattern due to the absence of an inner distal rim cycle.

Mattioli et al. (2004) distinguished *Discorhabdus* by its circular outline and attributed slightly to broadly elliptical forms to *Biscutum, Paleopontosphaera* or *Similiscutum* in their work on Lower Jurassic coccoliths. *Biscutum* was considered to contain forms with a bright inner tube cycle of elements formed by R-crystal units extending up from the proximal shield as shown in text-figure 4. Their diagnosis followed that of Black (1972), which included broadly elliptical to nearly circular forms. The authors proposed including in *Biscutum* elliptical to nearly circular forms with a "discrete distal-shield inner tube cycle, which is conspicuously bright" in polarized light (Mattioli et al. 2004, p. 25). They designated *Paleopontosphaera* Nöel 1965 a junior synonym of *Biscutum*.

In the present work, *Biscutum* is defined according to Mattioli et al. (2004). text-figures 4 and 5 demonstrate the idealized structure of *Biscutum*. *Discorhabdus* is herein considered distinct from *Biscutum* based on its circular outline. Some

nannofossil workers (e.g., de Kaenel and Bergen 1993) have wisely questioned the validity of separating genera based on coccolith outline. Covington (1985) discussed morphological variation of *B. zulloi* coccoliths on a single coccocylinder and noted that as curvature increases towards the ends of the coccocylinder, the shape of the coccoliths changes accordingly. As such, morphologically variable coccoliths from the same coccocylinder found separated in a sample, could be described as separate taxa. This emendation is beyond the scope of this work. *Discorhabdus* is herein considered generically distinct from *Biscutum*. The distinction of *Discorhabdus* from *Biscutum* based on coccolith morphology has been followed by other nannofossil workers (e.g., Mattioli et al. 2004, López-Otálvaro et al. 2012). The framework of Mattioli et al. (2004) is most appropriate for the current study because it emphasizes characteristics readily visible using optical microscopy techniques and does not rely on ultrastructure characteristics visible only in SEM which is infrequently used in routine nannofossil studies. The descriptive and taxonomic nomenclature herein follows terminology outlined by Young et al. (1997).

In addition to confusion at the generic level, many species concepts within *Biscutum* have been misinterpreted. The generotype, *Biscutum testudinarium*, consists of a broken specimen. The holotypes of *B. constans* and *B. ellipticum* are comprised of simple hand drawn line drawings lacking detail. Taxonomic revisions of these taxa have been carried about by several authors (e.g., Perch-Nielsen 1968, Bukry 1969, Grün and Allemann 1975, Grün and Zweili 1980) and yet no consensus exists with respect to many commonly used *Biscutum* species concepts. In addition to the obvious taxonomic problems, misapplication of species concepts can render nannofossils that may serve as paleoceanographic proxies useless through the merging of species with discrete paleoceanographic affinities (Lees, Bown and Mattioli 2005). This further stresses the need for clearly defined species concepts, especially in potential proxy taxa.

Perhaps the most prominent example of incongruent species concepts is the distinction between and definitions of *Biscutum constans* and *Biscutum ellipticum*. Görka's (1957) holotypes of
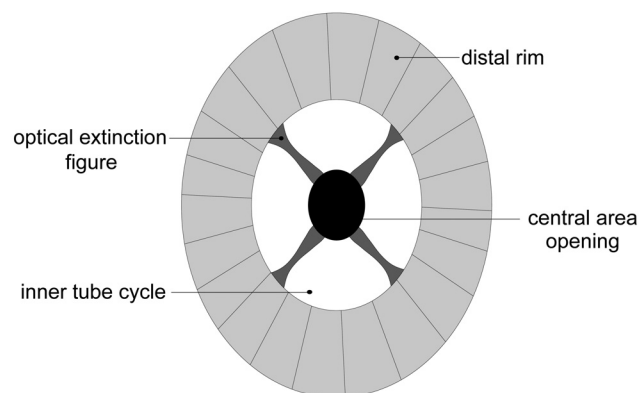
TEXT-FIGURE 5
Distal view of generalized *Biscutum* with relevant structures. Gray=V-crystal unit, extinct in cross polarized light, white=R-crystal unit, birefringent in cross polarized light, dark gray=optical extinction figure. After Mattioli et al. (2004). The inner tube cycle is composed of individual R-crystal units (as shown in text-figure 4), although these are not discernible via light microscopy.

Discolithus constans (the basionym for *Biscutum constans*) and *Tremalithus ellipticus* (the basionym for *Biscutum ellipticum*) are simple hand drawn line drawings. *Discolithus constans* was originally described by Görka (1957) as elliptical and elongate, with 15-20 radially arranged elements and a smooth central area. The accompanying illustration consists of a normally elliptical form with an eccentricity of 1.4, a smooth central area comprising 23% of the total area of the coccolith and 15 radial elements. Black included no morphological emendations in his 1967 transfer of *D. constans* into *Biscutum*.

Görka (1957) described *Tremalithus ellipticus* as an elliptical form with a smooth margin containing 10 curved elements. The holotype drawing consists of a broadly elliptical form with an eccentricity of 1.2, a smooth central area comprising 10% of the total surface area and 10 dextrally curved elements. The type material of *D. constans* and *T. ellipticus* is from the upper Maastrichtian of Poland. The differences between the two forms as originally described are the number (15-20 versus 10) and orientation (radial versus curved) of distal rim elements, as well as eccentricity (1.4 versus 1.2) and relative proportion of central area to total coccolith area (23 versus 10 percent). Based on the published dimensions as well as general appearance of the holotypes, the two forms are lacking in differential diagnoses. It should also be noted that forms with as few as 10 elements were not observed in this study.

Grün in Grün and Allemann's 1975 study of Berriasian nannofossils from Spain transferred *Tremalithus ellipticus* into *Biscutum* as the new generotype and declared *B. testudinarium* Black 1959, *B. castrorum* Black 1959, *B. constans* (Görka 1957) Black 1967 and *Paleopontosphaera dubia* Nöel 1965, along with many other species, to be junior synonyms (see reference for complete list of synonymies). Grün's (1975) emendation broadened the morphological range of *Biscutum ellipticum* to include forms with eccentricity values of 1.1-1.45, lengths of 2-10µm, widths of 1.3-8µm and 13-32 shield ele-

ments. In 1980, Grün and Zweili established a similarly extensive synonymy list (see reference for complete list) to that of Grün and Allemann (1975). Grün and Zweili (1980) emended *Biscutum ellipticum* to include forms of 2-10.5µm in length, 1.3-8µm in width, central area lengths of 1.1-4.9µm and central area widths of 0.6-3.8µm. The coccolith length was to be 2 to 2.8 times the central area length with eccentricity of 1.1-1.3 and 14-22 elements. Both of these emendations excluded the holotype of *Biscutum ellipticum* which was originally described by Görka (1957) as having 10 distal rim elements.

Bornemann and Mutterlose (2006) used biometric data to demonstrate a morphological continuum between *B. constans* and *B. ellipticum*. They considered *B. constans* var. *constans* to include forms with narrow central areas and *B. constans* var. *ellipticum* to include forms with larger central areas. These designations are not in agreement with Görka's (1957) holotypes which actually show the central area of *B. ellipticum* as being smaller than that of *B. constans*, in addition to other morphological differences (e.g., number and shape of distal elements) not recognized by the authors.

The lack of photomicrographs and detail in the two illustrations in Görka's original manuscript, as well as the subsequent inclusion of multiple taxa into *Biscutum ellipticum* (including *B. constans*) by Grün, permits a wide range of interpretations. As such, many morphotypes have been incorporated into *B. ellipticum* or into *B. constans* (depending upon authorship).

Another taxonomic issue in *Biscutum* lies within the distinction of the Late Cretaceous species *B. thurowii* Burnett 1997 from *B. zulloi* Covington 1994. Burnett (1997) describes *B. thurowii* as a "small *Biscutum* with a small central area lined with blocks and two central area perforations separated by a transverse bar aligned with the short ellipse axis" (Burnett 1997, p. 134). The holotype is 4.0µm in length by 2.0µm in width. Burnett supplements her *B. thurowii* SEM holotype with a light microscope image from Gale et al. (1996), which had previously been identified in that publication as *B. gartneri*.

Covington (1994) describes *B. zulloi* as including forms with approximately 30 radial elements in the distal rim and a relatively large central area accounting for 52% and 67% of the total coccolith width and length, respectively. He also notes the presence of a distinct "collar" visible in both phase contrast and cross polarized light, as well as the occurrence of a small knob in the central area of well-preserved specimens. The holotype measures 4.4µm wide by 5.5µm long with central area length and width of 2.3 and 3.7µm, respectively. Complications in pairing Covington's (1994) SEM with light microscope images of calcareous nannofossils, as well as a lack of detail in central area morphology visible in his light microscope images has resulted in confusion distinguishing these two species from one another.

RESULTS

Examination of nannofossils from the temperate latitude North American composite section (text-figure 2) indicates the presence of thirteen species of *Biscutum*, six of which have not been previously described. Geochronologic age estimates to the nearest 0.5 million years for first and last occurrences are included on Table 1 and a proposed lineage of mid to Late Cretaceous evolution within *Biscutum* is presented in text-figure 6. *Biscutum* is represented by three species in the upper Albian at
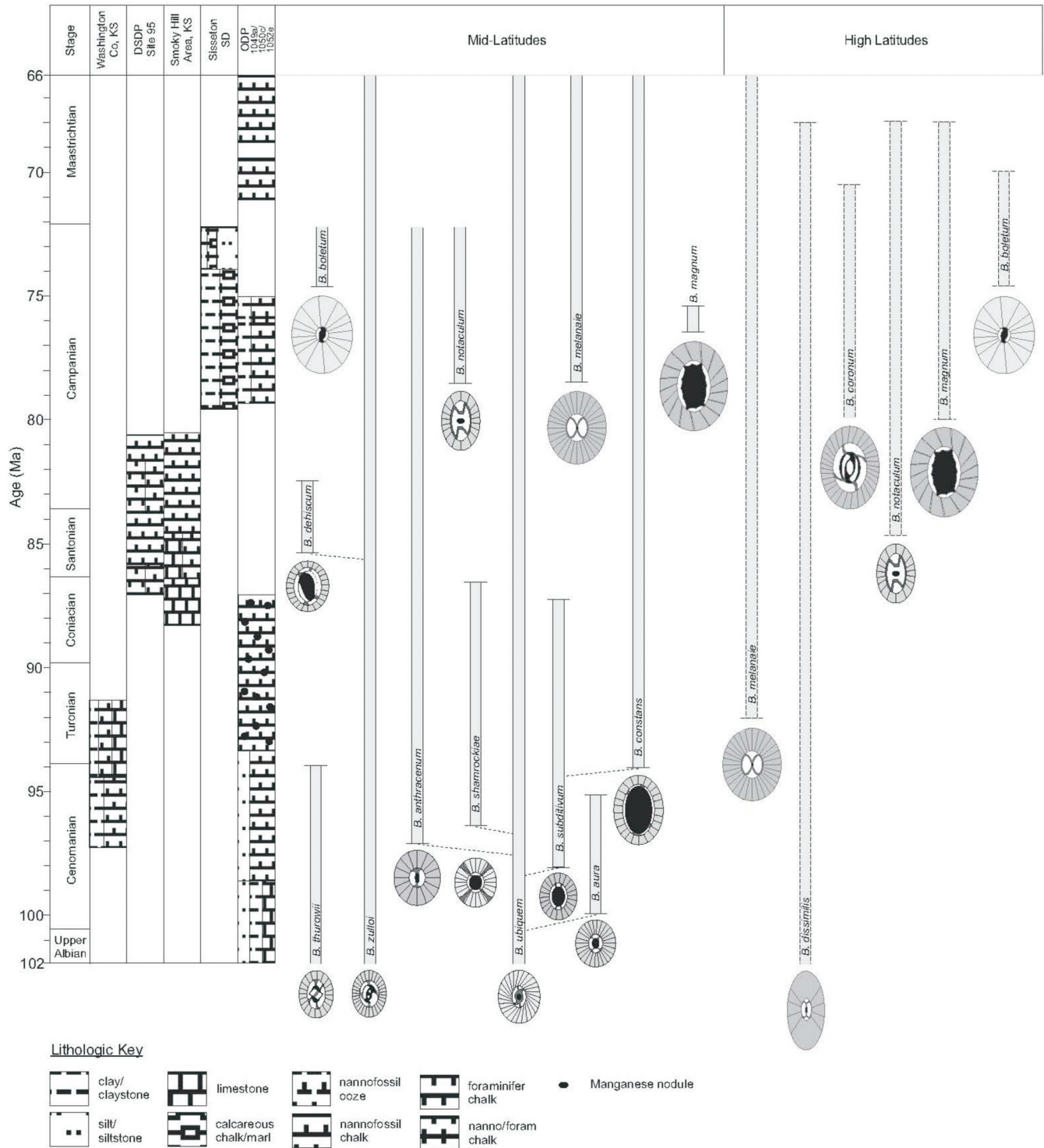
TEXT-FIGURE 6

Proposed lineage of *Biscutum* evolution during the Late Cretaceous. Mid-latitude forms on the left. High latitude forms on the right. High latitude ranges on the right are those documented by other workers (see text for specific references). Mid-latitude ranges on the left are documented in the current study. *Biscutum ubiquem* is present throughout both the high and mid-latitude sections.

TABLE 1

Geochronologic estimates (Ma) of first and last occurrences observed in the current study. 'NA' is listed for species encountered in the oldest and/or youngest sediments in the sample section.

*It should be noted that the listed ranges of high latitude species are those observed in mid-latitudinal sections and may differ from those in high latitudes.

† These dates should not be considered true first/last occurrences. These ages represent the end of a given sample set. The listed ranges are probable artifacts of sampling and true ranges likely extend beyond those listed in this study.

Species	First Occurrence	Last Occurrence
Biscutum ubiquem	NA	NA
Biscutum thurowii	NA	94.0
Biscutum zulloi	NA	NA
Biscutum aura	100.0	95.0
Biscutum subditivum	98.0	87.5
Biscutum anthracenum	97.0	72.0†
Biscutum shamrockiae	96.5	86.5
Biscutum constans s.s.	94.0	NA
Biscutum dehiscum	85.5	82.5
Biscutum notaculum*	78.5†	72.0†
Biscutum melaniae*	78.5	NA
Biscutum magnum*	76.5	75.5
Biscutum boletum*	74.5	72.0†

Blake Nose: *Biscutum ubiquem*, *Biscutum thurowii* and *Biscutum zulloi* (see Plate 1). *Biscutum zulloi* is only observed at Blake Nose until the lower Turonian when it appears in WIB sections. *Biscutum zulloi* is present through the rest of the Cretaceous and persists to at least the Cretaceous/Paleogene boundary.

Biscutum ubiquem is a broadly elliptical, medium form of Biscutaceae with 24 to 36 faintly birefringent distal rim elements as shown in Plate 1, Figures 1-6. Earlier forms tend to have the greatest number of elements. No structure is visible in the central area opening. Like *B. zulloi, Biscutum ubiquem* is found in both WIB and Blake Nose samples and persists at least to the top of the Cretaceous, ostensibly giving rise to several forms during its range as may be seen in text-figure 6. With the exception of *Biscutum dehiscum*, all of the newly-documented mid-latitude species appear to diverge from *B. ubiquem*. In addition, this is the only species encountered throughout both the mid- and high latitude composite sections.

In the uppermost Albian, a new form appears at Blake Nose, probably a descendant of *Biscutum ubiquem*. This small to medium coccolith, *Biscutum aura*, differs from its precursor in its more conspicuous distal rim elements and nearly closed central area as seen in Plate 2, Figures 1-4. As shown in text-figure 6, *Biscutum aura* persists into the Cenomanian where the last occurrence of it and *B. thurowii* are recorded.

As shown in text-figure 6, three new forms of *Biscutum* make their first appearance during a brief interval in the mid Cenomanian. *Biscutum subditivum* is first observed in the lower Cenomanian at Blake Nose and in the mid Cenomanian in WIB sediments and persists into the upper Coniacian. *Biscutum subditivum* may be distinguished from *Biscutum ubiquem* by its small size, approximately 24 distal rim elements, thin inner tube cycle and wide central area opening as shown in Plate 2, Figures 7-9.

The second form to appear during this mid Cenomanian interval of diversification is *Biscutum shamrockiae*. It is a small to medium coccolith primarily characterized by its unique extinction pattern as may be seen in Plate 2, Figures 10-12. *Biscutum shamrockiae* is observed only in WIB sediments and is last observed in the uppermost Coniacian.

The third and final form to appear during the mid Cenomanian is a very dark, small to medium *Biscutum* with 16 to 18 radial distal rim elements. In addition to its particularly dark distal rim, *Biscutum anthracenum* exhibits a distinct central area structure as shown in Plate 2, Figures 13-16. *Biscutum anthracenum* is observed in WIB sediments and persisted from the mid Cenomanian to the upper Campanian.

A medium *Biscutum* characterized by its wide, empty central area and thin inner tube cycle (see Plate 2, Figures 5-6) first appears in the upper Cenomanian. This form is consistent with Görka's (1957) *Discolithus constans* holotype illustration. Estimates of the holotype dimensions may be made based on a magnification of 1350x and a rim width of 1μm as stated by Görka (1957). Comparisons of the dimensions derived from the holotype with those obtained from the present work suggest that the observed morphotype is *Biscutum constans* (Görka 1957) Black 1967. The coccolith length, coccolith width, central area length and central area width all vary by less than 1μm. Coccolith eccentricity and central area eccentricity vary by less than 5%. The one substantial deviation from Görka's description and the forms observed here is the difference in number of distal rim elements. The morphotype in the current study averages 24 distal rim elements. Görka's holotype has 15 elements and her description indicates a range of 15 to 20 may be present. As such, it would appear that the element counts are incongruent; however, a closer view of the morphotype from this study shows a subtle grouping of distal rim elements. This grouping results in the appearance of fewer, thicker elements in the distal rim, but the individual elements may be resolved upon closer examination. It should be noted that Görka did not mention the presence of an inner tube cycle of elements in her diagnoses of *D. constans* and *T. ellipticus*.

Based on the similarity in appearance of the distal rim elements, central area and congruence of biometric data, the morphotype appearing in the upper Cenomanian in this study should be considered *B. constans sensu stricto*. text-figure 7 shows the congruence in appearance of *B. constans s.s.* from this study and *Discolithus constans* of Görka (1957). *Biscutum constans s.s.* is present at all sites, except Sisseton, SD. It appears in the upper Cenomanian at Cuba, KS and Blake Nose and later near the Coniacian/Santonian boundary in the Gulf of Mexico. It persists to at least the Cretaceous/Paleogene boundary.

During the early Santonian, *B. zulloi* diversified to give rise to a morphologically similar form, *Biscutum dehiscum*, shown in Plate 3, Figures 1-4. Both are small to medium coccoliths with relatively large central areas. *Biscutum dehiscum* may be distinguished from *B. zulloi* by its almost entirely black central area versus the two birefringent "knobs" visible in *B. zulloi* when oriented parallel to the polarizers. *Biscutum dehiscum* appears to have been endemic to the Gulf of Mexico and is observed from the lowermost Santonian into the lower Campanian.
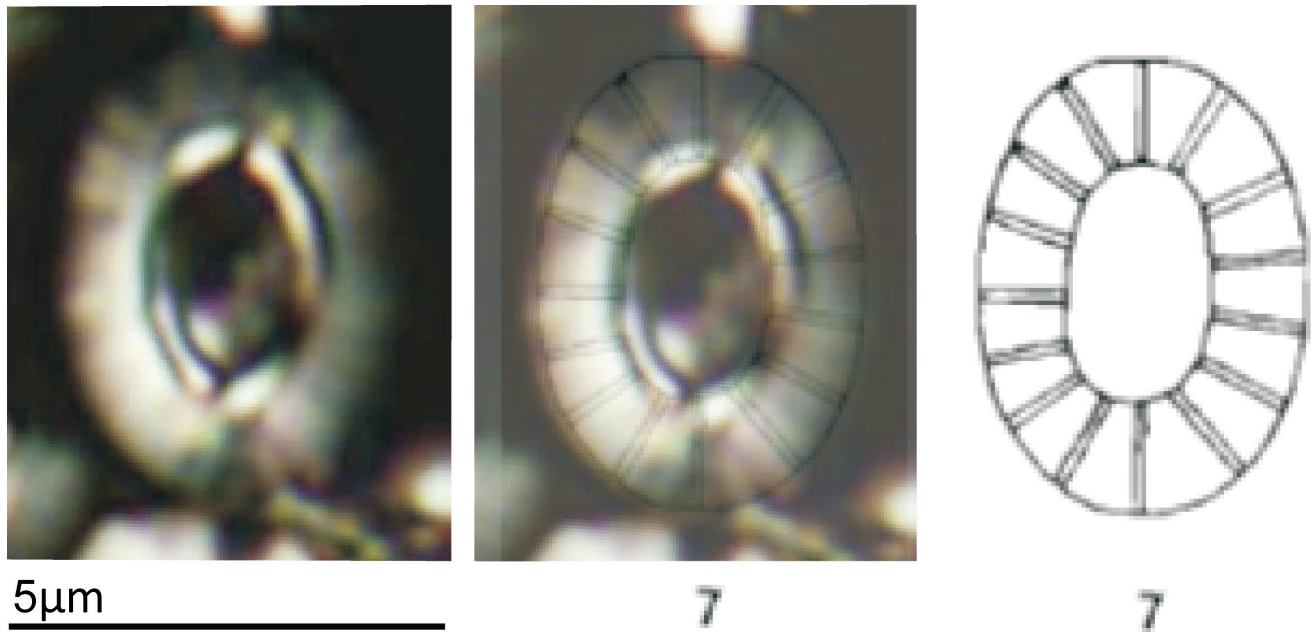
TEXT-FIGURE 7
Comparison of *Biscutum constan s.s* observed in the current study with Görka's 1957 holotype. The image on the left is *Biscutum constans* (Blake Nose – this study). The image on the right is Görka's 1957 *Discolithus constans* holotype to scale. The center image is an overlay of the holotype over *Biscutum constans s.s.* (Blake Nose – this study) to demonstrate congruence between the two images.

The following taxa were either described from or are common in high latitude settings. Their occurrence in the mid-latitudes represents brief migration events from higher latitudes. *Biscutum magnum* (Plate 3, Figures 5-7) is known from the high southern latitudes to first occur in the late early Campanian (Watkins et al. 1996) and have its last occurrence in the mid Maastrichtian (Wise and Wind 1977, Wise 1983, Watkins et al. 1996) as shown in text-figure 6. Its observed range in the WIB is relatively short, spanning a brief interval in the mid Campanian.

The first occurrence of *Biscutum notaculum* Wind and Wise 1977 (Plate 3, Figures 8-10) is in the mid Campanian of the WIB. In this study, *B. notaculum* is only observed in upper Campanian Sisseton core and Niobrara Formation samples, although its range is well documented in the Maastrichtian in high southern latitudes (Wise and Wind 1977, Watkins et al. 1996).

Another previously described form, *Biscutum melaniae* (Görka 1957) Burnett 1997, is shown in Plate 3, Figures 11-13 and was noted from the mid Campanian to the end of the Cretaceous in the sampled section. Burnett (1997) notes that *B. melaniae* is common in high latitude settings and that its first occurrence is in the upper Turonian as shown in text-figure 6.

The last species to appear in the Upper Cretaceous mid-latitudes is *B. boletum* Wind and Wise 1977, a previously documented high latitude form (Wise and Wind 1977) shown in Plate 3, Figures 14-16. Occurrences were rare and documented only from the late Campanian of the sampled mid-latitude section. This species has been reported in the high latitudes to range from upper Campanian to lower Maastrichtian (as shown

in text-figure 6). It should be noted that the common high latitude forms *B. coronum* and *B. dissimilis* were not observed in the mid-latitude study section.

DISCUSSION

Six new species of *Biscutum* are described herein from the mid to Upper Cretaceous of North America. This represents a major diversification in the genus *Biscutum* previously undocumented in mid-latitudes. Five of these species evolved within a relatively brief interval of diversification spanning the late Albian and Cenomanian of temperate North America. An additional species first occurred in the Santonian of the Gulf of Mexico. As is indicated in text-figure 6, the evolutionary appearances of these taxa do not occur at regular intervals, but are largely concentrated in the late Albian and Cenomanian. A general period of stasis followed this pulse of diversification until the Campanian. With the exception of *Biscutum dehiscum*, no new species of *Biscutum* can be demonstrated to have evolved in the mid-latitudes through the rest of the Late Cretaceous.

Biscutum magnum, *B. notaculum*, *B. melaniae* and *B. boletum* have all been described as common high latitude species and are observed in mid-latitudes in the current study. Contrasting mid- and high latitude ranges reveals evolutionary patterns that were previously unknown in *Biscutum*. Compared to its documented range in high latitudes, the stratigraphic range of *B. magnum* is truncated in the mid-latitude study section. *Biscutum magnum* is known from the high southern latitudes to first occur in the late early Campanian (Watkins et al. 1996) and have its last occurrence in the mid Maastrichtian (Wise and Wind 1977, Wise 1983, Watkins et al. 1996) as shown in text-figure 6. Thibault (2010) recorded the occurrence of *B. magnum* in the upper

Campanian of Denmark in boreal latitudes. Its observed range in the WIB spans a brief interval in the mid Campanian.

Biscutum magnum is rare in the study section, whereas it is a regular component of high southern latitude assemblages (Watkins et al. 1996). Its use as a marker species in the Maastrichtian (Watkins et al. 1996) of the Southern Ocean is indicative of its common occurrence in such settings. The diachroneity of occurrences and changes in abundance of *B. magnum* suggest that this species evolved in the high southern latitudes in the late early Campanian, expanded its range into mid-latitudes by the mid Campanian and moved into boreal latitudes by the late Campanian. Upon its geographic expansion, paleoceanographic conditions in the mid-latitudes may have been suboptimal, as indicated by the relative scarcity of this species in the study section compared to its higher abundances in high southern latitudes. It should be noted that Thibault (2010) does not comment on the relative abundance of *B. magnum* in his boreal study sections.

Biscutum notaculum is observed from the mid to upper Campanian in the mid-latitude study section (text-figure 6), although its range is well documented into the Maastrichtian in high southern latitudes (Wise and Wind 1977, Watkins et al. 1996). Its last occurrence corresponds with the top of the sampled section in the WIB, so that its last occurrence may be an artifact of sampling. It has not been recognized from the Maastrichtian section on Blake Nose; however, its range is well-documented into the Maastrichtian in high southern latitudes (Wise and Wind 1977, Watkins et al. 1996). Further examination of uppermost Cretaceous sections will be required to determine the true last occurrence of *B. notaculum* in the WIB. Thibault (2010) documented the occurrence of *B. notaculum* near the Campanian/Maastrichtian boundary in boreal latitudes. Similar to the case of *B. magnum,* the diachroneity in occurrences of *B. notaculum* suggests a similar pattern of evolution and dispersal. *Biscutum notaculum* evolved in Santonian high southern latitudes, expanded its range to at least the WIB by the mid Campanian and was present in the boreal realm by the latest Campanian.

As with *B. notaculum* and *B. magnum*, the first occurrences of *B. melaniae* are diachronous between mid- and high latitude settings. Its first occurrence has been noted in the lower Turonian austral Indian Ocean by Burnett (1998), but it is not observed in the present study until the mid-Campanian. Thibault (2010) documented the occurrence of *B. melaniae* in high northern latitudes in the upper Maastrichtian. Again, *B. melaniae* appears to show a pattern of high southern latitude evolution and northward range expansion. It first occurs in lower Turonian high southern latitude sections, disperses to the North American mid-latitudes by the Campanian and is present in the boreal realm by the latest Maastrichtian.

Biscutum boletum appears to show a contrasting evolutionary history in comparison with the other high latitude forms observed in this study; however, the amount of data available concerning the occurrence of *B. boletum* is comparatively small. The first occurrences of *B. boletum* in the mid-latitude study section and in high southern latitudes in the late Campanian (Watkins et al. 1996) are ostensibly coeval. This does not preclude the evolution of *B. boletum* in high southern latitudes in a fashion similar to other forms observed in this study, but more sections need to be examined to determine if the first occur-

rences are truly coeval or if *B. boletum* originated in high southern latitudes and migrated north like other *Biscutum* species in this study.

Biscutum dissimilis has been documented from the mid Albian (Wise 1983) to lower Maastrichtian (Watkins et al. 1996) in high southern latitudes. Burnett (1998) noted its occurrence in the lower to mid Campanian of northeast England. It is probable that *B. dissimilis* also underwent a similar pattern of evolution and dispersal to other high latitude taxa, crossing through mid-latitudes between the mid Albian and early Campanian. Its absence in the study section is likely due to its rarity in mid-latitudes. Further examination of samples from temperate regions will be required to ascertain the true range of *B. dissimilis* and determine if its evolutionary history is congruent with the other high latitude forms encountered in this study. Similarly, *B. coronum* was not observed in the current study, but has been documented to first occur in the lower Campanian and persist into the early Maastrichtian of high southern latitudes (Wise 1983, Watkins et al. 1996). It has been recorded in the upper Campanian in boreal settings (Thibault 2010). This again suggests a high southern latitude origin in the early Campanian followed by dispersal to higher latitudes and incursion of the boreal realm by the late Campanian. As with *B. dissimilis*, further study of mid-latitude samples will be required to ascertain its true range and evolutionary patterns.

Because a study of Jurassic and Early Cretaceous Biscutaceae is beyond the scope of this work, we cannot definitively state the age of the origin of these forms that extend into the Upper Cretaceous. Based on the work of other authors, many forms documented in older stratigraphic sections are conspecific with *Biscutum ubiquem*. For example, this is evident in the studies of Bischoff and Mutterlose (1998) and Herrle and Mutterlose (2003) on Aptian sections, as well as the work on the lower Valanginian by Bown and Concheyro (2004).

Huber and Watkins (1992) observe a Late Cretaceous diversification interval within Biscutaceae in the Southern Ocean which includes the appearance of four *Biscutum* species during the late Campanian and Maastrichtian. The authors also call attention to a marked shift in the degree of provincialism during the Late Cretaceous. The change from cosmopolitan assemblages in the Cenomanian to Campanian interval to the strongly divided temperate and polar assemblages of the Maastrichtian appears to have begun in the late Campanian. Their examination of sections from the Southern Ocean indicates the number of nannofossils with distinctly polar affinities increases markedly beginning in the upper Campanian.

These results further suggest that the primary site of *Biscutum* evolution shifted from the mid-latitudes in the mid Cretaceous to high southern latitudes in the Late Cretaceous. Nannofossil evidence suggests that significant cooling of the Southern Ocean surface water mass began by at least the early Maastrichtian and was most pronounced during the mid-Maastrichtian (Huber and Watkins 1992). The cooling of surface water masses during the Late Cretaceous may have facilitated expansion of species previously restricted to high latitude settings into lower latitudes, although detailed comparisons of Cretaceous paleoceanography and nannofossil distribution would be required to determine if this was the case.

SUMMARY AND CONCLUSIONS

One of the most commonly cited species of *Biscutum*, *B. constans*, is herein taxonomically restricted to include forms conforming to the *B. constans* holotype. The form previously referred to by many authors to be *B. constans* based on its lack of central area structure is distinguished from *B. constans s.s* as *Biscutum ubiquem*. *Biscutum ellipticum* is considered a junior synonym of *B. constans* until and unless a form congruent with its original description is documented. Six previously undocumented species of *Biscutum* are described, increasing the utility of *Biscutum* for biostratigraphy.

Mid-latitude diversification of *Biscutum* in the mid Cretaceous followed by Late Cretaceous diversification in high southern latitudes is indicated by the general trends of first occurrences as shown in text-figure 7. It is also supported by the evolutionary histories of individual species. All of the high latitude species considered in this study, with the exception of *B. boletum*, clearly exhibit patterns of high southern latitude origin, followed by migration to mid- and finally high northern latitudes.

This study clearly shows a shift in the evolutionary epicenter of *Biscutum* through both time and space. The brief migratory appearances of forms which evolved in the high latitudes may have been facilitated by cooling, linking the evolution of this group of nannoplankton to changes in Late Cretaceous climate and oceanography.

SYSTEMATIC PALEONTOLOGY

Class PRYMNESIOPHYCEAE (Hibberd 1976)
Order PODORHABDALES (Rood, Hay and Barnard 1971) Bown 1987
Family BISCUTACEAE (Black 1971) Bown 1987
Genus *Biscutum* (Black *in* Black and Barnes 1959)

Biscutum shamrockiae Brace and Watkins, **n. sp.**
Plate 2, figures 10-12

Etymology: In honor of Dr. Jamie Shamrock

Diagnosis: Small to medium, broadly to narrowly elliptical *Biscutum* displaying a unique extinction pattern in which the x-shaped extinction figure traverses the entire coccolith, not just the inner tube cycle as is common in most forms.

Description: Species of *Biscutum* with broadly to narrowly elliptical rim comprised of 20-24 radial elements. The thin inner tube cycle surrounds a relatively large central area opening which may comprise of to 40% of the total surface area of the coccolith.

Measurements:

Length = 3.6-5.7μm (σ=0.6, μ=4.5, n=26)
Central Area Length = 1.7-3.2μm (σ=0.5, μ=2.4, n=26)
Width = 2.3-5.2μm (σ=0.7, μ=3.7, n=26)
Central Area Width = 1.1-3.3μm (σ=0.3, μ=1.7, n=26)
Eccentricity = 1.1-1.9μm (σ=0.2, μ=1.3, n=26)
Central Area Eccentricity = 1.2-1.9μm (σ=0.2, μ=1.5, n=26)
Central Area/Total Surface Area = 0.1-0.4 (σ=0.1, μ=0.3, n=26)

Occurrence: Cenomanian to Coniacian; Western Interior Basin (Washington County, KS and Smoky Hill type area, KS)

Type section: Fort Hays Member, Niobrara Chalk, Hattin (1982)

Type level: Fort Hays Member, Niobrara Chalk, 10.6 m

Holotype: Plate 2, figures 10-12

Biscutum constans (Görka 1957) Black 1967, emended herein
Plate 2, figures 5-6

Discolithus constans GÖRKA 1957, pl. 4, fig. 7
Tremalithus ellipticus GÖRKA 1957, pl. 1, fig. 11
non Biscutum testudinarium BLACK 1959, pl. 10, fig. 1
non Biscutum castrorum BLACK 1959, pl. 10, fig. 2
Biscutum constans (Görka 1957) BLACK 1967, p. 139
Biscutum ellipticum (Görka 1957) GRÜN *in* GRÜN and ALLEMANN 1975, Text-fig. 3; pl. 1, figs. 5-7

Emended diagnosis: Medium, broadly to narrowly elliptical species of *Biscutum* with a thin inner tube cycle and very wide central area opening. The distal rim is comprised of 18-28 radial elements, although the individual elements are difficult to discern. The central area opening is smooth and devoid of any structures. The large central area opening is a diagnostic characteristic of this species.

Description: This species has a broad to narrowly elliptical outline. The inner rim is very thin and exhibits first order white birefringence. The outer rim is approximately 1μm wide and displays second order gray birefringence or is extinct. The outer rim contains 18-28 thin, radial elements, although the individual elements are difficult to discern. The elements appear to "clump" or "group" together in the outer rim, creating the illusion of fewer, wider elements. The central area opening is large with a smooth inner rim and comprises 30 to 40% of the total surface area of the coccolith. No structures are present in the central area.

Measurements:

Length = 5.0-6.5μm (σ=0.5, μ=5.4, n=11)
Central Area Length = 3.1-3.8μm (σ=0.2, μ=3.4, n=11)
Width = 3.6-4.4μm (σ=0.3, μ=4.1, n=11)
Central Area Width = 1.7-2.6μm (σ=0.3, μ=2.2, n=11)
Eccentricity = 1.2-1.5μm (σ=0.1, μ=1.3, n=11)
Central Area Eccentricity = 1.3-1.8μm (σ=0.2, μ=1.5, n=11)
Central Area/Total Surface Area = 0.2-0.4 (σ=0.1, μ=0.3, n=11)

Occurrence: upper Cenomanian to upper Maastrichtian; North Atlantic Ocean, Gulf of Mexico, Western Interior Basin (Washington County, KS and Smoky Hill type area, KS)

Remarks: The description in the current work emphasizes the original description as outlined by Görka (1957). *Biscutum constans* has frequently been used as a catch-all for species of *Biscutum* lacking a central area structure. Future definition of *B. constans* in accordance with the original description will facilitate taxonomic and biostratigraphic refinement by reducing the "lumping" of taxa into *B. constans*. Furthermore, there appears to be no clear, definitive distinction between *B. constans* and *B. ellipticum* according to the original descriptions. As such, it is suitable to consider *B. ellipticum* (Görka 1957) Grün 1975 a junior synonym until and unless a species matching the original description is described.

Biscutum anthracenum Brace and Watkins, **n. sp.**
Plate 2, figures 13-16

Etymology: (L.) anthracenus coal-black, referring to the very dark distal rim

Diagnosis: Small to medium, circular to normally elliptical species of *Biscutum* with a very dark distal rim and small central area opening.

Description: Small to medium species of *Biscutum* with circular to normally elliptical outline comprised of 16-18 radial elements. The distal rim is unusually dark for *Biscutum*. The inner tube cycle is relatively thick and may fill the entire central area opening, thus obscuring the x-shaped extinction figure typically apparent in *Biscutum* specimens when oriented oblique to the polarizers. This results in the appearance of one longitudinal extinction line bisecting the central area in many specimens. In less extreme cases, small portions of the tube cycle may be visible in between the upper and lower branches of the x-shaped extinction figure.

Measurements:

Length = 3.6-6.4µm (σ=0.7, µ=4.9, n=44)
Central Area Length = 1.4-3.7µm (σ=0.5, µ=2.4, n=44)
Width = 3.0-6.2µm (σ=0.7, µ=4.3, n=44)
Central Area Width = 1.2-2.5µm (σ=0.3, µ=1.7, n=44)
Eccentricity = 1.0-1.4µm (σ=0.1, µ=1.2, n=44)
Central Area Eccentricity = 1.2-1.7µm (σ=0.1, µ=1.4, n=44)
Central Area/Total Surface Area = 0.1-0.3 (σ=0.1, µ=0.2, n=44)

Occurrence: upper Cenomanian to lower Campanian; Western Interior Basin (Washington County and Smoky Hill type area, KS; Sisseton, SD)

Type section: Gregory Member, Pierre Shale, Sisseton, SD, Core 20-3

Type level: Gregory Member, Pierre Shale, Sisseton, SD, Core 20-3, 5-6cm

Holotype: Plate 2, figures 13-16

Biscutum dehiscum Brace and Watkins, **n. sp.**
Plate 3, figures 1-4

Etymology: (L.) dehisco gape, referring to the very large central area opening

Diagnosis: Small to medium, broadly to normally elliptical species of *Biscutum* with a very large central area opening comprising up to 60% of the total coccolith surface area.

Description: Small to medium species of *Biscutum,* broadly to normally elliptical in outline with approximately 22-32 radial distal rim elements. The central area opening is very wide and may comprise up to 60% of the total area of the coccolith. *Biscutum dehiscum* may be distinguished from *B. zulloi* by its almost entirely black central area versus the two birefringent "knobs" visible in *B. zulloi* when oriented parallel to the polarizers. The extinction pattern of *B. dehiscum* is characterized by two transverse extinction lines near the top and bottom of the tube cycle when oriented parallel or perpendicular to the polarizers. The resulting appearance is two birefringent crescents along the longitudinal axis surrounding the central area opening, with two smaller portions at the top and the bottom. When specimens are rotated oblique to the polarizers, the extinction figure traversing the inner tube cycle is comprised of a set of extinction lines parallel to the longitudinal and transverse axes of the coccolith.

Measurements:

Length = 3.9-5.4µm (σ=0.4, µ=4.5, n=17)
Central Area Length = 2.3-3.5µm (σ=0.3, µ=4.5, n=17)
Width = 3.1-4.3µm (σ=0.4, µ=3.7, n=17)
Central Area Width = 1.6-3.3µm (σ=0.4, µ=2.1, n=17)
Eccentricity = 1.0-1.4µm (σ=0.1, µ=1.2, n=17)
Central Area Eccentricity = 1.0-1.6µm (σ=0.2, µ=1.4, n=17)
Central Area/Total Surface Area = 0.3-0.6 (σ=0.1, µ=0.3, n=17)

Occurrence: Santonian to lower Campanian; Gulf of Mexico

Type section: DSDP Leg 10, Site 95, Core 17-3

Type level: 10-95-17-3, 126-127cm

Holotype: Plate 3, figures 1-4

Biscutum subditivum Brace and Watkins, **n. sp.**
Plate 2, figures 7-9

Biscutum ellipticum (Görka 1957) Grün *in* Grün and Allemann 1975 - GALE et al. 1996, fig. 6p. – BOWN 1998, pl. 6.5, figs. 21a-c
Biscutum constans Görka 1957 – WISE AND WIND 1977, pl. 50, fig. 1b. – PROTO DECIMA AND TODESCO 1978, pl. 15, figs. 1a-c. – PERCH-NIELSEN 1985, fig. 19 (6-7)
Biscutum constans (Görka 1957) Black *in* Black and Barnes 1959 var. *ellipticum* (Görka 1957). – THIBAULT 2010, pl. 4, fig. 15

Etymology: (L.) subditivus spurious, referring to the common misidentification of this species

Diagnosis: Small, broadly to narrowly elliptical species of *Biscutum* with very thin inner tube cycle resulting in a relatively large central area opening.

Description: Small species of *Biscutum,* broadly to normally elliptical in outline with approximately 24 distal rim elements. The central area comprises 30% of the total area of the coccolith which is a common value for *Biscutum* in the Upper Cretaceous; however, the inner tube cycle is comparatively thin resulting in a relatively large central area opening. *Biscutum subditivum* may be distinguished from *Biscutum ubiquem* and *Biscutum aura* by its small size, 24 distal rim elements and larger central area opening. A small central knob is observed in well-preserved specimens.

Remarks: This form has been misidentified as *Biscutum constans* and *B. ellipticum*. As mentioned previously in text and in the systematic description of *B. constans s.s.*, *B. ellipticum*

should be considered a junior synonym of *B. constans.* Species fitting the above description which had been previously ascribed to one of these species should now be considered *B. subditivum.*

Measurements:

Length = 3.6-4.8μm (σ=0.5, μ=4.3, n=6)
Central Area Length = 1.9-3.3μm (σ=0.5, μ=2.6, n=6)
Width = 2.8-4.4μm (σ=0.5, μ=3.8, n=6)
Central Area Width = 1.3-2.2μm (σ=0.4, μ=1.7, n=6)
Eccentricity = 1.1-1.5μm (σ=0.1, μ=1.2, n=6)
Central Area Eccentricity = 1.0-2.2μm (σ=0.4, μ=1.5, n=6)
Central Area/Total Surface Area = 0.2-0.4 (σ=0.1, μ=0.3, n=6)

Occurrence: Cenomanian to Coniacian; North Atlantic Ocean, Western Interior Basin (Washington County, KS; Smoky Hill type area, KS)

Type section: ODP Leg 171b, Site 1050c, Core 25-2

Type level: ODP Leg 171b, Site 1050c, Core 25-2, 39.5-40.5cm

Holotype: Plate 2, figures 7-9

Biscutum aura Brace and Watkins, **n. sp.**
Plate 2, figures 1-4

B. cf *B. ellipticum* (Görka 1957) Grün *in* Grün and Allemann 1975 - GALE et al. 1996, fig. 6q,r

Etymology: (L.) aura glow, referring to the slight birefringence in the distal rim

Diagnosis: Small to medium, broadly to narrowly elliptical species of *Biscutum* with small central area. The distal rim display slight birefringence in cross polarized light.

Description: An extinction pattern in which the two longitudinal portions of the central area take on a subtle reniform appearance is visible when oriented parallel or perpendicular to the polarizers. The relatively small size of the central area may obscure this characteristic. When positioned oblique to the polarizers, a cross-like extinction figure is apparent, separating the central area in to four equal quadrants. No structure is visible in the central area opening. The distal rim displays slight birefringence. *Biscutum aura* differs from *Biscutum ubiquem* in its more conspicuous and radial, 24 distal rim elements, as well as its nearly closed central area.

Measurements:

Length = 3.4-5.6μm (σ=0.5, μ=4.4, n=19)
Central Area Length = 1.6-2.8μm (σ=0.4, μ=2.2, n=19)
Width = 2.8-5.3μm (σ=0.6, μ=3.7, n=19)
Central Area Width = 1.0-1.8μm (σ=0.2, μ=1.4, n=19)
Eccentricity = 1.1-1.5μm (σ=0.1, μ=1.2, n=19)
Central Area Eccentricity = 1.2-2.1μm (σ=0.2, μ=1.5, n=19)
Central Area/Total Surface Area = 0.1-0.3 (σ=0.1, μ=0.2, n=19)

Type section: ODP Leg 171b, Site 1052e, Core 38-5

Type level: 171b-1052e-38-5, 111-113cm

Occurrence: Cenomanian; North Atlantic Ocean

Biscutum thurowii Burnett 1997
Plate 1, figures 7-10

non Biscutum gartneri Black 1971. – GALE et al. 1996, fig. 6s

Remarks: Burnett's (1997) description of *B. thurowii* based on her SEM image conforms with the light images of this study clearly showing the transverse minor axis bar oriented perpendicular to the long axis separating two distinct perforations. The transverse bar is birefringent and the perforations are extinct in cross polarized light. Although *B. zulloi* has two birefringent "knobs" in the central area, these are not equivalent to the perforations of Burnett's *B. thurowii* which should appear black and not birefringent. In addition, Burnett's holotype has approximately 19 radial distal rim elements as do the specimens observed in this study.

Measurements:

Length = 4.4-5.2μm (σ=0.3, μ=4.8, n=12)
Central Area Length = 2.0-3.4μm (σ=0.4, μ=2.8, n=12)
Width = 3.2-4.2μm (σ=0.3, μ=3.7, n=12)
Central Area Width = 1.4-2.3μm (σ=0.3, μ=1.8, n=12)
Eccentricity = 1.2-1.4μm (σ=0.1, μ=1.3, n=12)
Central Area Eccentricity = 1.2-2.0μm (σ=0.3, μ=1.6, n=12)
Central Area/Total Surface Area = 0.2-0.5 (σ=0.1, μ=0.3, n=12)

Occurrence: upper Albian to lower Cenomanian; North Atlantic Ocean

Biscutum ubiquem Brace and Watkins, **n. sp.**
Plate 1, figures 1-6

Biscutum constans – PROTO DECIMA 1974, pl. 4, figs. 11-13. – HILL 1976, pl. 1, figs. 32-37. – POSPICHAL 1991, pl. 3, figs. 3a-b. – BOWN 1998, pl. 5.10, figs. 21-22. – LADNER AND WISE 1998, pl. 3, figs. 5, 10. – WEI AND POSPICHAL 1991, pl. 1, fig. 9. – ERBA, WATKINS AND MUTTERLOSE 1995, pl. 1, figs. 4, 7-8
Biscutum castrorum – PERCH – NIELSEN 1985, fig. 19 (2-3)

Etymology: (L.) ubique everywhere
Diagnosis: Small to medium species of *Biscutum* with variable eccentricity. Exhibits an extinction pattern in which the two longitudinal portions of the central area take on a reniform appearance. When positioned oblique to the polarizers, a cross-like extinction figure is apparent, separating the central area in to four equal quadrants.

Description: Small to medium species of *Biscutum* with variable eccentricity and 24 to 36 dextrally oblique, faintly birefringent distal rim elements. Earlier forms tend to have the greatest number of elements. *Biscutum ubiquem* is distinguished from *B. zulloi* and *B. thurowii* by a lack of central area structure. It is distinguished from *B. constans* by its much smaller central area opening, thicker inner tube cycle and extinction pattern.

Remarks: This form has been misidentified as *Biscutum constans* and *B. ellipticum.* As mentioned previously in text and in the systematic description of *B. constans s.s.*, *B. ellipticum* should be considered a junior synonym of *B. constans.* Species fitting the above description which had been previously ascribed to one of these species should now be considered *B. ubiquem.*

Measurements:

Length = 3.4-6.4μm (σ=0.7, μ=4.7, n=41)
Central Area Length = 1.4-3.7μm (σ=0.4, μ=2.5, n=41)

Width = 2.2-5.4µm (σ=0.6, µ=4.0, n=41)
Central Area Width = 1.2-2.8µm (σ=0.3, µ=1.6, n=41)
Eccentricity = 1.0-1.6µm (σ=0.1, µ=1.2, n=41)
Central Area Eccentricity = 1.1-1.9µm (σ=0.2, µ=1.6, n=41)
Central Area/Total Surface Area = 0.2-0.4 (σ=0.1, µ=0.2, n=41)

Type section: ODP Leg 171b, Site 1052e, Core 55-1

Type level: 171b-1052e-55-1, 146-147cm

Occurrence: upper Albian to upper Maastrichtian; all localities

Biscutum zulloi Covington 1994
Plate 1, figures 11-16

Biscutum sp. – COVINGTON 1985, fig. 2a-b
Biscutum zulloi COVINGTON 1994, pl. 1, figs. 1-5
Biscutum sp. 1 – POSPICHAL AND BRALOWER 1992, pl. 3, figs. 1-2

Description: Small to medium species of *Biscutum* 28-32 radial distal rim elements. *Biscutum zulloi* is characterized by its large central area comprising up to 60% of the total surface area. Covington also notes the presence of a distinct "collar" visible in both phase contrast illumination and cross polarized light, as well as the occurrence of a small knob in the central area of well-preserved specimens. In this study, a single small knob was observed in specimens oriented oblique to the polarizers in cross polarized light, while two birefringent knobs are visible when the specimens are oriented parallel to the polarizers in cross polarized light.

Measurements:

Length = 3.2-6.6µm (σ=0.6, µ=4.3, n=69)
Central Area Length = 1.9-3.9µm (σ=0.5, µ=2.6, n=69)
Width = 2.5-5.2µm (σ=0.5, µ=3.6, n=69)
Central Area Width = 1.1-3.0µm (σ=0.3, µ=1.8, n=69)
Eccentricity = 1.0-1.6µm (σ=0.1, µ=1.2, n=69)
Central Area Eccentricity = 1.0-2.3µm (σ=0.2, µ=1.5, n=69)
Central Area/Total Surface Area = 0.2-0.6 (σ=0.1, µ=0.3, n=69)

Occurrence: upper Albian to upper Maastrichtian; all localities

Other Calcareous Nannofossil Species Considered in this Report

Biscutum boletum Wind and Wise 1977

Biscutum coronum Wind and Wise 1977

Biscutum dissimilis Wind and Wise 1977

Biscutum magnum Wind and Wise 1977

Biscutum melaniae (Görka 1957) Burnett 1997

Biscutum notaculum Wind and Wise 1977

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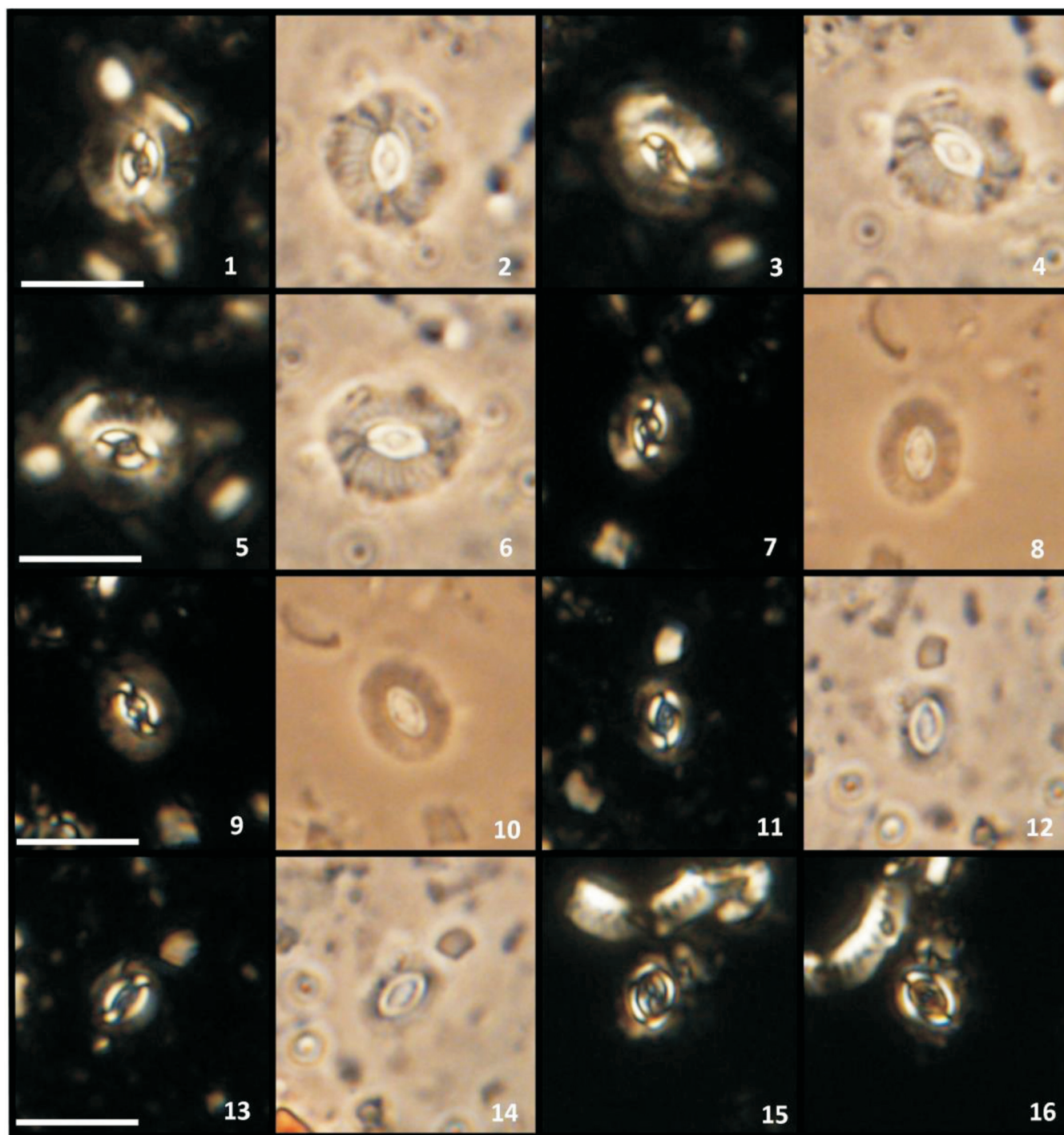
PLATE 1
Bar scale = 5µm. Figures 1, 3, 5, 7, 9, 11, 13, 15 and 16 are in cross-polarized light.
All others are in phase contrast illumination.

1–6   *Biscutum ubiquem* n. sp., (holotype specimen) ODP
       Leg 171b-1052e-55-1, 146–147cm

7–10   *Biscutum thurowii* Burnett 1997, ODP Leg 171b-
       1050c-23-4, 77–78cm

11–16 *Biscutum zulloi* Covington 1994; figures 11–14 from
       ODP Leg 171b-1052e-58-3, 30–31cm; figures 15–16
       from Gregory Mbr., Pierre Shale, Core 20-3, 5–6cm

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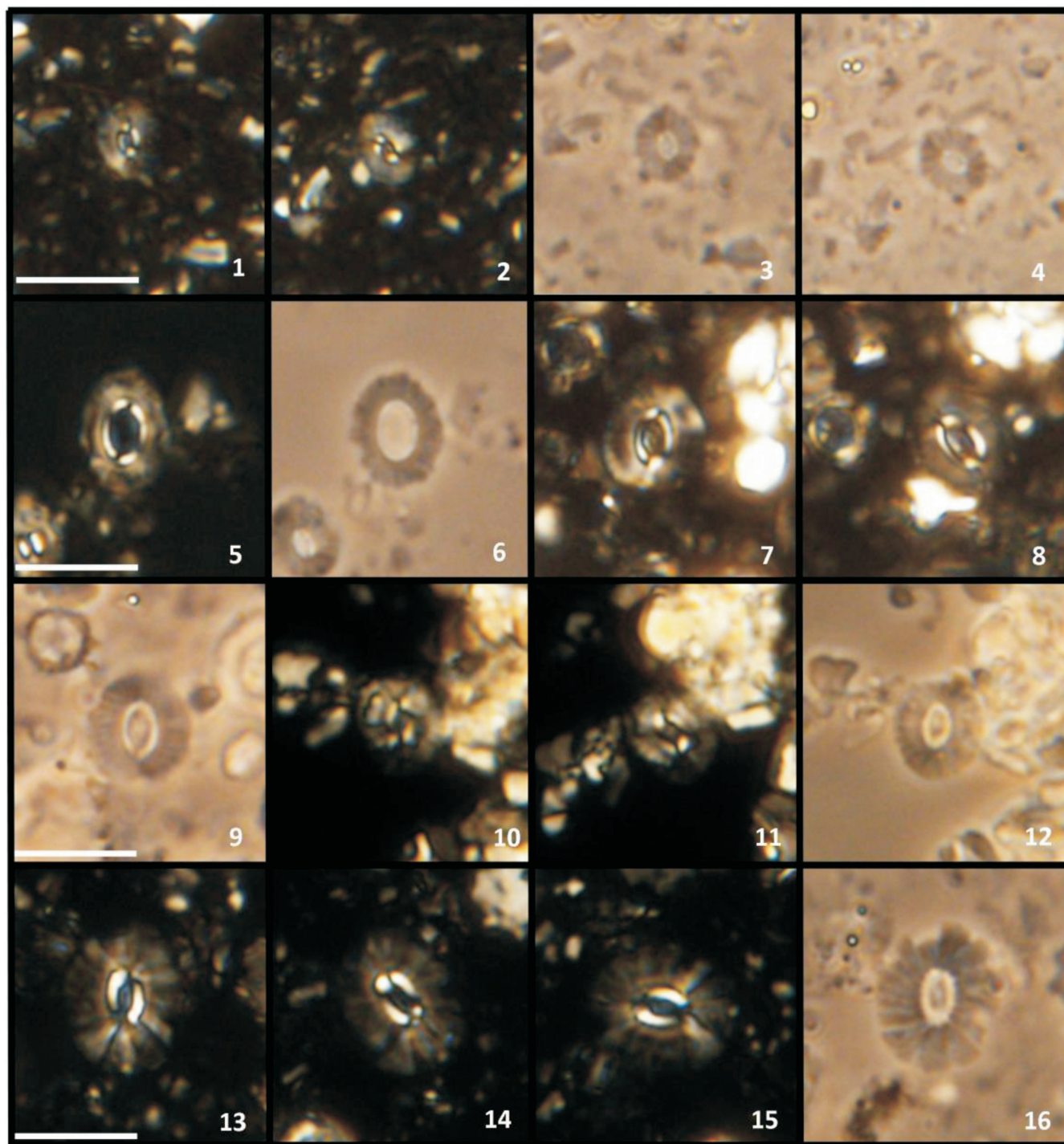
PLATE 2

Bar scale = 5µm. Figures 1, 2, 5, 7, 8, 10, 11, 13-15 are in cross polarized light. All others are in phase contrast illumination.

1–4   *Biscutum aura* n. sp., (holotype specimen) ODP Leg171b-1052e-38-5, 111–113cm

5–6   *Biscutum constans* s.s. Görka 1957, ODP Leg 171b-1050c-21-1, 109–110cm

7–9   *Biscutum subditivum* n. sp., (holotype specimen) ODP Leg 171b-1050c-25-2, 39.5–40.5cm

10–12   *Biscutum shamrockiae* n. sp., (holotype specimen) Ft. Hays Mbr., Niobrara Chalk, Loc. B, 10.6 m

13–16   *Biscutum anthracenum* n. sp., (holotype specimen) Gregory Mbr., Pierre Shale, Core 20-3, 5–6cm

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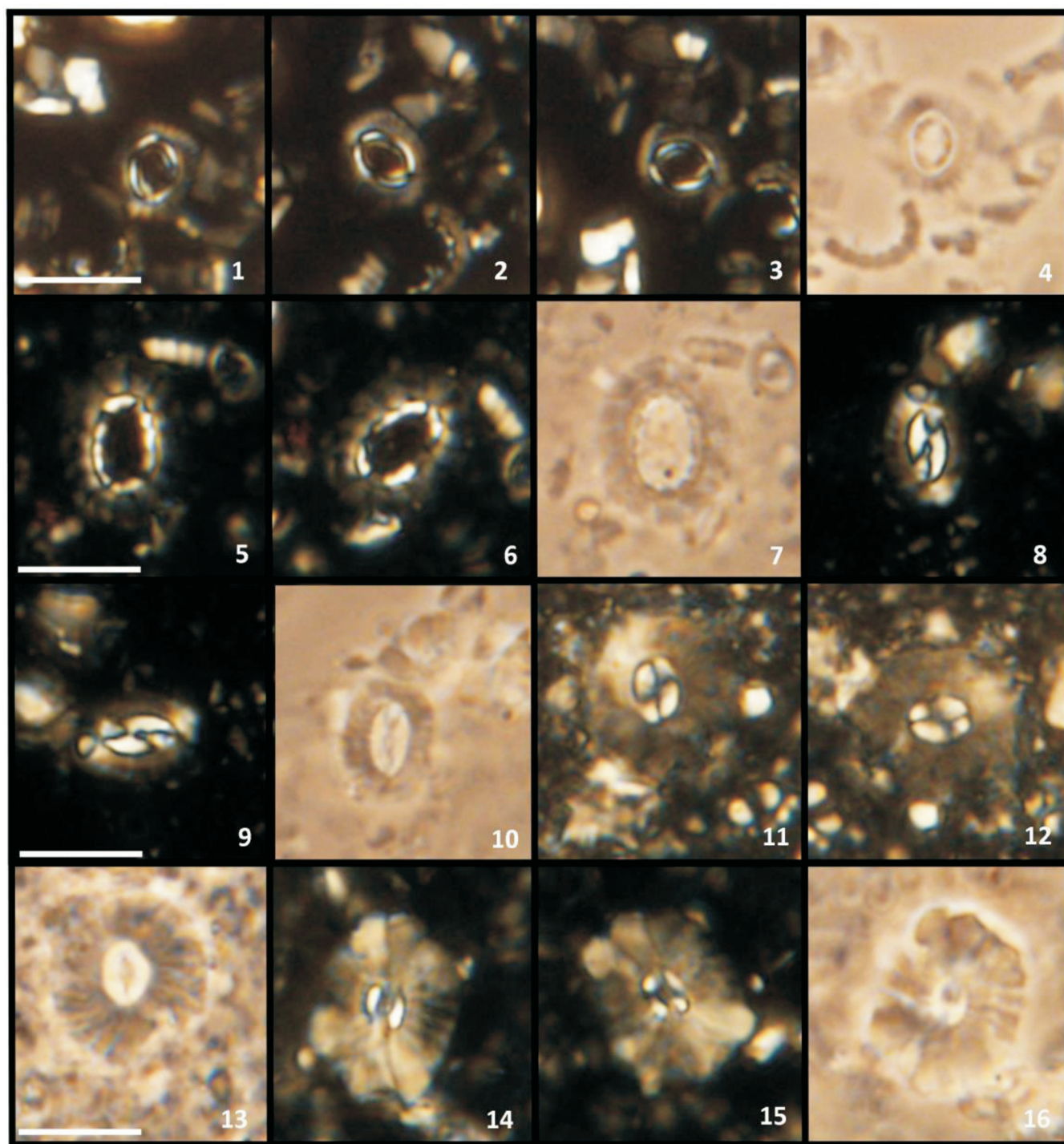
PLATE 3
Bar scale = 5µm. Figures 1-3, 5, 6, 8, 9, 11, 12, 14 and 15 are in cross-polarized light.
All others are in phase contrast illumination.

1–4   *Biscutum dehiscum* n. sp., (holotype specimen) DSDP Leg 10-95-17-3, 126–127cm

5–7   *Biscutum magnum* Wind and Wise 1977, Gregory Mbr., Pierre Shale, Core 21-3, 21–22cm

8–10   *Biscutum notaculum* Wind and Wise 1977, Crow Creek Mbr., Pierre Shale, Core 11-5, 17–19cm

11–13 *Biscutum melaniae* (Görka 1957) Burnett 1997, ODP Leg 171b-1047a-17-2, 22–29.5cm

14–16 *Biscutum boletum* Wind and Wise 1977, Crow Creek Mbr., Pierre Shale, Core 11-5, 17–19cm