

THE FIRST RADIATION OF THE FASCICULITHS: MORPHOLOGIC ADAPTATIONS OF THE COCCOLITHOPHORES TO OLIGOTROPHY

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ABSTRACT

The Qreiya section (Upper Egypt) contains a well-preserved record of the first radiation of the fasciculiths, an evolutionary event that affected the coccolithophores of the Order Discoasterales during the late Danian. At Qreiya it unfolds across the so-called Neo-Duwi Event. We describe the morphostructural changes that affected coccoliths and document a trend towards increased surface area of the coccoliths of the Order Discoasterales. Our isotopic data do not support earlier interpretation(s) that the Neo-Duwi Event may correspond to a Paleocene hyperthermal. We interpret the first radiation of the fasciculiths as an adaptive response to increased oceanic oligotrophy through the appearance of coccoliths adapted to food collection in nutrient-poor oceanic waters.

1. INTRODUCTION

Since the early 1980s there has been considerable interest devoted to mass extinction events. In contrast, little attention has been paid to diversification events, even though the dynamics of diversification may illuminate the dynamics of extinction. The latest Danian (~63-62 Ma; Westerhold et al., 2008) was a significant time in the Cenozoic diversification of the planktonic calcifiers (e.g., d'Hondt et al., 1994; Aubry, 1998; Coxall et al., 2006; Bown, 2005). This is when coccolithophores of the Order Discoasterales Hay 1977 emend Aubry (in press) began their Cenozoic diversification that led ~3.5 Myr later to the successive radiations of the families Helio-discoasteraceae and Eu-discoasteraceae (Aubry, 1998; Aubry and Bord, 2009). These two families, in turn, contributed almost half of the components of nannofossil oozes at low- and mid-latitudes, both in terms of relative abundance and (to a lesser degree) species diversity, from the Late Paleocene to the late Pliocene.

The early Paleocene diversification of the Order Discoasterales has been documented in terms of species richness (Bown, 2005) and abundance patterns (Fuqua et al., 2008), but the fundamental morphological transformations that affected coccoliths at this time have not been described. The recovery of well preserved assemblages across the Danian/Selandian boundary (as defined by Schmitz et al., 2011) in the Qreiya section of Upper Egypt provides us with the first opportunity to discuss the significance of the "first radiation of the fasciculiths", the expression generally used following Romoin (1979) to refer to a burst of diversification in the Order Discoasterales. We discuss this in the light of the Neo-Duwi Event (Speijer, 2003; Guasti et al., 2005) which is recorded in Egypt shortly after the radiation event.

2. THE QREIYA SECTION

The outcrop at Gebel Qreiya (26° 21'N, 33° 01' E) is located

at the southeastern end of Gebel Abu Had in the Egyptian Eastern Desert on the eastern side of the Wadi Qena (Fig. 1). Situated ~50 km ENE of the town of Qena, it is accessible by the road running essentially West to East from Qena to Safaga and then along a track in the desert. The almost 300 m high outcrop exposes, in stratigraphic succession, the Dakhla (Said, 1961), Tarawan (Awad and Ghobrial, 1965), Esna Shale (Said, 1960) and Thebes Limestone (Said, 1960) formations. The Maastrichtian to Ypresian stratigraphy was first described by Barron and Hume (1902) and revisited by Said (1962), Abd El Razi (1969, 1972), Faris et al. (1985) and Luger (1988) among others.

The base of the steep upper slope is formed by the upper part of the Dakhla Formation, consisting essentially of hemipelagic, homogeneous laminated shales of middle to outer neritic origin (Speijer, 2003). This monotonous succession is interrupted by a thin but distinctive organic-rich interval that occurs throughout Upper Egypt (Speijer and Schmitz, 1998;

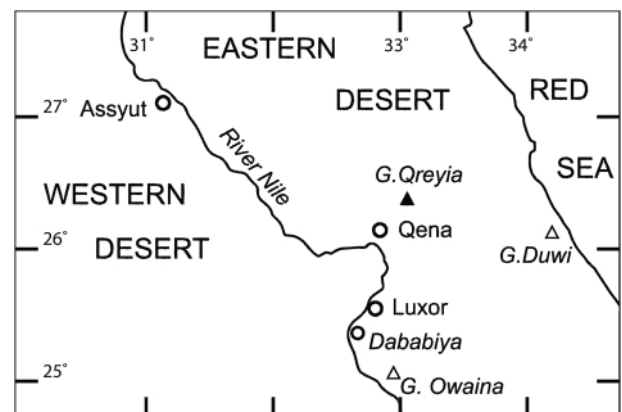


FIGURE 1: Location map.

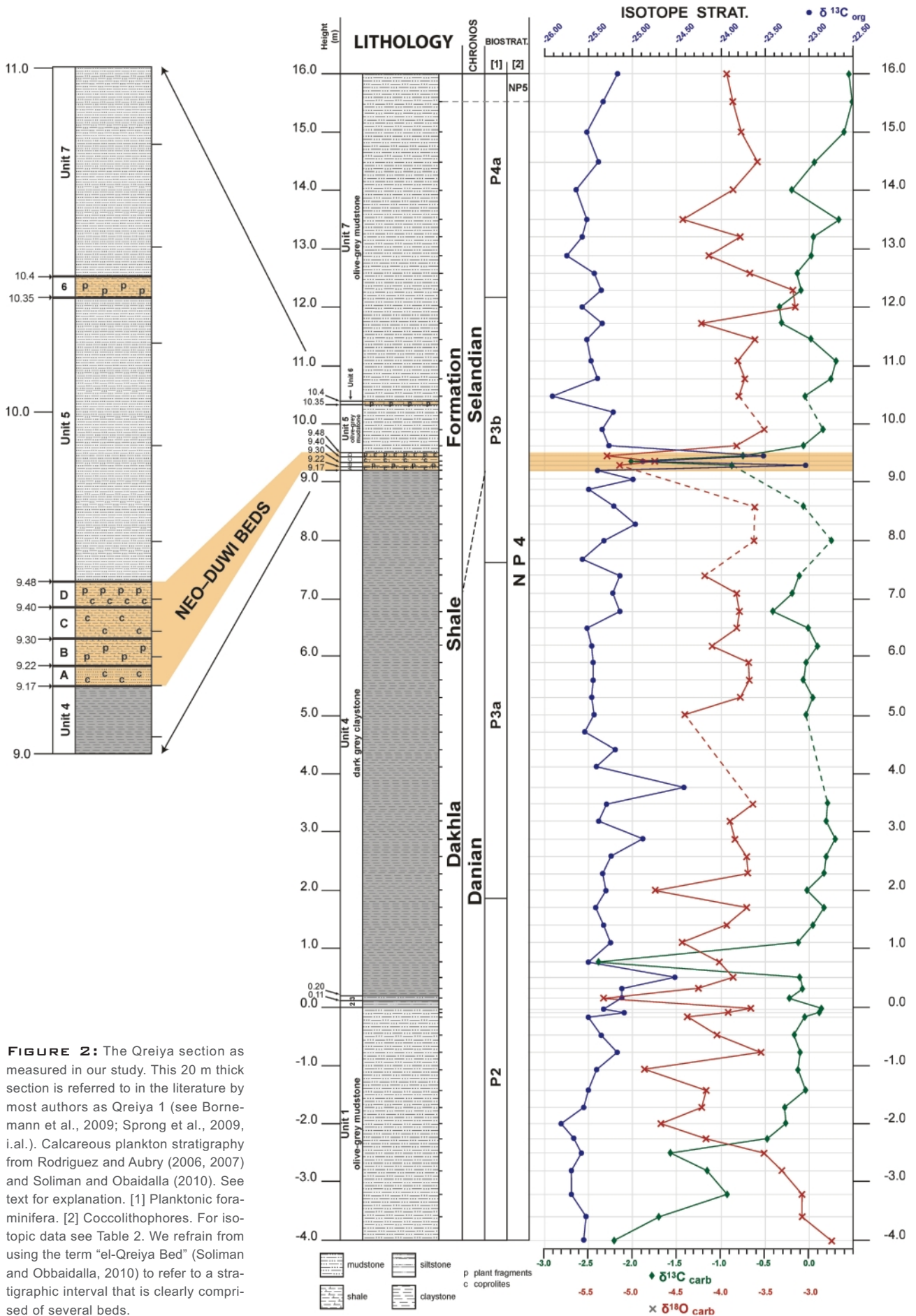


FIGURE 2: The Qreiya section as measured in our study. This 20 m thick section is referred to in the literature by most authors as Qreiya 1 (see Borne-mann et al., 2009; Sprong et al., 2009, i.a.). Calcareous plankton stratigraphy from Rodriguez and Aubry (2006, 2007) and Soliman and Obaidalla (2010). See text for explanation. [1] Planktonic foraminifera. [2] Coccolithophores. For isotopic data see Table 2. We refrain from using the term “el-Qreiya Bed” (Soliman and Obaidalla, 2010) to refer to a stratigraphic interval that is clearly comprised of several beds.

Speijer, 2003), albeit with varying thickness from a few centimeters to several decimeters. This distinct lithologic interval is associated with a sudden incursion of the shallow water benthic foraminifera *Neoponides duwi* into benthic foraminiferal assemblages typical of deep-water shelf environments. This abrupt event was referred to as the “Neo-Duwi Event” by Guasti et al. (2005), and as the “Late Danian Event [LDE]” by Sprong et al. (2011). We here refer to the phosphatic organic-rich interval that includes the Neo-Duwi Event as the Neo-Duwi beds. These correspond to the “el-Qreiya Bed” of Soliman and Obaidalla (2010).

At least three sections have been sampled at Gebel Qreiya around the Neo-Duwi beds in recent years, and studied for planktonic foraminifera (Qreiya 1, 3: Sprong et al., 2009; Qreiya 1: Soliman and Obaidalla, 2010), benthic foraminifera (Qreiya unspecified: Guasti et al., 2005; Qreiya 3: Sprong et al., 2011), coccolithophores (Qreiya 3: Steurbaut and Sztrákos, 2008, Sprong et al., 2009, 2011; Qreiya 1, 2: Youssef, 2009), carbonate isotope stratigraphy (Qreiya 1, 3: Bornemann et al., 2009), and mineralogy and geochemistry (Qreiya 1: Soliman and Obaidalla, 2010; Qreiya 3: Sprong et al., 2011). The 20 m-thick Qreiya 1 section was sampled in 2004 by two of us (RK, BS) (Fig. 2). It consists of mudstone and includes three distinct lithologic markers. The lowest marker (unit 2 of Figure 2) consists of 11 cm of homogeneous pale grey siltstone. Its base constitutes Level 0 of the measured section. The highest marker (unit 6 of Figures 2 and 3) consists of brown, organic-rich shale with plant fragments.

The middle marker (comprising beds A to D of Figures 2 and 3) is the most prominent, consisting of 31 cm of fissile mudstone with coprolites. This phosphate-bearing interval corresponds to the Neo-Duwi beds. It consists of four beds that are, in stratigraphic succession: Bed A: 9.17 to 9.22 m: a black fissile mudstone with rare coprolites; Bed B: 9.22 to 9.30 m: an organic-rich brown grey shale, friable and moderately fissile, with abundant plant fragments and phosphatic material; Bed C: 9.30 to 9.40 m: an indurated, grey shale with scattered coprolites, and Bed D: 9.40 to 9.48 m: an organic-rich brown grey shale with coprolites and plant fragments, moderately fissile, forming the top of a prominent ledge. The Qreiya 1 section is Lower and Middle Paleocene (spanning the Danian/Selandian boundary, although authors differ in the location of the boundary with respect to the Neo-Duwi beds). It belongs to planktonic foraminiferal Zones P2 to P4a (Sprong et al., 2009; Soliman and Obaidalla, 2010; zonal scheme of Berggren and Pearson, 2005), and calcareous nannofossil Zone NP4 and lowermost Zone NP5 (zonal scheme of Martini, 1971; Rodriguez and Aubry, 2006, 2007). The interval investigated here belongs to Subzones P3a-P3b and Zone NP5, Subzones NTp7B and NTp8 (zonal scheme of Varol, 1989).

3. METHODS

3.1 MICROPALAEONTOLOGIC ANALYSIS

Two conspicuous changes in the nannofossil assemblages

occur in Qreiya section 1. One is a sudden drop (from ~40 to <10%) in the abundance of *Ellipsolithus* species between levels 3.2 and 5 m (unit 4; Rodriguez and Aubry, unpublished data, based on counts of 300 coccoliths/smear slide). The other, beginning at 7.1 m (also in unit 4), involves the sequential lowest occurrences (LOs) of taxa with a radial structure (Order Discoasterales), for which the new generic names *Diantholitha* and *Lithoptychius* have recently been introduced (Aubry et al., 2011). We are concerned here with this qualitative change, documented from a suite of twenty (20) samples taken from Level 6.8 m to Level 12.3 m (upper unit 4 to lower unit 7; Fig. 2). Sample spacing is 30 cm, except in the Neo-Duwi beds where samples were taken <10 cm apart.

The procedures followed for calcareous nannofossil analysis are given in Aubry et al. (2011). Only smear slides were used. The frequency of the taxa discussed here is variable, constituting generally <1% of the otherwise highly diversified assemblages (see counting method above). Preservation is good at most levels. Dissolution occurs at Levels 8.9 and 9.05 m and the group is poorly represented and poorly preserved in the Neo-Duwi beds (9.17–9.42 m). This reduction in diversity may be due, at least partly, to ecological factors since new occurrences are observed at these levels.

The taxonomic descriptions of *Diantholitha* and *Lithoptychius* species are given in Aubry et al. (2011). The morphostructure of their respective coccoliths is described in detail in Aubry (in press) from whom the terminology is borrowed. The Order Discoasterales is based on structural unity among its coccoliths, including, among other characters, the direction of imbrication of the elements in their proximal (column) and distal (calyptra) structural units (see Aubry, 1998, for a general description of the structure of coccoliths). Elements of the column are non-imbricate with radial or slightly clockwise sutures. Elements of the calyptra have dextral imbrication with anticlockwise sutures.

Although the practice is sometimes discouraged (Young et al., 1997), it is useful to group coccoliths into morphostructural groups (biantholiths, fasciculoliths, sphenoliths, in this paper). In as much as they are based on homology of characters as in cladistics methodologies (Table 1), we regard these groupings as scientifically sound. Moreover, generic and specific concepts for fossil taxa are based almost entirely on isolated coccoliths because coccospheres are disarticulated during sedimentation. This is in contrast with taxonomic concepts of species and genera in living taxa which are based on both coccoliths and coccospheres. For the coccolithophores, taxonomic concepts in paleontology are much narrower than taxonomic concepts in biology. The use of morphostructural groups, which are short and precise ways to refer to coccoliths of (a) specific genus(era), is a recognition of the insufficiency (not superficiality) of the paleontologic concepts of genera in coccolithophore studies.

3.2 ISOTOPE CHEMISTRY

Organic carbon isotopes were analyzed by CF-IRMS at Rutgers University using a Eurovector EA coupled with a GVI Iso-

Genus	Column	Calyptra D. imbrication	Calyptra S. imbrication	Collaret	Central Body
<i>Biantholithus</i>	1	1	0	0	0
<i>Diantholitha</i>	1	1	0	0	0
<i>Fasciculithus</i>	1	1	0	0	0
<i>Gomphiolithus</i>	1	0	0	0	1
<i>Lithoptychius</i>	1	1	0	1	0
<i>Sphenolithus</i>	1	0	1	0	1

TABLE 1: Distribution of homologous characters in the genera discussed here. D: dextral; S: senestral. Note that the structure of *Gomphiolithus* is poorly established. (See Aubry in press for further explanation).

prime after carbonate had been removed with 25% HCl. An approximately equal amount of V₂O₅ as sediment was added to the tin capsule, and the samples were normalized against NBS 22 (Coplen et al., 2006) and a secondary sediment standard. Organic C concentrations were determined concurrently using the major ion intensity and an acetanilide calibration curve.

Stable carbon and oxygen isotopic composition of marine carbonates

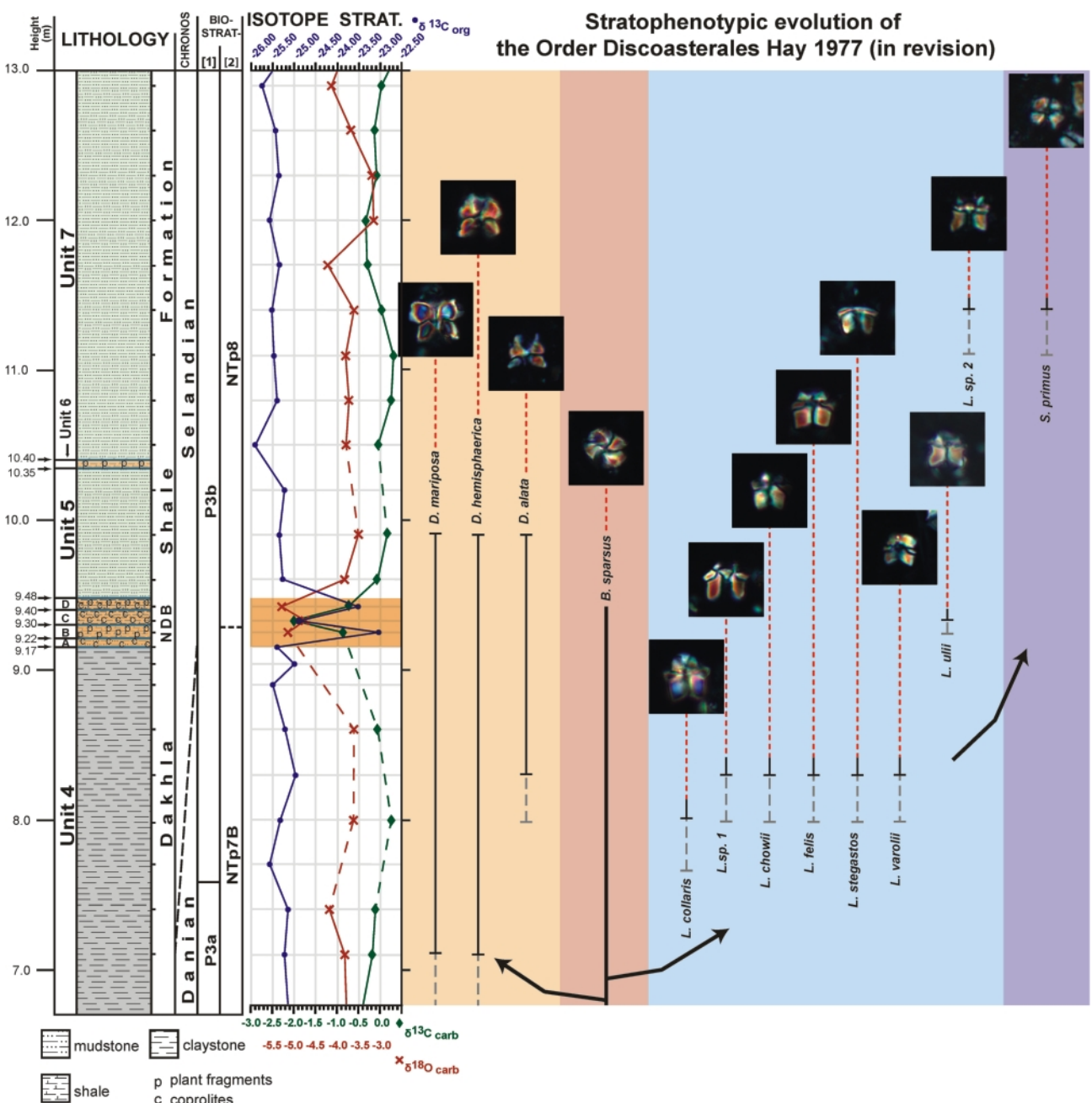


FIGURE 3: Distributions of the representatives of the Order Discoasterales in the vicinity of the Neo-Duwi beds. Taxonomic framework follows Aubry (in press) and Aubry et al. (2011). [1] Planktonic foraminifera. [2] Coccolithophores.

were studied on whole rock samples at the University of Göteborg. Analyses were performed with a VG Prism Series II mass

spectrometer attached to an Isocarb automated carbonate preparation system.

For both organic matter and carbonates isotopic values are expressed as per mil differences with respect to the PDB standard (Table 2).

Sample	WT% OC	N ppm	C _{org} /N _T	δ ¹³ C _{org}	δ ¹³ C _{carb}	δ ¹⁸ O
Q16	0.58	725.79	9.27	-25.16	0.46	3.94
Q15.5	0.56	738.18	8.80	-25.33	0.64	3.88
Q15	0.59	798.75	8.68	-25.51	0.40	3.78
Q14.5	0.50	707.06	8.22	-25.38	0.07	3.60
Q14	0.57	753.82	8.77	-25.63	0.19	3.88
Q13.5	0.53	726.88	8.57	-25.52	0.34	4.42
Q13.2	0.57	756.43	8.84	-25.57	0.06	3.79
Q12.9	0.62	761.39	9.48	-25.74	0.03	4.14
Q12.6	0.57	657.70	10.12	-25.44	0.12	3.67
Q12.3	0.56	663.07	9.80	-25.35	0.09	3.20
Q12	0.63	710.68	10.29	-25.57	0.34	3.17
Q11.7	0.53	635.97	9.69	-25.36	0.31	4.22
Q11.4	0.50	648.07	8.99	-25.50	0.03	3.62
Q11.1	0.46	625.24	8.61	-25.47	0.31	3.81
Q10.8	0.54	624.44	10.07	-25.40	0.26	3.73
Q10.5	0.54	613.63	10.19	-25.89	0.04	3.80
Q10.2	0.93	1077.63	10.05	-25.04	no calcite	
Q10.2	0.92	960.66	11.13	-25.40		
Q9.9	0.61	702.69	10.10	-25.34	0.16	3.51
Q9.6	0.77	789.12	11.36	-25.27	0.06	3.82
Q9.42	4.81	736.17	76.26	-23.51	0.74	5.30
Q9.32	1.51	1515.69	11.62	-24.72	2.02	4.76
Q9.32	1.53	1433.38	12.48	-25.08		
Q9.25	7.41	6213.78	13.91	-23.02	0.86	5.17
Q9.17	0.61	612.06	11.66	-25.39	no calcite	
Q9.05	0.48	450.93	12.30	-24.99	no calcite	
Q8.9	0.44	555.01	9.27	-25.51	no calcite	
Q8.6	0.40	471.93	9.78	-25.21	0.06	3.62
Q8.3	0.23	263.62	10.23	-24.98	no calcite	
Q8.0	0.46	571.50	9.40	-25.32	0.26	3.63
Q7.7	0.53	680.52	9.15	-25.57	no calcite	
Q7.4	0.39	513.74	8.93	-25.14	0.11	4.20
Q7.1	0.45	517.12	10.23	-25.14	0.17	3.83
Q7.1	0.53	543.93	11.32	-25.22		
Q6.8	0.50	936.17	6.18		0.40	3.80
Q6.8	0.49	598.94	9.61	-25.14		
Q6.5	0.41	584.85	8.18	-25.51	0.01	3.82
Q6.2	0.35	568.08	7.13	-25.47	0.08	4.12
Q5.9	0.39	588.71	7.74	-25.46	0.03	3.68
Q5.6	0.43	575.97	8.66	-25.45	0.04	3.68
Q5.3	0.40	592.30	7.96	-25.45	0.04	3.77
Q5.0	0.33	578.14	6.74		0.03	4.41
Q5.0	0.39	599.06	7.61	-25.43		
Q4.7	0.35	562.54	7.30	-25.55	no calcite	
Q4.4	0.36	545.50	7.74	-25.21	no calcite	
Q4.1	0.33	524.67	7.23	-25.40	no calcite	
Q3.8	0.36	519.78	8.19	-24.42	no calcite	
Q3.5	0.35	548.70	7.54	-25.29	0.22	3.65
Q3.2	0.36	600.44	6.95	-25.39	0.21	3.90
Q2.9	0.40	620.35	7.58	-24.89	0.30	3.84
Q2.6	0.32	586.23	6.43	-25.26	0.20	3.71
Q2.3	0.37	622.56	7.01	-25.34	0.17	3.70
Q2.0	0.38	577.01	7.75	-25.30	0.02	4.74
Q1.7	0.35	603.72	6.73	-25.41	0.18	3.72
Q1.4	0.33	605.72	6.30	-25.33	0.05	3.95
Q1.1	0.35	589.32	6.86	-25.25	0.13	4.44
Q0.8	0.40	636.04	7.26	-25.50	2.40	4.03
Q0.5	0.35	765.13	5.40	-24.52	0.10	3.88
Q0.3	0.31	590.64	6.06	-25.12	0.07	4.26
Q0.15	0.38	543.59	8.08	-25.13	0.23	5.34
Q-0.02	0.18	290.88	7.27	-25.32	0.14	3.69
Q-0.1	0.33	508.11	7.55	-25.10	0.13	3.92
Q-0.2	0.33	545.52	7.15	-25.50	0.04	4.38
Q-0.5	0.39	550.12	8.33	-25.35	0.17	4.05
Q-0.8	0.34	586.06	6.72	-25.17	0.08	3.55
Q-1.1	0.38	535.88	8.17	-25.42	0.11	4.86
Q-1.4	0.36	614.97	6.78	-25.50	0.03	4.18
Q-1.7	0.40	601.16	7.86	-25.56	0.28	4.23
Q-2	0.47	622.98	8.78	-25.81	0.26	4.68
Q-2.25	0.41	603.64	7.88	-25.66	0.47	4.17
Q-2.5	0.44	619.90	8.23	-25.58	1.57	3.51
Q-2.8	0.40	620.94	7.60	-25.70	1.15	3.33
Q-3.2	0.38	652.91	6.82	-25.69	0.93	3.52
Q-3.6	0.23	361.49	7.41	-25.53	1.69	3.08
Q-4	0.36	647.67	6.45		2.21	-2.76
Q-4	0.44	671.94	7.70	-25.55		

TABLE 2: Results from isotopic analyses from the Qreiya 1 section.

4. RESULTS

4.1 COCCOLITHOPHORES OF THE ORDER DISCOASTERALES

Sixteen biostratigraphic events concerning this order occur in the 5 m thick interval (7.1 m to 12.5 m) encompassing the Neo-Duwi beds (Fig. 2). These include the lowest (LO) and highest (HO) occurrences of three species of *Diantholitha*, the LOs of eight species of *Lithoptychius*, and the LO of the oldest species of *Sphenolithus*. The ranges of *Diantholitha* species are well delineated in the section, but the upward ranges of several species of *Lithoptychius* were difficult to establish because of scarcity as well as poor preservation in the Neo-Duwi beds.

4.2 ISOTOPE CHEMISTRY

The δ¹³C_{org} is essentially constant in the section, varying by 0.5‰ around a mean of 25.5‰ (Fig. 2). However two major positive excursions occur in the NDI, one of 2.5‰ between 9.17 m and 9.25 m across beds A and B, the other of 1.5‰ between 9.32 m and 9.42 m across beds C and D (Fig. 3).

The δ¹³C_{carb} and δ¹⁸O_{carb} are much less stable, and some degree of covariance occurs (Fig. 2). However marked negative excursions of ~1.5‰ (δ¹⁸O_{carb}) between 8.6 m and 9.25 m, and ~1.2‰ (δ¹³C_{carb}) between 9.25 m and 9.32 m occur in the Neo-Duwi beds (Fig. 3).

5. DISCUSSION

5.1 THE FIRST RADIATION OF THE FASCICULITHS: CHARACTERIZATION AND MODALITIES

The first radiation of the fasciculiths is not about transitional forms between the genera that participated in it. Rather it concerns the sequential appearances of important morphostructural groups that can be shown to consist of homologous structural units on the basis of shared characters that are exclusive to them. Our interpretation thus results from a methodological mix of cladistics and stratophenotypy. The discovery of *Diantholitha* was significant in this regard; it showed that the column and calyptra of biantholiths have expanded during phylogeny, confirming previous inferences that fasciculiths were derived from biantholiths (e.g., Prins, 1971; Romein, 1979).

The first radiation of the fasciculiths involved coccoliths belonging to three morphostructural groups (Fig. 3): biantholiths, fasciculiths and sphenoliths. The first group diversified; the second group appeared and diversified very rapidly (i.e., radiated); the last group appeared but did not diversify in earnest until the Early Eocene.

Biantholiths (species *Biantholithus sparsus*) evolved imme-

diately after the Cretaceous/Paleogene boundary. These are disc-shaped, circular in proximal and distal view. Their column and calyptra are of similar diameter and thickness (Fig. 4). The biantholiths of *Diantholitha mariposa* are similar to those of *Biantholithus sparsus*, except for being much thicker. Both consist of two homologous, monocyclic structural units that are easily related to one another. The evolution of *Diantholitha* from *Biantholithus* entailed the distal and proximal expansions of, respectively, the calyptra and the column. Diversification within *Diantholitha* essentially involved the broadening of the calyptra and differential orientation of its elements.

The fasciculiths of *Lithoptychius* differ from biantholiths in several structural characters. They consist of four structural units (column, calyptra, collaret, central body; Fig. 4). Their evolution involved the thickening of the disc-shaped column of biantholiths into the cylindrical column characteristic of fasciculiths. In comparison the calyptra evolved little from biantholiths to fasciculiths. In the oldest species of *Lithoptychius* it is thicker than in *Biantholithus* spp. The main difference between biantholiths and these older fasciculiths is the presence of the collaret, a distinct cycle with dextrally imbricate elements as seen in distal view. Morphologic diversification in *Lithoptychius* affected mostly the shape of the calyptra and collaret and their relative proportions, but also the shape and size of the central body, and the shape of the column.

Sphenoliths evolved from biantholiths. The relationship between these two morphostructural groups is less readily established than between biantholiths and fasciculiths. The elements of the column and calyptra are imbricate in opposite fashion in the two groups, implying deep re-organization during the evolutionary transition (Aubry, in press).

Biantholiths remained little diversified until their disappearance near the Paleocene/Eocene boundary (Aubry, 1998), but the late Danian radiation of the Discoasterales is rooted in them. They gave rise to the dominant coccolithophores of the Paleocene, from *Lithoptychius* to *Fasciculithus* (that led to the second radiation of the fasciculiths in the late Paleocene), itself at the origin of *Heliolithus* from which the successful genus *Helio-discoaster* arose (Aubry, in press). *Sphenolithus* also diversified considerably, forming a significant component of coccolithophore communities until the mid-Pliocene.

5.2 CAUSAL MECHANISMS FOR THE FIRST RADIATION OF THE FASCICULITHS

The radiation event in Qreiya 1 provides an opportunity to examine a possible relation with the Neo-Duwi beds. It has been suggested that these beds reflect a global change in sea level (Speijer et al., 2003; Guasti et al., 2005) and possibly also a Paleocene hyperthermal with injection of isotopically light carbon in the ocean atmosphere system (Bornemann et al., 2009; Sprong et al., 2011). The isotopic data we present here do not support the latter view. The concentration of organic C through most of the section at Gebel Qreiya varies between 0.3 and 0.6 wt %. There are 2 prominent increases in concentration to 7.4 and 4.8 wt % about 1.2 and 1.4 m above

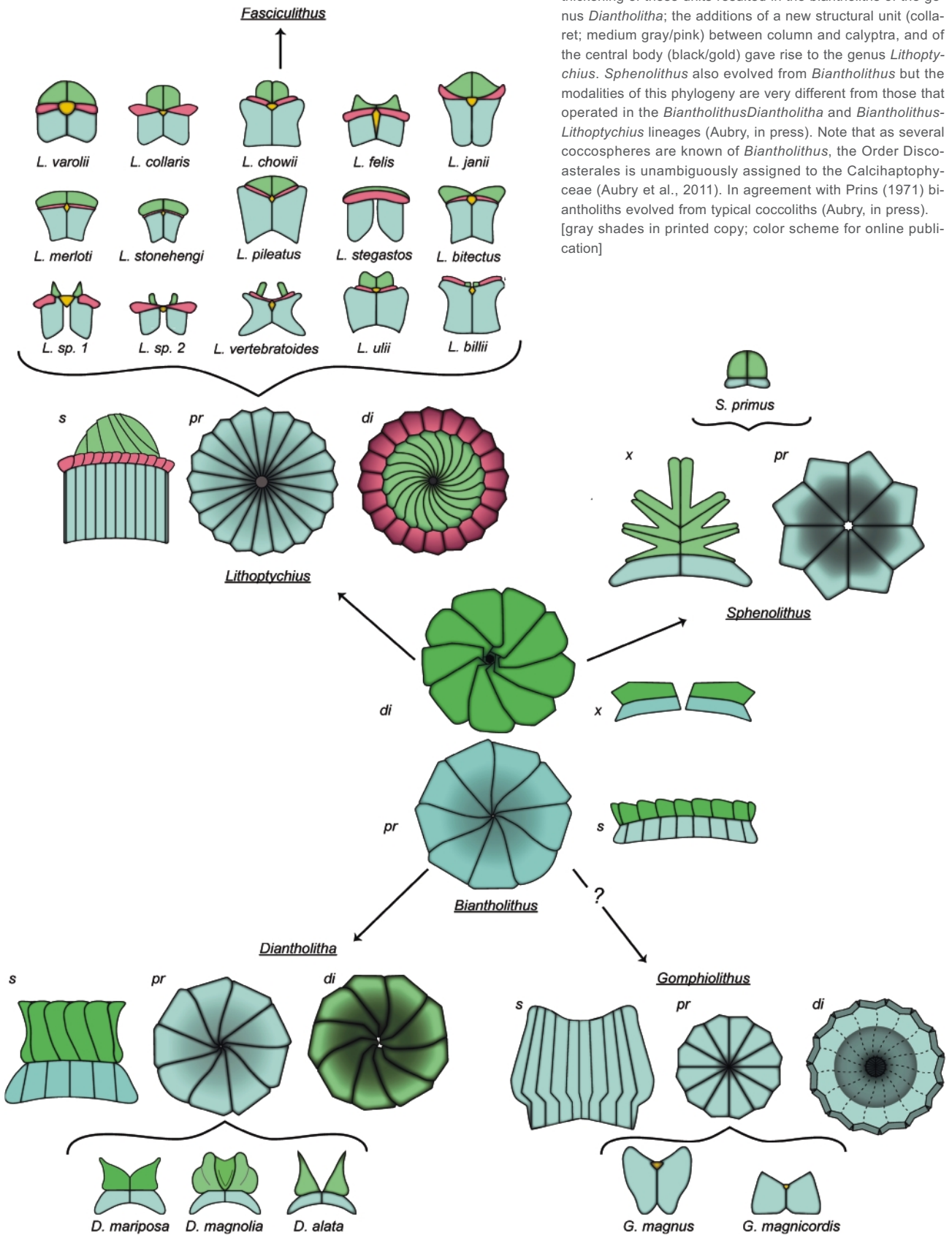
the base of the Dakhla Shale Formation and in the Neo-Duwi beds, respectively, and a third much smaller increase in organic C concentration occurs another 0.8 m up-section. The sediments that contain the highest concentrations of organic C have $\delta^{13}\text{C}$ compositions that are 1.5 to 2 per mil enriched in ^{13}C relative to a background of -26 to -25 ‰. These organic-rich sediments contain plant fragments and scattered coprolites (which were avoided in sampling for organic C analyses) demonstrating increase deposition of terrestrial matter. The coincidence of low $\delta^{18}\text{O}$ in carbonate further suggests increased fluvial input, as it is possible that if this caused an increase in nutrient availability, increase productivity could have led to an increase in marine organic $\delta^{13}\text{C}$ (Eek et al., 1999). However, at 9.42 m, a high C/N ratio was measured (65.4 whereas elsewhere in the section the ratios vary between 5 and 12) suggesting that an increased contribution of terrestrial organic matter was the primary driver increasing $\delta^{13}\text{C}_{\text{org}}$. The excursion to higher $\delta^{13}\text{C}$ compositions does not support addition of ^{12}C -enriched CO_2 to the atmosphere-ocean that has been suggested as an explanation of the $\delta^{13}\text{C}$ minima in carbonate that have been observed here (Bornemann et al., 2009). Consequently, the minimum in carbonate $\delta^{13}\text{C}$ is most likely caused by deposition of carbonate cements incorporating ^{13}C depleted C derived from remineralized organic matter during diagenesis (Allen and Matthews, 1977; Hudson, 1977).

Although significant changes in the composition of the planktonic foraminiferal assemblages were noted at the base of the Neo-Duwi beds (Soliman and Obaidalla, 2010) no changes were recorded in this group at level 7.1 m of Qreiya 1, i.e., the level where the initiation of the first radiation of the fasciculiths is recorded. The radiation of the Order Discoasterales occurs at Qreiya within uniform lithologies (units 4 to 7) and is clearly unrelated to the Neo-Duwi Event however significant this event was. The LOs of the oldest representatives of the radiation (*Diantholitha mariposa* and *Lithoptychius collaris*) are located, respectively, >2 m and ~1 m below the Neo-Duwi beds. The LO of *Sphenolithus primus* is > 2 m above the Neo-Duwi beds. We do not have the means currently to determine the duration between these events in the Qreiya section. The oldest are <0.2 and 0.1 Myr if rates of sedimentation (~1 cm/10³ yr) for oceanic oozes are used, which is likely too low for shales (but see discussion in Soliman and Obaidalla, 2010).

5.3 THE LATE DANIAN ADAPTIVE RADIATION OF THE DISCOASTERALES

The late Danian diversification of the planktonic foraminifera has been firmly linked to increased oligotrophy (e.g., Boersma et al., 1987; Coxall et al., 2006), the acquisition of photosymbionts representing adaptation by non-spine (muricate) taxa to low nutrient conditions. By association, the radiation of the Order Discoasterales has also been thought to reflect intensification of oceanic oligotrophy during the Paleocene (Aubry, 1998; Fuqua et al., 2008), although no adaptive mechanism has been proposed. The functional morphology of coccoliths is generally poorly understood (Young, 1994; Young et al., 2009),

FIGURE 4: Morphostructural diversification in the Order Discoasterales associated with the First radiation of the fasciculiths near the Danian/Selandian boundary. "Second radiation of the fasciculiths" (Bernaola et al., 2009) is another name for this event. Justification for using the first expression is given in Aubry et al. (2011). *Fasciculith* is a morphostructural term that designates the coccoliths secreted by the genera *Lithoptychius*, *Fasciculithus* and *Gomphiolithus* [the latter two not discussed here although *Gomphiolithus* is illustrated]. Although they were first assigned to *Fasciculithus*, the coccoliths of *Diantholitha* are not fasciculiths. The coccoliths (biantholiths) of *Biantholithus* consist of two monocyclic structural units, the (proximal) column (dark gray/blue) and (distal) calyptra (light gray/green). The thickening of these units resulted in the biantholiths of the genus *Diantholitha*; the additions of a new structural unit (collaret; medium gray/pink) between column and calyptra, and of the central body (black/gold) gave rise to the genus *Lithoptychius*. *Sphenolithus* also evolved from *Biantholithus* but the modalities of this phylogeny are very different from those that operated in the *Biantholithus*/*Diantholitha* and *Biantholithus*/*Lithoptychius* lineages (Aubry, in press). Note that as several coccospheres are known of *Biantholithus*, the Order Discoasterales is unambiguously assigned to the Calcihaptophyceae (Aubry et al., 2011). In agreement with Prins (1971) biantholiths evolved from typical coccoliths (Aubry, in press). [gray shades in printed copy; color scheme for online publication]



but the suggestion that coccoliths may be food traps has opened new possibilities for understanding adaptive radiations (Aubry, 2009). The *Qreyia* record sheds new light on the relationship between evolutionary radiation and oligotrophy. The first radiation of the fasciculiths is associated with an increase in volume of coccoliths, but even more clearly and importantly, with an increase of the surface of the coccoliths (Fig. 4). The evolution of *Diantholitha* from *Biantholithus* is the first evidence of a substantial increase in the surface area of coccoliths for enhanced contact with sea-water. The next step in this trend is the acquisition of the collaret in *Lithoptychius*. The evolution of sphenoliths (directly from biantholiths, Aubry, in press) is further evidence of selection for maximum contact with sea-water. Sphenoliths are composed of unusual elements arranged so as to delineate deep alveoli in the calyptra and deep furrows in the column (Aubry, in press; during diagenesis, the alveoli are filled with secondary calcite whereas the original elements are dissolved). Selection for increased surface area of the coccoliths in the Order Discoasterales is further exemplified by the late Paleocene evolution of the fasciculiths of *Fasciculithus* from those of *Lithoptychius*. This involved the loss of the collaret but the acquisition of deep alveoli all over the column of the fasciculiths (Aubry, in press), resulting in unprecedented morphologic convergence in sister families (Aubry, 2011).

In the light of the evidence presented above, it would seem reasonable to interpret biantholiths, fasciculiths and sphenoliths as food collectors. In this perspective, the sequential divergences of the coccoliths of *Diantholitha*, *Lithoptychius* and *Sphenolithus* from *Biantholithus* represent a marked trend towards increased efficiency at gathering food particles, a trend that would only strengthen through the late Paleocene (Aubry, 2011; Berggren and Aubry, 2011). We conclude that the first radiation of the fasciculiths represents the first stage in the long history of the Cenozoic families of the Order Discoasterales at enhancing mixotrophic capabilities in an ever-changing ocean.

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