



A high-resolution late Paleocene–early Eocene organic-walled dinoflagellate cyst zonation of the United States Atlantic Coastal Plain

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Abstract. Over the past decades, many expanded sedimentary records from the US Atlantic Coastal Plain (ACP) have been studied in detail to assess causes and consequences of the Paleocene–Eocene Thermal Maximum (PETM; ~56 Ma). In ACP sections, the PETM, which is globally marked by a distinct negative carbon isotope excursion (CIE) lasting ~180 kyr following a large input of ¹³C-depleted carbon into the ocean–atmosphere system, has been recorded near the base of the Marlboro Clay. However, truly detailed site-to-site correlations within the CIE interval remain difficult in view of the absence of suitable stratigraphic markers offering the required resolution. Here, augmenting earlier studies involving various other marine microfossil groups, we present a high-resolution regional organic-walled dinoflagellate cyst (dinocyst) zonation scheme covering the uppermost Paleocene to lowermost Eocene sediments of the Aquia and Marlboro Clay formations at six ACP localities. We propose five latest Paleocene (ACP Pv–Pz) and six earliest Eocene (all within the PETM interval; ACP E0a–E0f) regional informal dinocyst zones. In addition, we emend the genus *Hystrichokolpoma* and employ several new species, of which four, viz. *Impagidinium witmeri* sp. nov., *Nematosphaeropsis elongatus* sp. nov., *Hystrichokolpoma heroldiae* sp. nov., and *Cannosphaeropsis frielingii* sp. nov., are formally described. Furthermore, we calibrate the dinocyst zones against magneto-, bio-, and ecostratigraphic records to allow robust regional correlation and age assessments with an average time resolution of < 10⁵ years for the late Paleocene and < 10⁴ years within the PETM interval. The scheme provides new opportunities for portraying the environmental and sedimentological evolution across the US Atlantic Coastal Plain during the PETM in unprecedented detail.

1 Introduction

The “Paleocene–Eocene Thermal Maximum”, or PETM interval (~56 Ma), is a distinct, geologically short-lived interval marked by strong global warming and a pronounced negative stable carbon isotope excursion (CIE) in the global exogenic carbon pool (Dickens et al., 1995; Kennett and Stott, 1991; McInerney and Wing, 2011). The CIE comprises three phases: a 1–5 kyr “onset phase” (Kirtland Turner et al., 2017; Zeebe et al., 2016), followed by a 100–170 kyr

“CIE body” (Giusberti et al., 2007; Zeebe and Lourens, 2019) and a 30–145 kyr “recovery phase” (Bowen and Zachos, 2010; Piedrahita et al., 2025; Röhl et al., 2007). On the US Atlantic Coastal Plain (ACP), the PETM is associated with increased runoff from land, eutrophication (Sluijs and Brinkhuis, 2009), deoxygenation (Stassen et al., 2015) (Babila et al., 2016; Robinson and Spivey, 2019), sea level rise (Sluijs et al., 2008), ocean warming (John et al., 2008; Sluijs et al., 2007; Zachos et al., 2006), acidification, and stratification (Babila et al., 2016), all reflecting a general intensifica-

tion of the hydrological cycle (Carmichael et al., 2017; Kopp et al., 2009; Rush et al., 2021; Self-Trail et al., 2017; Sluijs and Brinkhuis, 2009; Stassen et al., 2012, 2015).

To better understand aspects of the global carbon cycle perturbation and concomitant climate change during the PETM, many stratigraphically expanded sections along the ACP in New Jersey, Maryland, Delaware, and Virginia have been extensively studied over the past decades (Fig. 1a) (e.g., Gibbs et al., 2006b; Sluijs et al., 2007; see overview in Robinson et al., 2024). The Virginia/Maryland sites are situated near a major outflow of the “paleo-Potomac” River (Fig. 1). The New Jersey sites are situated near the “paleo-Susquehanna” River (Fig. 1). Generally, the sediment load of these paleo-rivers to the ACP during the late Paleocene was low, and average sedimentation rates were $< 1 \text{ cm kyr}^{-1}$ (Cramer et al., 1999; Kopp et al., 2009; Lyons et al., 2019; Stassen et al., 2012). During the PETM, sedimentation rates increased by approximately 10-fold (e.g., John et al., 2008; Kopp et al., 2009; Li et al., 2022; Stassen et al., 2012). Sites proximal to the paleo-Potomac River, such as Mattawoman Creek–Billingsley Road (MCBR) and Oak Grove, were subjected to even higher temporal sediment supply compared to the more distal New Jersey sites (Babila et al., 2022; Kopp et al., 2009; Poag and Sevon, 1989; Self-Trail et al., 2017).

This shift towards a river-dominated setting during the PETM is marked by the widespread onset of the silty clay of the Marlboro Clay (Cramer et al., 1999; Gibbs et al., 2006b; Gibson et al., 2000). The PETM sections in the Marlboro Clay are considered to have an expanded “CIE onset” in up-dip sites and an expanded “CIE body” in the more distal sites due to progradation of sediments (op. cit. Podrecca et al., 2021; Robinson et al., 2024). The completeness of the PETM sections varies along the ACP due to the presence of unconformities between the Marlboro Clay and the up to 2 Myr younger overlying post-PETM sediments (e.g., John et al., 2008; Doubrawa et al., 2022).

The several-meters-thick PETM successions of the Marlboro Clay from the ACP provide a unique opportunity to study paleoenvironmental changes on the shelf during the PETM at decadal- to millennial-scale resolution. Indeed, as mentioned, the past decade has seen a large volume of studies targeting the chrono-biostratigraphic and paleoenvironmental analysis of these successions in various boreholes and outcrops at many locations. So far, biostratigraphic analyses (Gibbs et al., 2006b; Stassen et al., 2012) have primarily focused on calcareous microfossils (Aubry, 1996; Martini, 1971). However, these calcareous fossil groups have not achieved the stratigraphic resolution necessary to support the high-resolution correlation of PETM intervals across the inshore-to-offshore transect. Integrated marine palynological analysis, emphasizing organic-walled dinoflagellate cysts (dinocysts), has been shown to be particularly useful for biostratigraphic and paleoenvironmental assessment in these cases, as these microfossils are particularly well suited for marginal marine to terrestrial (including lacustrine) settings

and “land-sea correlation” (Frieling and Sluijs, 2018; Iakovleva et al., 2021; Pross and Brinkhuis, 2005; Vieira and Jolley, 2020). While previous studies indicate that the US Coastal Plain PETM sections are indeed rich in organic-walled microfossils suitable for high-resolution correlations between sites in New Jersey (e.g., Sluijs and Brinkhuis, 2009), no truly integrated studies present a basin-wide overview so far. Here, we aim to extend the earlier studies and employ quantitative dinocyst analysis to establish a robust, highly resolved, and well-calibrated regional zonation scheme allowing detailed infra-PETM site-to-site correlations. Such a scheme should provide a solid basis for future integral quantitative palynological analysis also involving the other co-occurring remains of aquatic algae and sporomorphs.

2 Materials and methods

2.1 Materials

The Salisbury Embayment comprises a southern domain, which includes Maryland, Virginia, and Delaware, and a northern domain in New Jersey (Fig. 1). We selected two sites from Maryland for analysis, viz. Mattawoman Creek–Billingsley Road (MCBR) and South Dover Bridge (SDB), and a site from Virginia (Oak Grove). Additionally, we revisited two sites from an earlier study from New Jersey, Wilson Lake and Bass River (Sluijs and Brinkhuis, 2009), and added another site from this area (Clayton). Bass River was drilled as part of Ocean Drilling Program (ODP) Leg 174AX (Miller et al., 1998). All other sites were drilled by the United States Geological Survey (USGS) (Gibson et al., 1993; Reinhardt et al., 1980; Self-Trail, 2011; Self-Trail et al., 2017; Stassen et al., 2012) (Table 1).

Generally, the upper Paleocene deposits consist of grayish-green clayey and glauconitic quartz sands of the Aquia Formation in the southern and central part of the Salisbury Embayment (Virginia and Maryland) and the Vincentown Formation in the northern part (Delaware and New Jersey) (Gibson and Bybell, 1994b; Liu et al., 1997). The lowermost Eocene deposits are marked by the widespread distribution of fine-grained silty clayey marine sediments referred to as the Marlboro Clay (Bybell and Gibson, 1991; Gibson et al., 1980, 2000). Typically, an unconformity separates the Marlboro Clay from the overlying glauconitic quartz sands of the lower Eocene Nanjemoy Formation (Maryland/Virginia) (Self-Trail, 2011) and the lower Eocene Manasquan Formation (New Jersey) (Cramer et al., 1999). However, the expression of the lowermost Eocene (PETM) varies among sites across the Salisbury Embayment, and several stratigraphic gaps have been recognized at these unconformities (Cramer et al., 1999; Gibbs et al., 2006a; Gibson et al., 1993). Moreover, due to these unconformities, the completeness of the PETM interval varies between sites. In particular, the PETM “recovery interval” is often truncated near the top. Typically, New Jersey sites are more complete compared to the Mary-

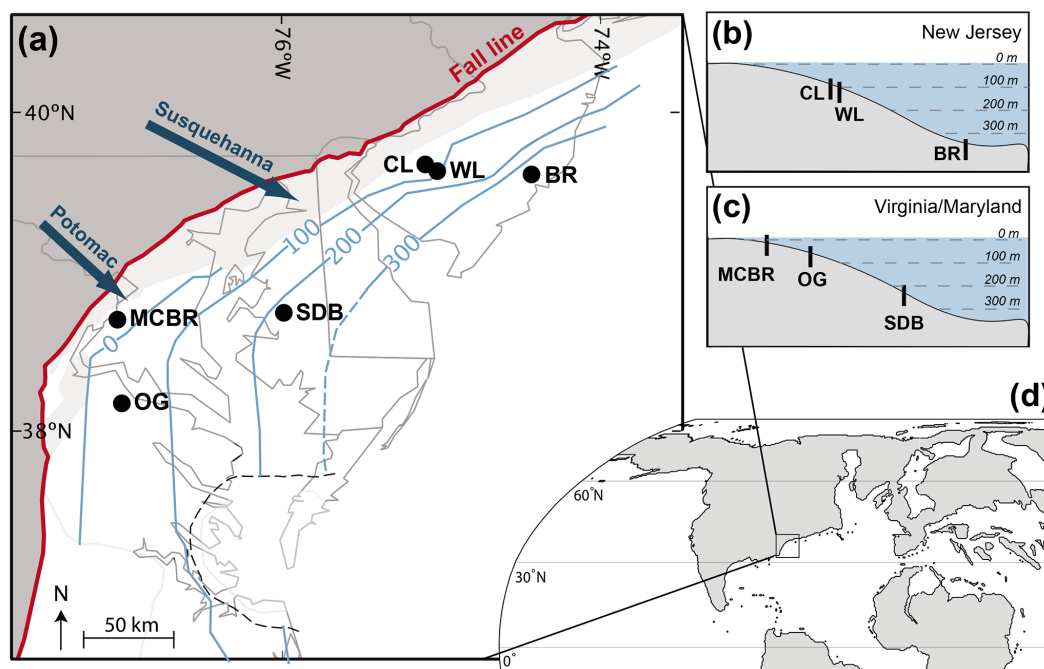


Figure 1. Map of the US Atlantic Coastal Plain and studied sites. **(a)** Map showing location of the six studied sites: Oak Grove (OG), Mattawoman Creek–Billingsley Road (MCBR), South Dover Bridge (SDB), Clayton (CL), Wilson Lake (WL), and Bass River (BR). Blue isopach lines indicate the depth below sea level of the Marlboro Clay from Kopp et al., 2009. The fall line is indicated by the red line. Approximate location of the “paleo-Potomac” and “paleo-Susquehanna” indicated by arrows (modified from Poag and Sevon, 1989; Kopp et al., 2009). Figure modified from Kopp et al. (2009). **(b, c)** Cross-section of the New Jersey sites **(b)** and Maryland/Virginia **(c)** showing the inshore-to-offshore transect. Depths indicate the depth below sea level of the Marlboro Clay from Kopp et al. (2009). The exact water depths have not been constrained and may have varied substantially during the PETM. Nevertheless, these illustrate the inshore-to-offshore transect on which these sites are located. **(d)** Plate configuration at 56 Ma and location of the Atlantic Coastal Plain, modified from Carmichael et al. (2017).

land and Virginia sites, typically containing an interval assigned to the upper NP10 calcareous nannoplankton zone (Self-Trail, 2011; Self-Trail et al., 2012).

To assess the potential of the dinocyst distribution within the selected sections for regional correlation, we first compiled all previously published information regarding the lithology, biozones, carbon isotope data, and other chrono- and biostratigraphic constraints for the six studied sites, discussed below (see also Table 1).

2.1.1 Mattawoman Creek–Billingsley Road (MCBR)

At MCBR, the upper Paleocene Aquia Formation consists of glauconite-rich quartz sands overlain by laminated gray–red-brown very fine sandy silt to silty clay of the Marlboro Clay (Self-Trail et al., 2017). The boundary between these formations is placed at 12.16 m (Self-Trail et al., 2017). Records of $\delta^{13}\text{C}_{\text{bulkcarb}}$ show a -26‰ shift over a 2 m interval, interpreted to reflect the CIE onset (Self-Trail et al., 2017). The Marlboro Clay at MCBR contains a stacked succession of muddy packages with internal laminations, interpreted to represent episodic deposition from river-derived sediments (Self-Trail et al., 2017). Earlier palynological analyses re-

vealed that strata with coarser sediments at MCBR are nearly barren of dinocysts, but common *Apectodinium* spp. and *Phthanoperidinium crenulatum* are encountered in the top part of the Marlboro Clay (Self-Trail et al., 2017). The latter has been proposed to serve as a local marker species to correlate sites in the Salisbury Embayment, as this species was also recorded from SDB (Self-Trail et al., 2017). In addition to dinocysts, planktic foraminifera and calcareous nannoplankton abundances were previously used to stratigraphically correlate between the SDB and MCBR sites (Self-Trail et al., 2017). At MCBR, this is complicated by the absence of CaCO_3 in the lowest 2.3 m of the Marlboro Clay (Self-Trail et al., 2017), which was correlated to a similar carbonate-free 1.3 m thick interval in SDB (Self-Trail et al., 2012). At MCBR, six cores were drilled. In this study, we analyzed samples from MCBR-1 and MCBR-2, with samples from MCBR-2 being supplemented by MCBR-1 to include upper Paleocene sediments. In total, 34 samples were analyzed: 26 samples from MCBR-1 and 8 samples from MCBR-2 (see Nelissen et al., 2025).

Table 1. Overview of the drilled sites, with coordinates and dates, and references for the lithologic descriptions, zonation schemes, and carbon isotope values used in this study.

	Site	Drilled	Coordinates	Lithology	Zonation	Carbon isotope
Maryland/Virginia	MCBR	USGS, 2011/12	38°36′ N, 77°02′ W,	Self-Trail et al. (2017)	–	$\delta^{13}\text{C}_{\text{bulkcarb}}$: Self-Trail et al. (2017)
	Oak Grove	USGS, 1976	38°10′ N, 77°2′ W	Reinhardt et al. (1980)	Gibson et al. (2000)	–
	SDB	USGS, 2007	38°44′ N, 76°0′ W	Doubrawa et al. (2022), Self-Trail et al. (2012)	Self-Trail et al. (2012)	$\delta^{13}\text{C}_{\text{bulkcarb}}$: Self-Trail et al. (2012) $\delta^{13}\text{C}_{\text{bulkorg}}$: Lyons et al. (2019)
New Jersey	Clayton	USGS, 1977	39°39′ N, 75°03′ W	Gibson et al. (1993)	Gibson et al. (1993)	$\delta^{13}\text{C}_{\text{bulkcarb}}$: Stassen et al. (2012), Kent et al. (2003)
	Wilson Lake	USGS, 2000	39°39′ N, 75°03′ W	Gibson et al. (2000), Gibbs et al. (2006b)	NP: Gibbs et al. (2006a), Stassen et al. (2012)	$\delta^{13}\text{C}_{\text{bulkcarb}}$: Zachos et al. (2006) $\delta^{13}\text{C}_{\text{dino}}$: Sluijs et al. (2007)
	Bass River	ODP Leg 174AX, 1996	39°36′ N, 74°26′ W	Cramer et al. (1999), Miller et al. (1998)	NP: Gibbs et al. (2006a), Aubry et al. (2000), Stassen et al. (2012)	$\delta^{13}\text{C}_{\text{bulkcarb}}$: John et al. (2008) $\delta^{13}\text{C}_{\text{dino}}$: Sluijs et al. (2007)

2.1.2 Oak Grove

In the Oak Grove core, the contact between the glauconitic sands of the Aquia Formation and the Marlboro Clay was placed at a depth of 103.6 m based on lithologic changes (Reinhardt et al., 1980). The overlying Nanjemoy Formation was placed at a depth of 98.2 m (Reinhardt et al., 1980). To date, there are no carbon isotope data available from the Oak Grove site. In the Aquia Formation calcareous nannofossil Zone NP9 was identified in samples from 108.8 to 103.9 m, but the Marlboro Clay was barren of calcareous nannofossils (Gibson et al., 2000). Zone NP10 was recorded in the Nanjemoy Formation between 97.4 and 92.4 m (Bybell et al., 2021; Gibson et al., 2000).

We included the palynological analyses from Oak Grove from the unpublished PhD thesis of Roger J. Witmer (Witmer, 1987, Virginia Polytechnic Institute and State University). His thesis includes counts and photoplates, allowing us to ensure taxonomic consistency between his work and our study. A total of 29 samples from his thesis are included in the present study (nos. 303 to 331; Witmer, 1987), which include 17 samples from the Aquia Formation (103.5 to 138.9 m), 5 samples from the Marlboro Clay (98.4 to 102.1 m), and 7 samples above that interval (up to 79.6 m). We scanned 20 additional slides from Oak Grove ranging between 61.72 and 137.65 m (Frederiksen, 1979) for presence or absence.

2.1.3 South Dover Bridge (SDB)

At SDB, the contact between the glauconitic quartz sands of the Aquia Formation and the silty clays of the Marlboro Clay is placed at 204.0 m (Self-Trail, 2011). Within the Aquia Formation, a clay-rich layer preserves a recently recognized “pre-PETM onset” stable isotope excursion (POE), interpreted to reflect a similar excursion reported by Bowen et al. (2015) from 206.7 to 205.9 m, marking a 1‰–1.5‰ negative $\delta^{13}\text{C}$ excursion in bulk carbonates (Babila et al., 2022; Lyons et al., 2019; Self-Trail et al., 2012). The CIE is constrained by a −4‰ $\delta^{13}\text{C}_{\text{bulkcarb}}$ excursion between 204.2 and 204.0 m and stable low carbon isotope values up to 190.5 m (Self-Trail et al., 2012). Bulk $\delta^{13}\text{C}_{\text{org}}$ data show a similar trend with decreasing values in the first meter from the CIE onset. Higher values within the body of the CIE were attributed to fossil carbon reworked into the organic carbon pool (Lyons et al., 2019). Above the main body interval, $\delta^{13}\text{C}_{\text{bulkcarb}}$ values gradually increase towards the unconformable contact with the Nanjemoy Formation at 188.4 m (Self-Trail et al., 2012). The overlying Nanjemoy Formation is lithologically similar to the Aquia Formation and consists of silty glauconitic and quartz sands, often intensely burrowed (Gibson and Bybell, 1994b).

Previous palynological analyses employed the top of the dinocyst species *Apectodinium augustum* and the base of *Phthanoperidinium crenulatum* (Self-Trail et al., 2017) as local marker species to correlate sites in the Salisbury Em-

bayment. Calcareous nannofossils at SDB placed the Aquia Formation in Zone NP9a, which ranges up into the Marlboro Clay and is followed by a thin interval containing the first occurrence of excursion taxa (Zone NP9b). Zone NP10 ranges up into the Nanjemoy Formation (Self-Trail, 2011). The Nanjemoy Formation represents calcareous nannofossil zones NP10 through NP13 (Gibson and Bybell, 1994a). We analyzed a total of 64 samples from SDB ranging between 182.64 and 210.02 m.

2.1.4 Clayton

At Clayton, the uppermost Paleocene sediments of the Vincetown Formation consist of glauconite-bearing bioturbated siltstones that gradually transition into the finer-grained Marlboro Clay (Gibson et al., 1993). The onset of the CIE in $\delta^{13}\text{C}_{\text{bulkcarb}}$ is between 97.7 and 97.8 m, and low $\delta^{13}\text{C}$ values remain up to the erosional contact at the base of the Shark River Formation at 88.7 m (Gibson et al., 1993; Kent et al., 2003; Stassen et al., 2012). Initially, calcareous nannoplankton Zone NP8 was documented from the Vincetown Formation at 106.7 m, Zone NP9 was documented in samples between 99.1 and 94.5 m, Zone NP10 was documented in samples between 93.0 and 88.7 m, and Zone NP14 was documented from the Shark River Formation (Gibson et al., 1993). These NP zones were later refined into subzones NP9a and NP9b based on the first occurrence of excursion taxa, while Zone NP14 was recognized in the Shark River Formation above the unconformity (Stassen et al., 2012). No previous palynological data have been published from Clayton to our knowledge. We analyzed a total of 62 samples between 89.02 and 107.3 m.

2.1.5 Wilson Lake

At Wilson Lake, the boundary between the Vincetown Formation and the Marlboro Clay is marked by a transition from glauconitic clayey sandstones below to silty claystones at ~ 109.5 m (Gibbs et al., 2006b; Stassen et al., 2012). The absence of carbonate between 109.5 and 109.9 m hampers precise placement of the CIE onset based on $\delta^{13}\text{C}_{\text{bulkcarb}}$ (Zachos et al., 2006). Eventually, it was placed at approximately 110 m based on dinocyst $\delta^{13}\text{C}_{\text{dino}}$ records (Sluijs et al., 2007). Bulk carbonate data (Zachos et al., 2006) and dinocyst $\delta^{13}\text{C}_{\text{dino}}$ data record low values up to the unconformity at 96.32 m. The Manasquan Formation, which overlays the Marlboro Clay, consists of yellow-green to olive-green calcareous clays to fine sands (Gibson et al., 2000). Calcareous nannoplankton subzone NP9a was identified in the Vincetown Formation followed by NP9b. The boundary between subzones NP9b and NP10a is placed at a depth of around 105.75 m (Stassen et al., 2012).

Previous palynological analyses have documented diverse and rich dinocyst assemblages at Wilson Lake, with marked variations in species abundances during the PETM (Sluijs

and Brinkhuis, 2009). These dinocyst events have previously been used to correlate between Wilson Lake and Bass River (Sluijs and Brinkhuis, 2009). We re-examined 73 samples ranging between 91.51 and 112.76 m to update taxonomy and species occurrences.

2.1.6 Bass River

At Bass River, the uppermost Paleocene sediments of the Vincetown Formation consist of glauconite-bearing siltstones, which are overlain at 356.92 m by the kaolinite-rich Marlboro Clay representing the PETM (Cramer et al., 1999; Miller et al., 1998; Sluijs et al., 2007). Paleomagnetic data documented reversed polarity representing Chron C24r between 346.56 and 363.20 m, and the boundary between C25n and C24r is between 363.20 and 363.63 m (Cramer et al., 1999). Based on $\delta^{13}\text{C}$ records of dinocysts, bulk carbonate, and foraminifera, the depth of the CIE onset was placed at 357.3 m (Cramer et al., 1999; John et al., 2008; Sluijs et al., 2007). The boundary between calcareous nannoplankton zones NP8 and NP9 and subzones NP9a and NP9b were placed at 368.80 m and between 356.95 and 356.89 m, respectively. Subzone NP10b (base) was identified at 346.98 m (Aubry et al., 2000) immediately above an unconformity at 347.05 m, representing the Manasquan Formation/Marlboro Clay contact (Cramer et al., 1999).

Previous palynological analyses have documented diverse and rich dinocyst assemblages at Bass River, with variations in abundances during the PETM (Sluijs and Brinkhuis, 2009). These dinocyst events have previously been used to correlate between Wilson Lake and Bass River (Sluijs and Brinkhuis, 2009). We re-examined the 91 samples ranging between 345.17 and 374.61 m to update taxonomy and species occurrences.

2.2 Palynological processing and counting

We generated new palynological data from South Dover Bridge, Mattawoman Creek–Billingsley Road, and Clayton, and we re-examined slides that were previously analyzed from Bass River and Wilson Lake (Sluijs and Brinkhuis, 2009). In addition, we re-analyzed samples from Oak Grove, augmenting data and images from the unpublished PhD thesis of Witmer (1987), and we scanned 20 slides from the Oak Grove that were processed by Frederiksen (1979). See his publication for full preparation details.

Samples from MCBR and SDB were processed by the USGS. These samples were dried at 60 °C, weighed, and spiked with *Lycopodium* spores for quantitative analyses. HCL and HF were used to remove carbonates and silicates, respectively. Samples were then sieved using 150 and 10 μm mesh sieves. These residues were stained with Bismarck brown and mounted on slides in glycerin jelly.

Samples from Clayton, Wilson Lake, and Bass River were processed following the procedures of Sluijs and Brinkhuis

(2009). Briefly, freeze-dried and pre-weighed samples were spiked with *Lycopodium* spores for quantitative analyses and treated with 30 % HCl and 38 % HF to dissolve carbonates and silicates, respectively. Residues were sieved over a 15 µm nylon mesh and mounted on microscope slides.

Analyses were carried out using a light microscope (Leica DM2500 LED) at 400x magnification, and pictures were taken with a Leica MC170HD. A minimum of 200 dinocysts were counted to ensure a statistically representable assemblage, with an exception for the Oak Grove slides, which were scanned. In some samples from MCBR, dinocyst abundances were too low and 200 counts could not be reached (see Nelissen et al., 2025 for an overview of the number of dinocysts counted per sample). In the abundance plots, we have included all samples with a minimum count of 100 dinocysts. In all samples with counts < 100 dinocysts, we indicated the presence of taxa with an X in Nelissen et al. (2025). We adhere to the taxonomy cited in Fensome et al. (2019), except for wetzeliielloid taxa, for which we follow the recommendations of Bijl et al. (2016).

We describe four new dinocyst species that are of potential stratigraphic importance. Other taxa are left in “open nomenclature” due to their low abundances and/or association with genera that are not well defined, and all these are informally described in the annotated species list (Sect. 6.3). Groups of morphologically related dinocyst species are organized into informal “complexes” (see annotated species list in Sect. 6.3). Importantly, for the purpose of this work, we use different complexes compared to Sluijs and Brinkhuis (2009), for example. Relative abundance data of stratigraphically important dinocyst taxa and groups are available in Nelissen et al. (2025) and in the annotated species list (Sect. 6.3). When species were encountered outside of the counts of Sluijs and Brinkhuis (2009) or outside of regular counts, their presence was indicated with a p (present). All slides and type materials are stored in the collection of the Laboratory of Palaeobotany and Palynology, Department of Earth Sciences, Utrecht University, the Netherlands. For all photoplates, we have indicated the sites with MCBR (Mattawoman Creek–Billingsley Road), SDB (South Dover Bridge), CL (Clayton), WL (Wilson Lake), and BR (Bass River), and we have indicated the average sampling depth in meters for each sample. We used England finder coordinates to give the location of the cyst on the respective slide. An overview of the depths in meters and feet, along with other naming that is used for each slide, is provided in Nelissen et al. (2025).

3 Results

3.1 Atlantic Coastal Plain PETM dinocyst distributions and events

Virtually all samples from the various locations contain rich, diverse, and reasonably preserved to well-preserved palynological assemblages, dominated by dinocysts, various cate-

gories of prasinophyte algae, and sporomorphs. Across the PETM, all sites reveal a high diversity of dinocyst species and large variations in the abundances of various taxa. These variations may be taken to indicate changing paleoenvironmental conditions during the PETM and are in line with previous records from the Bass River and Wilson Lake samples (Sluijs and Brinkhuis, 2009). Importantly, besides quantitative events, our records indicate a large number of consistent first and last occurrences of taxa, including some undescribed ones, among the dinocysts, providing a solid basis for establishing a detailed zonal scheme. Since SDB and Bass River are the most expanded and complete sections, we base the main body of our zonal scheme and calibrations on these sections in particular (Fig. 2). The (informal) zones we erect in this paper are Oppel zones (as in Hedberg, 1976). We employ first occurrences (FOs) and last occurrences (LOs), as well as first and last “consistent occurrences” (FCOs, LCOs), implying the beginning or ending of consistent, continuous presence in a given series of samples. Additionally, we note characteristic taxa and bio-events for these by categorizing abundances of dinocysts as common (1 %–10 %), abundant (10 %–40 %), and very abundant/acme (> 40 %). For these abundances, we only included samples in which a minimum of 100 dinocysts were identified (see Nelissen et al., 2025, for dinocyst counts per sample).

The dinocyst assemblages from SDB, Bass River, and the other sections (Fig. 2) contain several globally recognized late Paleocene–early Eocene index events which allow us to correlate in broad terms to established “global” schemes, such as the one shown by Gradstein and Ogg (2020) (for an overview, see Fig. S1 in the Supplement). For example, the first and last occurrences of the index PETM species *Apectodinium augustum* (Denison, 2021; Steurbaut et al., 2003) are accordingly recognized at both SDB and Bass River (Fig. 2). The FO of *A. augustum* corresponds to the CIE onset at both sites, locally calibrated against the top of calcareous nannoplankton subzone NP9a, matching the global correlations shown in Gradstein and Ogg (2020), for example (Fig. 2).

Furthermore, starting from the lowest section in the Paleocene interval in the Bass River core, the LCO of *Alisocysta margarita* (at Bass River at 370.18 m) corresponds to the upper part of calcareous nannoplankton Zone NP8 and falls in paleomagnetic Chron C25n (Fig. 2), again matching that shown in Gradstein and Ogg (2020). In the Northern Hemisphere, the LCO of *A. margarita* is widely used as a marker species for the late Paleocene. In the UK North Sea sectors, the LO of this species defines the boundary between the late Paleocene subzones Pb5 and P6a (Mudge and Bujak, 1996). In Western Siberia, the *Alisocysta margarita* zone is placed below the *Apectodinium hyperacanthum* zone (Iakovleva and Aleksandrova, 2013). Powell (1992) calibrated the *A. margarita* zone to nannoplankton Zone NP8 in Europe, which is consistent with what is recorded in Bass River.

Above this event, an increase in *Apectodinium* spp. (excluding *A. augustum*) precedes the CIE onset, as recorded

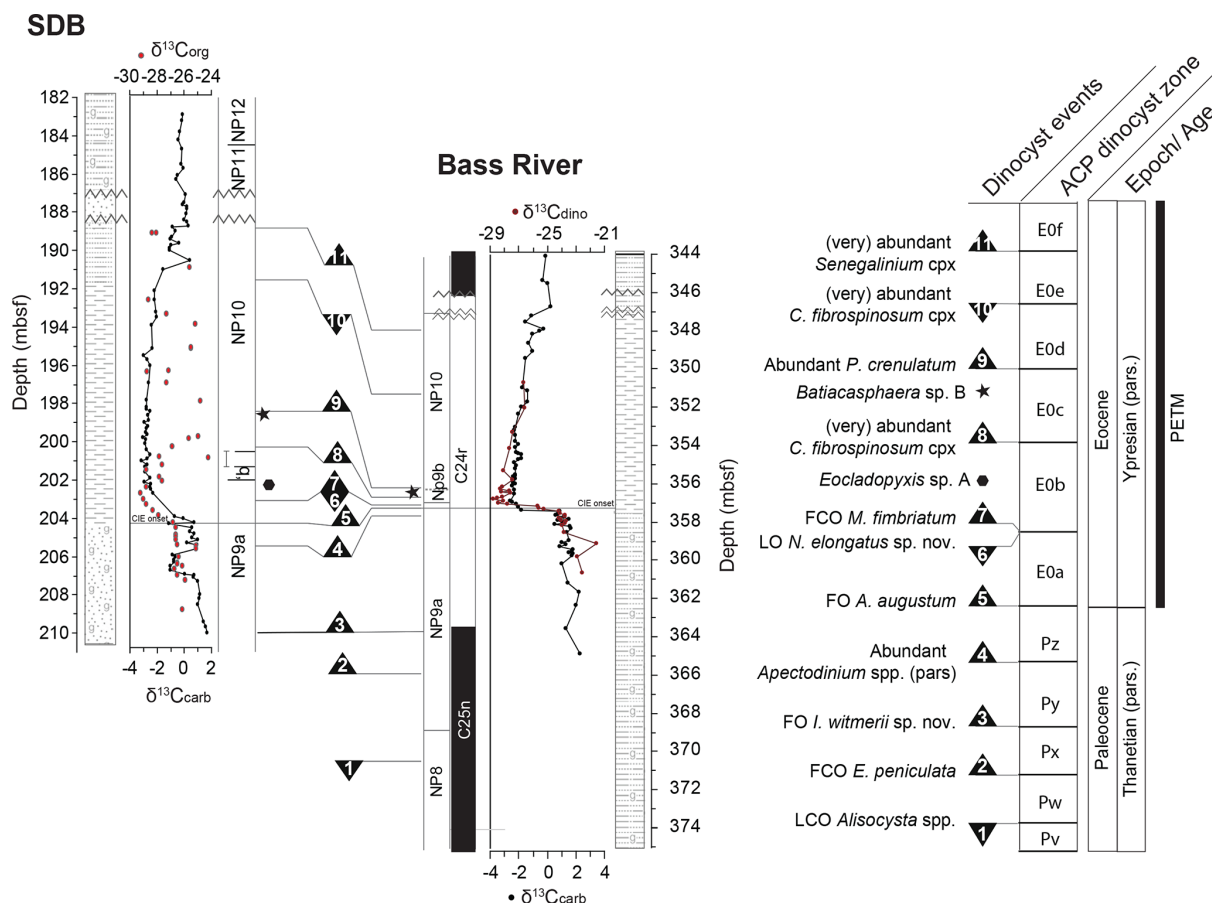


Figure 2. Dinocyst events recorded at South Dover Bridge and Bass River and associated informal ACP dinocyst zones, calibrated against established magnetostratigraphic data, NP zones, and carbon isotope data. From South Dover Bridge (SDB), we show $\delta^{13}\text{C}_{\text{bulkcarb}}$ (Self-Trail et al., 2012) and $\delta^{13}\text{C}_{\text{org}}$ data (Lyons et al., 2019) and the NP zones from Self-Trail (2011). From Bass River, we show the paleomagnetic data with the Chron C24r/C25n reversal (Cramer et al., 1999), $\delta^{13}\text{C}_{\text{bulkcarb}}$ (Cramer et al., 1999; John et al., 2008) and $\delta^{13}\text{C}_{\text{dino}}$ data (Sluijs et al., 2007), and NP zones from Aubry et al. (2000). We show 11 dinocyst events that can be correlated between the two sites, based on the LCO (last consistent occurrence), FCO (first consistent occurrence), FO (first occurrence), and LO (last occurrence) of key taxa, and increases/decreases in relative abundance. For an overview of taxa and complexes, see remarks in the annotated species list in Sect. 6.3. All dinocyst data are available in Nelissen et al. (2025).

in SDB and Bass River (Fig. 2) and previously reported in Sluijs and Brinkhuis (2009), and is often used in global correlations. The genus *Apectodinium* has a first occurrence in the Selandian at low latitude sites (e.g., Awad and Obboh-Ikuenobe, 2016; Brinkhuis et al., 1994) and is usually recorded in the Thanetian at mid- and high-latitude sites (e.g., Crouch et al., 2014; Powell et al., 1996). An acme of *Apectodinium* spp. has been widely recognized in association with the PETM (Bujak and Brinkhuis, 1998; Crouch et al., 2001, 2003; Denison, 2021). In effect, an increase in *Apectodinium* species, notably *A. homomorphum* and *A. hyperacanthum*, is recorded prior to the FO of *A. augustum* and/or the CIE onset at many locations, e.g., the South Pacific (Bijl et al., 2013), Western Siberia (Iakovleva and Aleksandrova, 2013), Kazakhstan (Radionova et al., 2001), the North Sea (Jolley et al., 2022; Mudge and Bujak, 1996; Powell et al., 1996;

Vieira et al., 2020), France (Iakovleva et al., 2021), and the equatorial Atlantic (ODP Site 959; Frieling et al., 2018). The increase we record in SDB and Bass River shows a similar pattern, with the FO of *A. augustum* marking the Paleocene–Eocene boundary and CIE onset. In the North Sea, the first occurrence of *A. augustum* marks the base of subzone P6b (Mudge and Bujak, 1996; Powell et al., 1996). The presence of the species *A. augustum* at the CIE onset at many northern mid- and high-latitude sites, e.g., in Belgium (Steurbaut et al., 2003), New Jersey (Sluijs and Brinkhuis, 2009), Western Siberia (Frieling et al., 2014), and the Arctic (McNeil and Parsons, 2013), further demonstrates the unique value of the range of this species to serve as a marker for the PETM interval.

A subsequent early Eocene global index event is the first occurrence of the iconic Paleogene dinocyst genus *Wet-*

zeliella. Already early on, the FO of *W. articulata* was typically employed in many regional Eocene zonal schemes (Bujak and Mudge, 1994; Iakovleva and Aleksandrova, 2013; Powell et al., 1996), is still functional in Gradstein and Ogg (2020), and is also recognized in the ACP sections (see the overview in Fig. S1 in the Supplement).

3.2 Regional ACP high-resolution Paleocene–Eocene dinocyst events and informal zones

With SDB and Bass River as backbones (Fig. 2), we identified a consistent succession of bio-events at the six sites and employed these to construct a regional US Atlantic Coastal Plain (ACP) dinocyst zonal framework, calibrated against the magnetostratigraphic, carbon isotopic, and biostratigraphic zonal schemes shown in Fig. 2. Moreover, we compare these events to those that were previously used to correlate between Wilson Lake and Bass River (Sluijs and Brinkhuis, 2009). In total, we describe five late Paleocene (Thanetian pars. – ACP Pv–Pz) and six early Eocene (Ypresian, PETM; ACP E0a–E0f) informal dinocyst zones and associated bio-events (Fig. 2).

We chose the name E0 (or “E-zero”) for our suite of successive infra-PETM zones. This to avoid confusion with established North Sea dinocyst zones, in which the (back then earliest, now “early”) Eocene zone, representing post-PETM sediments, was labeled starting with “E1” in 1994 (Bujak and Mudge, 1994) – all this as a consequence of a revised positioning (i.e., lowering) of the Paleocene–Eocene boundary in the early 2000s by the International Commission on Stratigraphy (ICS). Our suite of E0 zones may thus be compared to the P6b subzone of Bujak and Mudge (1994) and Mudge and Bujak (1996), as both are based on the range of *Apectodinium augustum*. Our ACP Eocene regional zones are labeled chronologically starting with the beginning of the alphabet (a–b–c, etc.), while the Paleocene zones are labeled “anti-chronologically” (z–y–x, etc.). This allows future work to expand the Paleocene zonation downward and the Eocene upward. Based on the distributions of key dinocyst taxa, the regional informal zones proposed below have been recognized at all six studied sites where time-equivalence exists (Figs. 3–9; Table 2).

From older to younger, we define the following informal zones.

Regional Paleocene dinoflagellate cyst zone ACP Pv

- Age: Late Paleocene (Thanetian, pars.).
- Reference section: Bass River, Vincetown Formation (374.61–370.41 m).
- Calibration: Magnetostratigraphy: Chron C25n (pars.). Calcareous nannoplankton: NP8 (pars.).
- Definition: The base of the zone is not defined. The top is defined by the base of the LCO of *Alisocysta* spp. (notably

Table 2. Top and bottom depth (meters) of late Paleocene–early Eocene ACP dinocyst zones. Sites shown are Mattawoman Creek–Billingsley Road (MCBR), Oak Grove (OG), South Dover Bridge (SDB), Clayton (CL), Wilson Lake (WL), and Bass River (BR). For the boundaries between two zones, the average depth between two samples was taken. In Nelissen et al. (2025), an overview of all sample depths and zones is provided. Depths in bold show the depth of the sample above which the zone is truncated with an unconformity.

Zone	MCBR	OG	SDB	CL	WL	BR
?					?	?
?			?		93.15	?
			187.1		?	
?			?		94.79	?
					?	
E0f			188.53			347.30
			188.77			347.96
E0e						
			191.45			351.30
E0d					96.94	
			198.31		100.98	356.25
E0c				89.63		
			200.21	93.48	105.76	356.91
E0b	3.92	?				
	4.42	98.95	202.98	97.39	109.50	357.08
E0a						
	11.67	101.8	204.15	97.64	109.99	357.35
Pz						
	13.01	105.45	205.38	98.36	110.48	357.71
Py						
	Bottom	?	209.56	104.71	Bottom	363.81
Px						
			Bottom	105.93		365.99
Pw						
				Bottom		370.18
Pv						
						Bottom

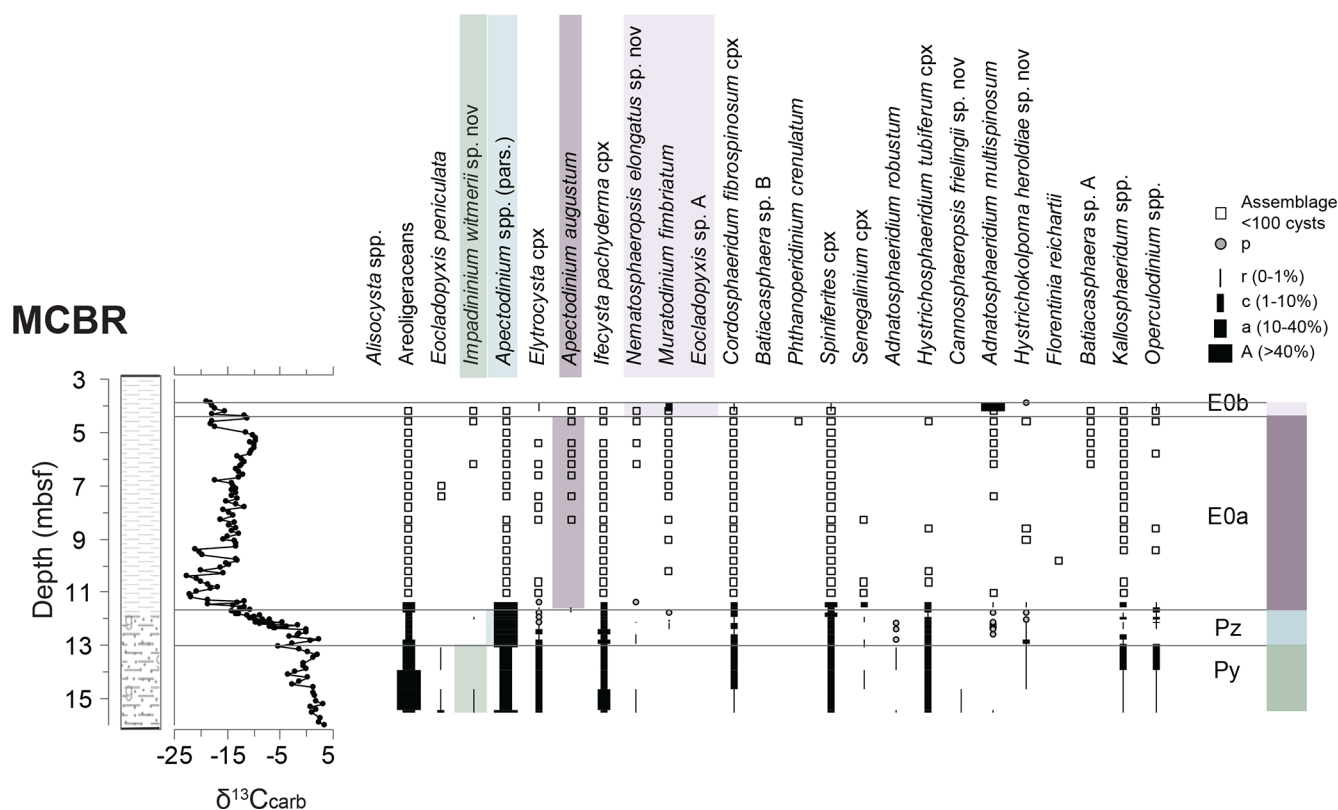


Figure 3. Relative abundances of stratigraphically important dinocyst species and taxa at Mattawoman Creek–Billingsley Road (MCBR). Abundances are indicated by rare (r, 0 %–1 %), common (c, 1 %–10 %), abundant (a, 10 %–40 %), or very abundant/acme (A, > 40 %). When taxa were encountered outside of regular counts, their abundance is indicated with an open gray circle, which means “present”. The relative abundances are plotted only when > 100 cysts per sample were counted. In some samples, dinocyst abundances were too low. In those cases, the presence of taxa is indicated with an open square. $\delta^{13}\text{C}_{\text{carb}}$ bulk carbonate data are from Self-Trail et al. (2017). At MCBR, the dinocyst zones Py to E0b are recognized.

Alisocysta heilmannii (Casas-Gallego et al., 2021), which defines overlying zone ACP Pw.

Characteristic taxa and bio-events: Other characteristic species: abundant to very abundant members of the Areoligeraceans, notably *Areoligera volata*.

Remark: This ACP zone is only recognized at Bass River.

Regional Paleocene dinoflagellate cyst zone ACP Pw

Age: Late Paleocene (Thanetian, pars.).

Reference section: Bass River, Vincetown Formation (369.95–366.20 m).

Calibration: Magnetostratigraphy: Chron C25n (pars.). Calcareous nannoplankton: top Zone NP8 to the bottom of Zone NP9a.

Definition: The base of the zone is defined by the LCO of *Alisocysta* spp. The top of the zone is defined by the FCO of *Eocladopyxis peniculata*, which marks the base of the overlying Px zone.

Characteristic taxa and bio-events: Within this zone, the first occurrence of *Apectodinium* spp., notably *Apectodinium homomorphum*, is recorded. At the base of this zone, repre-

sentatives of the *Spiniferites* complex (cpx) become abundant and remain abundant in this zone. *Elytrocysta* spp. become abundant and show varying abundance within this zone. Representatives of the *Senegalinium* cpx, notably *Senegalinium* spp. and *Deflandrea oebisfeldensis*, become abundant and common within this zone, respectively, before decreasing again near the top. Additionally, an increase in members of the *Hystrichosphaeridium tubiferum* cpx is recorded within this zone.

Remarks: ACP zone Pw is recognized at Clayton and Bass River. At Clayton, *Elytrocysta* spp. become very abundant near the top of this zone, and Areoligeraceans are abundant throughout. At Bass River, the *Spiniferites* cpx is more abundant when compared to Clayton, likely related to coastal proximity (e.g., Sluijs et al., 2008; Sluijs and Brinkhuis, 2009).

Regional Paleocene dinoflagellate cyst zone ACP Px

Age: Late Paleocene (Thanetian pars.).

Reference section: Bass River, Vincetown Formation (365.77–364.04 m).

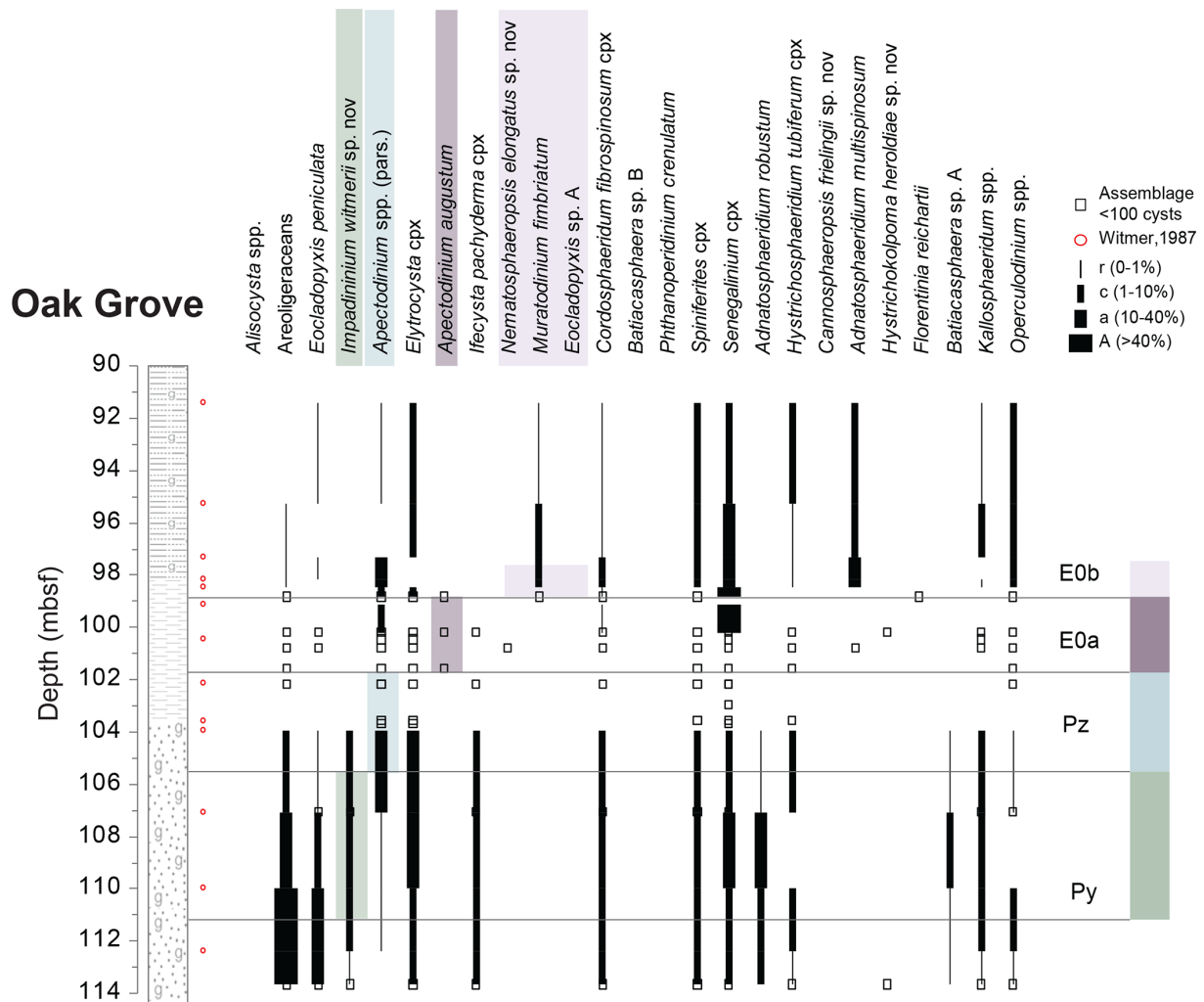


Figure 4. Relative abundances of stratigraphically important dinocyst species and taxa at Oak Grove. Abundances are indicated by rare (r, 0%–1%), common (c, 1%–10%), abundant (a, 10%–40%), or very abundant/acme (A, >40%). The relative abundances are plotted only when >100 cysts per sample were counted. In some samples, dinocyst abundances were too low. In those cases, the presence of taxa is indicated with an open square. Counts from the unpublished PhD thesis of Roger Witmer (Witmer, 1987) are indicated with a red circle. Other data are based on scanned slides from Frederiksen (1979). At Oak Grove, the dinocyst zones Py to E0b are recognized.

Calibration: Magnetostratigraphy: top Chron C25n. Calcareous nannoplankton: mid-subzone NP9a.

Definition: The base of the zone is defined by the FCO of *Eocladopyxis peniculata*, and the top of the zone is defined by the FO of *Impagidinium witmeri* sp. nov.

Characteristic taxa and bio-events: At the base of this zone, Areoligeraceans (notably *Areoligera volata*) become abundant, and the relative contribution of members of the *Spiniferites* cpx decreases. Towards the top of this zone, members of the *Spiniferites* cpx become more abundant. Like zone Pw, representatives of the *Senegalinium* cpx, notably *Senegalinium* spp., become abundant halfway into the zone, to decrease before the top of this zone.

Remarks: ACP zone Px is recognized at SDB, Clayton, and Bass River. At SDB, only one sample (the lowermost

sample studied here) is placed in zone Px, based on the presence of abundant *E. peniculata* and the absence of *I. witmeri* sp. nov. At Clayton, the Areoligeraceans, notably *A. volata*, are (very) abundant within this zone, along with common representatives of *Senegalinium* cpx, notably *Senegalinium* spp., *Spiniferites* cpx, and *Elytrocysta* spp. At Bass River, *Spiniferites* cpx is more abundant compared to the other sites, like Zone Pw.

Regional Paleocene dinoflagellate cyst zone ACP Py

Age: Late Paleocene (Thanetian, pars.).

Reference section: Bass River, Vincetown Formation (363.58–357.76 m).

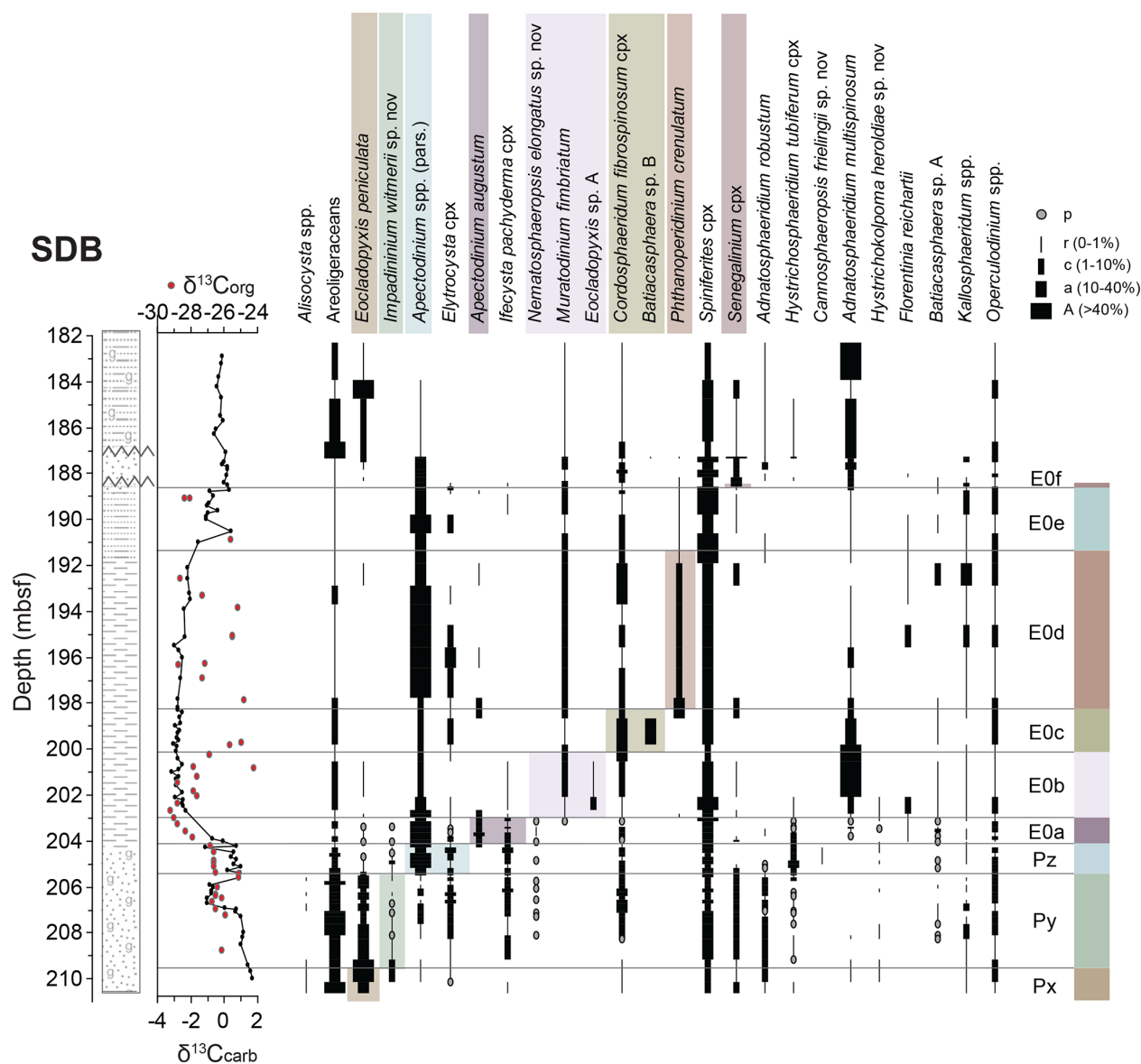


Figure 5. Relative abundances of stratigraphically important dinocyst species and taxa at South Dover Bridge (SDB). Abundances are indicated by rare (r, 0%–1%), common (c, 1%–10%), abundant (a, 10%–40%), or very abundant/acme (A, >40%). When taxa were encountered outside of regular counts, their abundance is indicated with an open gray circle, which means “present”. $\delta^{13}\text{C}$ bulk carbonate data are from Self-Trail et al. (2012), and $\delta^{13}\text{C}$ bulk organic data are from Lyons et al. (2019). At SDB, the dinocyst zones Px to E0f are recognized.

Calibration: Magnetostratigraphy: base Chron C24r. Calcareous nannoplankton: upper Zone NP9a.

Definition: The base of the zone is defined by the FO of *Impadinium witmeri* sp. nov. The top of the zone is defined by the base of the overlying zone, by the first consistent abundant occurrence of *Apectodinium* spp. (pars), which defines the base of zone Pz. Within this zone, a stepwise decrease in Areoligeraceans is recorded.

Characteristic taxa and bio-events: At the base of this zone, Areoligeraceans, notably *A. volata*, become (very) abundant and decrease in abundance towards the top of

this zone. Other abundant dinocysts within zone Py are *Spiniferites* spp. Representatives of the *Ifecysta pachyderma* cpx, notably *Ifecysta pachyderma*, commonly occur and remain present throughout. Halfway into this zone, *Eocladopyxis peniculata* becomes abundant and then decreases in abundance but remains in the entire zone. *Cannosphaeropsis frielingii* sp. nov. is sporadically present. Within this zone, an increase and decrease in *Apectodinium* spp. (pars) is recorded, which is followed by an increase in representatives of the *Cordosphaeridium fibrospinosum* cpx and *Elytrocysta* spp. towards the top of this zone.

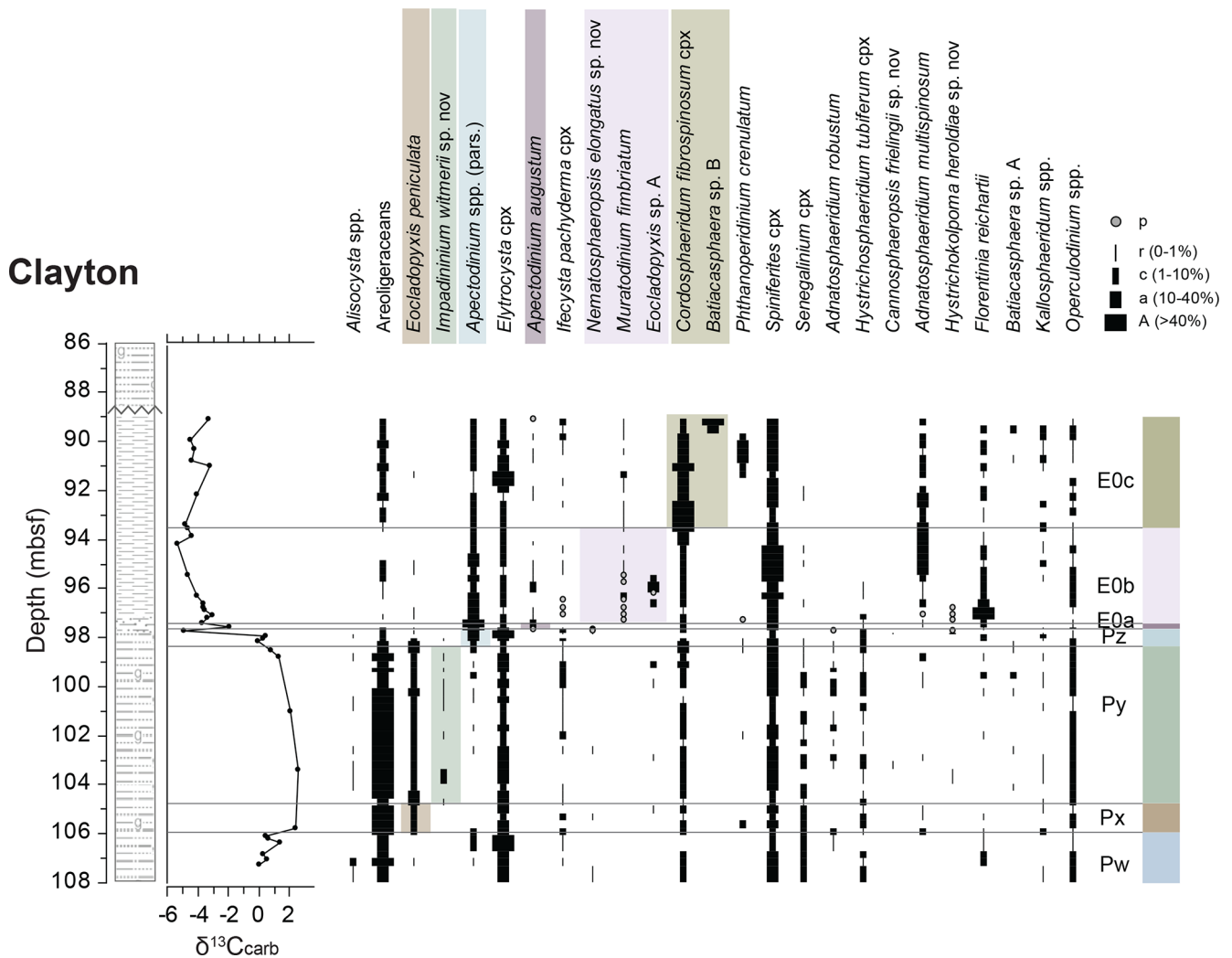


Figure 6. Relative abundances of stratigraphically important dinocyst species and taxa at Clayton. Abundances are indicated by rare (r, 0%–1%), common (c, 1%–10%), abundant (a, 10%–40%), or very abundant/acme (A, >40%). When taxa were encountered outside of regular counts, their abundance is indicated with an open gray circle, which means “present”. $\delta^{13}\text{C}$ bulk carbonate data are from Kent et al. (2003). At Clayton, the dinocyst zones Pw to E0c are recognized.

Remarks: ACP zone Py is recognized at MCBR, Oak Grove, SDB, Clayton, Wilson Lake, and Bass River. At SDB, representatives of the *Cordosphaeridium fibrospinosum* cpx and *Ifecysta pachyderma* cpx are more abundant than at Wilson Lake, Clayton, and Bass River. *Cannosphaeropsis frielingii* sp. nov. was not recorded at Bass River, Clayton, and Wilson Lake, but, since this species is quite rare, it may have been overlooked. The events we record in zone Py correlate to the decrease in Areoligeraceans (event “A”), the brief increase in *Eocladopyxis peniculata* (event “B”, collectively called Goniodomid taxa), and a second decrease in Areoligeraceans (event “C”) from Sluijs and Brinkhuis (2009). We point out that, at MCBR, *Apectodinium* spp. (pars) are very abundant in the lowermost sample, which would place the interval between 13.01 and 15.04 m in zone

Pz. Nevertheless, an increase in *Apectodinium* spp. (pars) is recorded at SDB, Clayton, Bass River, and Wilson Lake. The ecological affinity of *Apectodinium* spp. (pars) may explain its higher abundance at MCBR. Based on the observed step-wise decrease in Areoligeraceans at MCBR, we placed these depths in zone Py. Moreover, we point out that the short-lived increase in *Apectodinium* spp. (pars) is not well expressed at SDB, again potentially due to ecological affinities of this taxon.

Regional Paleocene dinoflagellate cyst zone ACP Pz

Age: Latest Paleocene (Thanetian pars.).

Reference section: Bass River, Vincetown Formation (357.67–357.39 m).

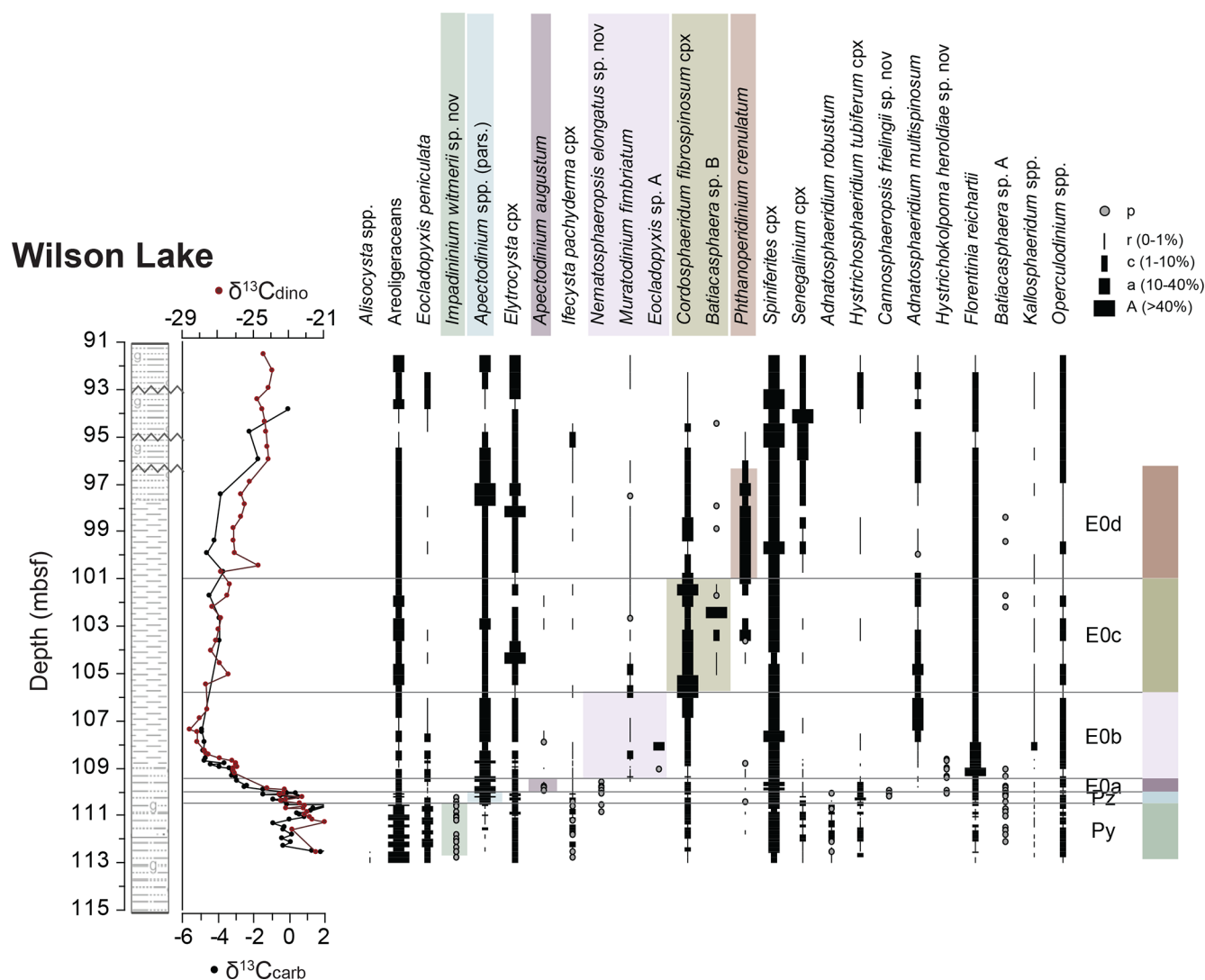


Figure 7. Relative abundances of stratigraphically important dinocyst species and taxa at Wilson Lake. Abundances indicated by rare (r, 0%–1%), common (c, 1%–10%), abundant (a, 10%–40%) or very abundant/acme (A, >40%). When taxa were encountered outside of regular counts, their abundance is indicated with an open gray circle, which means “present”. $\delta^{13}\text{C}$ bulk carbonate data are from Zachos et al. (2006), and $\delta^{13}\text{C}$ dinocyst data are from Sluijs et al. (2007). At Wilson Lake, the dinocyst zones Py to E0d are recognized.

Calibration: Magnetostratigraphy: lower Chron C24r. Calcareous nannoplankton: upper subzone NP9a.

Definition: The base of zone Pz is defined by the FAO of *Apectodinium* spp. (pars). The top of the zone is defined by the FO of *Apectodinium augustum*, which marks the base of Zone E0a.

Characteristic taxa and bio-events: Within this zone, *Elytrocyta* spp. peak, and representatives of the *Hystrichosphaeridium tubiferum* cpx show a brief increase in abundance. *Eoeladopyxis peniculata* and members of the *Cordosphaeridium fibrospinosum* cpx are present in low abundances and are sporadic in occurrence.

Remarks: ACP zone Pz is recognized at all sites. At MCBR, members of the *Ifecysta pachyderma* cpx are abun-

dant, and they are common in SDB. While this taxon is present at the New Jersey sites, it tends to be less common. *Apectodinium* spp. (pars) are very abundant at all sites. Notably, *Elytrocyta* spp. are most abundant at the New Jersey sites. The events we record in zone Pz correlate to the short-lived abundance of *Hystrichosphaeridium* spp. (event “D”), the onset of the *Apectodinium* acme (event “E”), and the abundance of *Elytrocyta* spp. (event “F”, previously identified as *Membranospaera* spp.) from Sluijs and Brinkhuis (2009).

Regional Eocene dinoflagellate cyst zone ACP E0a

Age: Earliest Eocene (Ypresian pars.).

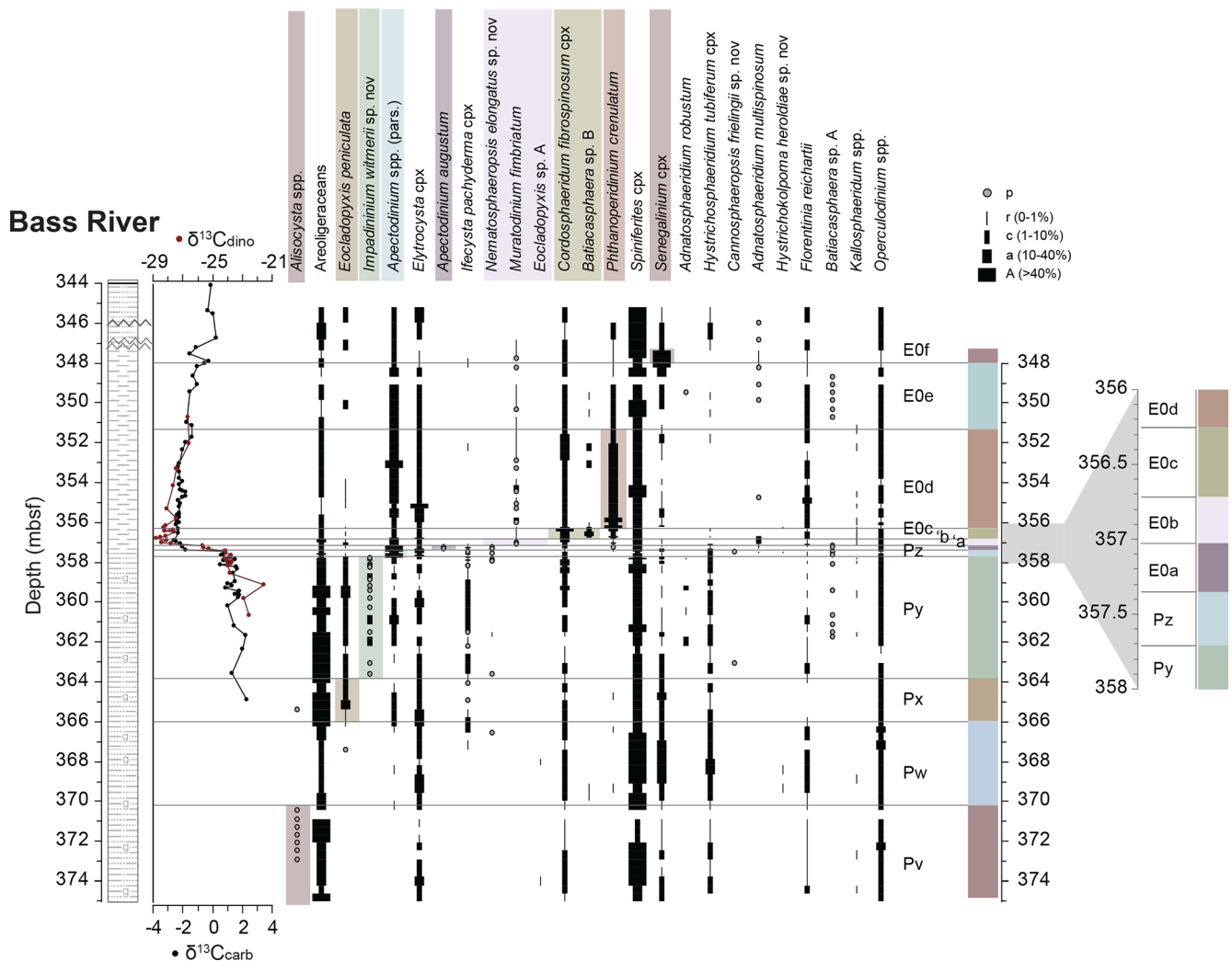


Figure 8. Relative abundances of stratigraphically important dinocyst species and taxa at Bass River. Abundances are indicated by rare (r, 0%–1%), common (c, 1%–10%), abundant (a, 10%–40%), or very abundant/acme (A, >40%). When taxa were encountered outside of regular counts, their abundance is indicated with an open gray circle, which means “present”. When taxa were encountered outside of regular counts, their abundance is indicated with a p (present). $\delta^{13}\text{C}$ bulk carbonate data are from John et al. (2008), and $\delta^{13}\text{C}$ dinocyst data are from Sluijs et al. (2007). At Bass River, the dinocyst zones Pv to E0f are recognized.

Reference section: South Dover Bridge, Marlboro Clay (204.05–203.01 m).

Calibration: Magnetostratigraphy: mid-Chron C24r. Calcareous nannoplankton: top subzone NP9a. First zone within the CIE of the PETM correlates with its onset.

Definition: The base of the zone is defined by the FO of *Apectodinium augustum*, and the top is defined by the FCO of *Muratodinium fimbriatum* and/or the LO of *Nematosphaeropsis elongatus* sp. nov.

Characteristic taxa and bio-events: This zone is marked by the LCO of representatives of the *Ifecysta pachyderma* cpx. The relative contribution of *Spiniferites* spp. increases towards the top of this zone. Other species within this zone include *Hystrichokolpoma heroldiae* sp. nov., *Florentinia reichartii*, and *Batiacasphaera* sp. A.

Remarks: ACP Zone E0a is recognized at all studied sites. Some variation in the abundance of taxa is recorded between sites. At MCBR, the highest abundances of members of the *Ifecysta pachyderma* cpx and *Kallosphaeridium* spp. are recorded. Importantly, *Apectodinium augustum* is rare and often only recorded outside of regular counts. No dinocyst events have been described in Sluijs and Brinkhuis (2009) that can be correlated within Zone E0a.

Regional Eocene dinoflagellate cyst zone ACP E0b

Age: Early Eocene (Ypresian, pars.).

Reference section: South Dover Bridge, Marlboro Clay (202.86–200.57 m).

Calibration: Magnetostratigraphy: lower Chron C24r. Calcareous nannoplankton: subzone NP9a. Second zone within the CIE of the PETM.

Definition: The base of Zone E0b is defined by the FCO of *Muratodinium fimbriatum* and the LO of *Nematosphaeropsis elongatus* sp. nov. The top of the zone is defined by an increase in abundance of members of the *Cordosphaeridium fibrospinosum* cpx. *Nematosphaeropsis elongatus* sp. nov. is rare, so this species was often observed outside of regular counts.

Characteristic taxa and bio-events: A peak in *Eocladopyxis* sp. A is often recorded within this zone. Additionally, is common to very abundant *Adnatosphaeridium multispinosum*, with highest abundances recorded at SDB and MCBR and lowest abundances recorded at Bass River. *Florentinia reichartii* becomes (very) abundant at the base of this zone at Clayton and Wilson Lake.

Remarks: ACP Zone E0b is recorded at all the studied sites, although the top of this zone is not recorded at MCBR and Oak Grove. Additionally, the peak in *Eocladopyxis* sp. A is not recorded at these sites, as Zone E0b is cut off. The highest abundance of *Adnatosphaeridium multispinosum* is recorded at MCBR, followed by SDB and Oak Grove. The New Jersey sites have the lowest abundances of *A. multispinosum*, particularly at Bass River. The events we record in Zone E0b correlate to the abundance of *Florentinia reichartii* (event “G”) from Sluijs and Brinkhuis (2009). *Florentinia reichartii* becomes the least abundant at the SDB site, potentially due to ecological affinities. Sluijs and Brinkhuis (2009) recognize event “I”, described as “a short-lived acme of goniodomid taxa”. The authors included both *Eocladopyxis* spp. and a taxon identified as “*Eocladopyxis*–*Spumadinium* sp.” from Bass River. Re-examination of these slides identified “*Eocladopyxis*–*Spumadinium* sp.” as *Batiacasphaera* sp. B. Event “I” from Sluijs and Brinkhuis (2009) corresponds to the short-lived peak in *Eocladopyxis* sp. A at Wilson Lake that is recorded in Zone E0b.

Regional Eocene dinoflagellate cyst zone ACP E0c

Age: Early Eocene (Ypresian, pars.).

Reference section: South Dover Bridge, Marlboro Clay (199.84–198.74 m).

Calibration: Magnetostratigraphy: lower Chron C24r. Calcareous nannoplankton: basal zone NP10. Third zone within the CIE of the PETM.

Definition: The base of Zone E0c is defined by a peak in members of the *Cordosphaeridium fibrospinosum* cpx, which become (very) abundant at the base of this zone. The top of the zone is defined by the FCO of (very) abundant *Phthanoperidinium crenulatum*. Within this zone, *Batiacasphaera* sp. B becomes abundant.

Characteristic taxa and bio-events: *Elytrocysta* spp. become (very) abundant, and *Apectodinium* spp. are present.

Remarks: ACP Zone E0c is recognized at SDB, Clayton, Wilson Lake, and Bass River. At Clayton, this zone is truncated by an unconformity (Gibson et al., 1993). *Cordosphaeridium fibrospinosum* cpx abundances are highest at Clayton and Wilson Lake, which are also where the highest abundances of *Batiacasphaera* sp. B are reached. An increase in *Phthanoperidinium crenulatum* in this zone is recorded in Bass River, Clayton, and Wilson Lake. At SDB, Zone E0c spans only two samples in 2 m, so the peak abundances of *Batiacasphaera* sp. B or *Elytrocysta* spp. in this zone are likely due to a low sampling resolution. As discussed above, event “I” from Sluijs and Brinkhuis (2009) represents the peak in *Batiacasphaera* sp. B, which was previously identified as “*Eocladopyxis*–*Spumadinium* sp.”. Furthermore, Sluijs and Brinkhuis (2009) tentatively correlate a peak abundance of *Cordosphaeridium* (event “J”) between 356.67 and 356.35 m at Bass River and 107.9 m at Wilson Lake (Sluijs and Brinkhuis, 2009). However, correlating the peak in *Batiacasphaera* sp. B places another peak in *Cordosphaeridium* spp. at a stratigraphically consistent place, which would place the depth of event “J” at 101.23 m in Wilson Lake. This event correlates to the top of Zone E0c.

Regional Eocene dinoflagellate cyst zone ACP E0d

Age: Early Eocene (Ypresian, pars.).

Reference section: South Dover Bridge, Marlboro Clay (197.88–192.07 m).

Calibration: Magnetostratigraphy: mid-Chron C24r. Calcareous nannoplankton: basal to mid-NP10. Fourth zone within the CIE of the PETM.

Definition: The base of Zone E0d is defined by a marked increase in the abundance of *Phthanoperidinium crenulatum*. The top of the zone is defined by the LO of very abundant members of the *Cordosphaeridium fibrospinosum* cpx.

Characteristic taxa and bio-events: Midway into Zone E0d, there is an optimum in the relative abundance of *Elytrocysta* spp., *Apectodinium* spp. become (very) abundant, and *Kallosphaeridium* spp. are common, particularly *Kallosphaeridium orchiesense*.

Remarks: ACP Zone E0d is recognized at SDB, Wilson Lake, and Bass River. The peak abundance of *Elytrocysta* spp. is most pronounced in Bass River and Wilson Lake, where it becomes very abundant. *Kallosphaeridium* spp. become abundant near the top of Zone E0d at SDB, while this taxon is only commonly present at Wilson Lake and Bass River. Highest relative abundances of *P. crenulatum* are recorded at Bass River at the base of Zone E0d. Also at SDB and Wilson Lake, *P. crenulatum* is abundant at the base of the zone. The relative abundance of *Apectodinium* spp. increases towards the top of this zone at all three sites. The events we record in Zone E0d correlate to the onset of abundant *Senegalinium* cpx from Sluijs and Brinkhuis (event “K”, in which the *Senegalinium* cpx includes *P. crenulatum*). The authors correlated this increase between 356.25 m at Bass River

and 103.80 m at Wilson Lake (Sluijs and Brinkhuis, 2009). Nevertheless, we show that an increase in *P. crenulatum* is observed in Zone E0c (prior to the peak in *Batiacasphaera* sp. B) at the New Jersey sites. The widespread increase in abundance of *P. crenulatum* that defines the base of Zone E0d can therefore be correlated to event “K” from Sluijs and Brinkhuis (2009), in which the depth of this event is updated to 100.72 m in Wilson Lake (which was previously assigned to event “M”, corresponding to “a second increase in *Senegalinium* cpx”). Furthermore, an increase in *Apectodinium* spp. is observed within Zone E0d, which was recognized as event “L” in Sluijs and Brinkhuis (2009). This event was previously placed at a depth of 102.6 m at Wilson Lake (Sluijs and Brinkhuis, 2009), but we show a more pronounced increase in *Apectodinium* spp. at 97.46 m in Zone E0d (which was previously assigned to event “N” corresponding to an “increase in *Apectodinium* abundance”).

Regional Eocene dinoflagellate cyst zone ACP E0e

Age: Early Eocene (Ypresian pars.).

Reference section: South Dover Bridge, Marlboro Clay (190.82–188.84 m).

Calibration: Magnetostratigraphy: mid-Chron C24r. Calcareous nannoplankton: mid-NP10. Fifth zone within the CIE of the PETM.

Definition: The base of Zone E0e is defined by a decrease in the abundance of the *Cordosphaeridium fibrospinosum* cpx, and the top is defined by an increase in representatives of the *Senegalinium* cpx, which defines the base of the overlying zone.

Characteristic taxa and bio-events: (very) abundant *Apectodinium* spp. and (very) abundant *Spiniferites* cpx.

Remarks: ACP Zone E0e is recognized at SDB and Bass River. Dinocyst assemblages are dominated by *Apectodinium* spp. and *Spiniferites* cpx. At SDB, a pulse of *Kallosphaeridium* spp. is recorded within this zone, becoming nearly abundant. This increase is not recorded at Bass River. At Bass River, *Elytrocysta* spp. become abundant towards the top of Zone E0e, which is not recorded at SDB. These differences potentially reflect the ecological affinities of these taxa. Within Zone E0e, no events were correlated between Wilson Lake and Bass River by Sluijs and Brinkhuis (2009), as Wilson Lake does not extend into this zone.

Regional Eocene dinoflagellate cyst zone ACP E0f

Age: Early Eocene (Ypresian pars.).

Reference section: South Dover Bridge, Marlboro Clay (188.69–188.53 m).

Calibration: Magnetostratigraphy: mid-Chron C24r. Calcareous nannoplankton: NP10 (pars.). Sixth zone within the CIE of the PETM.

Definition: The base of the zone is defined by the rapid increase in representatives of the *Senegalinium* cpx. The top

of the zone is truncated in SDB and Bass River and is therefore not defined. Characteristic taxa and bio-events: abundant *Senegalinium* cpx and *Spiniferites* cpx.

Remarks: The LO of *Apectodinium augustum* and the FO of *Wetzeliella* spp. may be used to approximate the top of this zone, coinciding with the top of the global dinoflagellate cyst subzone D5a (Fig. 2). At SDB and Bass River, Zone E0f is truncated by an unconformity and is only recorded in two samples dominated by members of the *Senegalinium* cpx and the *Spiniferites* cpx. At SDB, *Apectodinium* spp. remain abundant, whereas at Bass River this taxon is common.

4 Discussion

4.1 Comparison to previous ACP correlation schemes

Comparisons of previously established regional biostratigraphic zones to the ACP dinocyst zonation are in remarkable agreement across the six studied sections. Calcareous nannofossil NP zones have been recognized in the Paleocene–Eocene sediments at Oak Grove (Gibson et al., 1980; Bybell et al., 2021), at SDB (Rush et al., 2023; Self-Trail, 2011), and at Clayton, Wilson Lake, and Bass River (Aubry, 1996; Gibson et al., 1993; Stassen et al., 2012) (Fig. 9). These records show that the intercalibration we established at SDB and Bass River correlates consistently with NP zones at Clayton and Wilson Lake. In addition to the calcareous nannofossil zones, other correlation efforts have focused on benthic foraminiferal “ecozones” (Doubrawa et al., 2022; Stassen et al., 2012). A comparison of ecogroup and plankton abundance changes – stratigraphically correlated by Doubrawa et al. (2022) to our dinocyst zonation scheme – further demonstrates the strong agreement between the two schemes (Fig. S2). The base of the Marlboro Clay at SDB and MCBR is mostly barren of calcareous nannofossils due to dissolution (Robinson and Spivey, 2019; Self-Trail et al., 2017; Stassen et al., 2012). The dissolution interval broadly coincides with dinocyst Zone E0a. Above this interval, three ecogroups (A, B, and C) were recognized by Doubrawa et al. (2022). Group A and B seem to be roughly equivalent with the E0a/E0b and E0b/E0c boundaries, respectively, at SDB, Wilson Lake, and Bass River (Fig. S2). Ecogroup C, which is present in Zone E0e in Bass River, is not recorded in SDB and Wilson Lake. Additionally, the shifts in plankton, which were correlated across SDB, Wilson Lake, and Bass River, mostly follow the same stratigraphic zones we propose in this study (Doubrawa et al., 2022).

4.2 From depth to time domain for the new zonation

Collectively, where present, we have consistently recorded the defined top and bottom of our ACP dinocyst zones at the six sites (Table 2). Their stratigraphic occurrences are internally consistent with calcareous NP zones; carbon isotope stratigraphy; benthic foraminiferal ecozones at SDB, Clay-

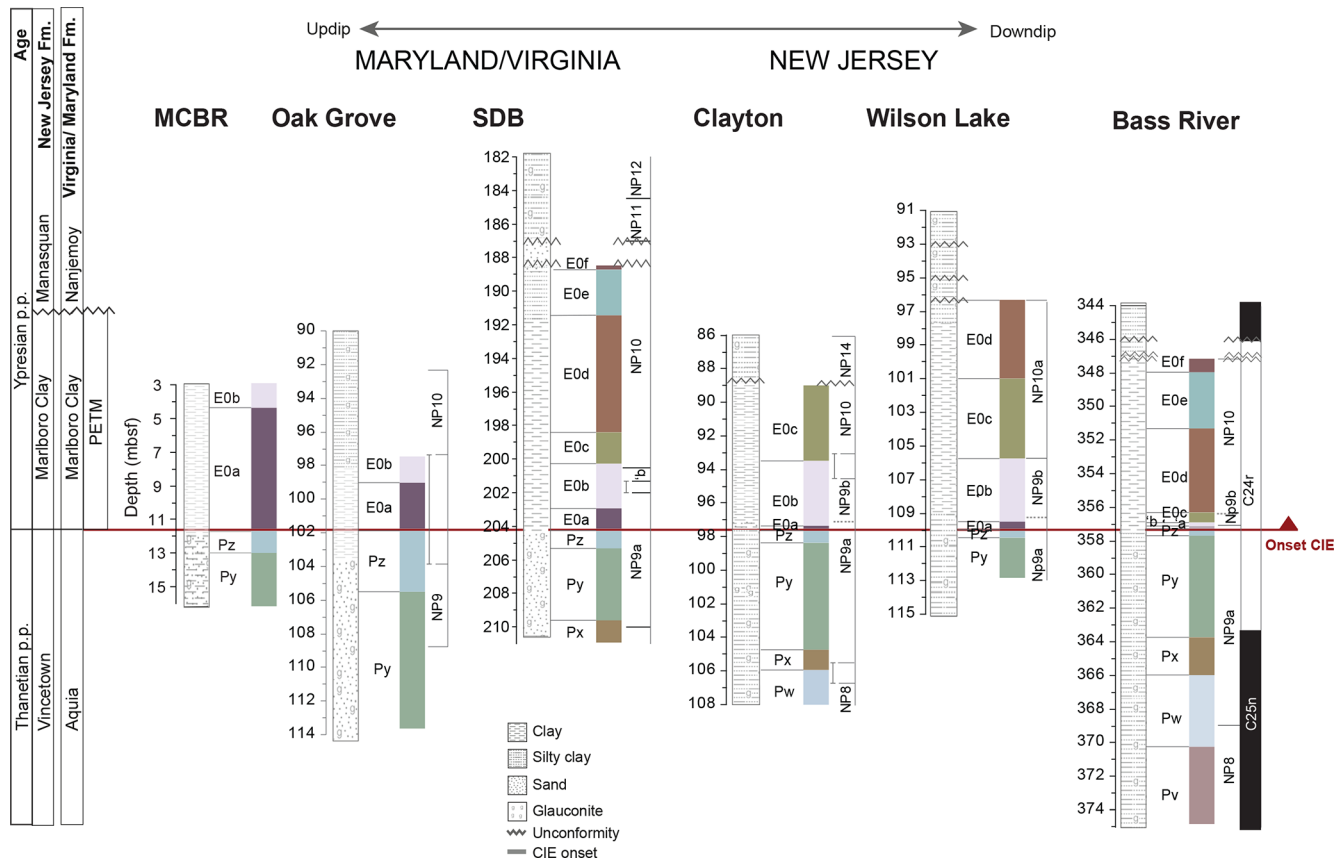


Figure 9. US Atlantic Coastal Plain integrated dinocyst zonation scheme of the late Paleocene and PETM. Sites shown are MCBR (Mat-tawoman Creek–Billingsley Road), Oak Grove, South Dover Bridge, Clayton, Wilson Lake, and Bass River. Lithologies and formation are shown. Dinocyst zones Pv–Pz are late Paleocene, and zones E0a–E0f are PETM; see Table 2 and Fig. 2 for corresponding depths and bio-events. In addition to the dinocyst zones, we show previously published calcareous nannoplankton zones, biofacies. Magnetostratigraphic data from Bass River are shown (Cramer et al., 1999). NP zones are from SDB (Rush et al., 2023), Clayton (Gibson et al., 1993), Wilson Lake (Stassen et al., 2012), and Bass River (Aubry et al., 2000). Biofacies zones from Wilson Lake and Bass River are from Stassen et al. (2015). The figure is adapted from Doubrava et al. (2022).

ton, Wilson Lake, and Bass River; and magnetostratigraphic data at Bass River (Figs. 9, S2). We show a large variation in the thickness of the ACP dinocyst zones across the studied sites, which indicates sediment supply to have varied across the paleo-shelf during the PETM (Fig. 10). Although some zones are truncated by an unconformity and their exact original thickness cannot be determined, the overall pattern shows that the earliest PETM zones are condensed at Bass River. The updip sites (MCBR and Oak Grove) show an expanded Zone E0a, which represents the earliest phase of the PETM. The intermediate sites Clayton and Wilson Lake show expanded zones E0b and E0c, while the downdip sites SDB and Bass River show expanded zones E0d and E0e (Fig. 10). This pattern has previously been recognized and interpreted to reflect the seaward progradation of the delta (Podrecca et al., 2021). Interestingly, while such seaward progression of sedimentation typically reflects forced regression (e.g., Vail et al., 2002), in this case, it reflects eustatic rise (Harris et al.,

2010; Sluijs et al., 2008) combined with massive sediment supply.

To broadly constrain the time that is captured within these ACP dinocyst zones, we calibrate them against known established ages for critical boundaries and assumptions regarding the duration of CIE phases at Bass River and SDB (see Fig. S3 and Nelissen et al., 2025). For the late Paleocene zones in Bass River, we interpolate the depths and ages for the boundary between NP8 and NP9 (57.21 Ma) following Gradstein et al. (2012) and the magnetic reversal between Chrons C25n to C24r (57.1 Ma) and the Paleocene–Eocene boundary (~ 56 Ma) following Gradstein and Ogg (2020). Interpolating these depths and ages gives an average sedimentation rate of 0.55 cm kyr^{-1} between the Paleocene–Eocene boundary and the Chron C24r/C25n reversal, which broadly corresponds to dinocyst zones Pz and Py (Fig. S3). This sedimentation rate is comparable to estimates from Maryland sites (Li et al., 2022; Lyons et al., 2019) and from other New Jersey sites (Stassen et al., 2012). Based on the

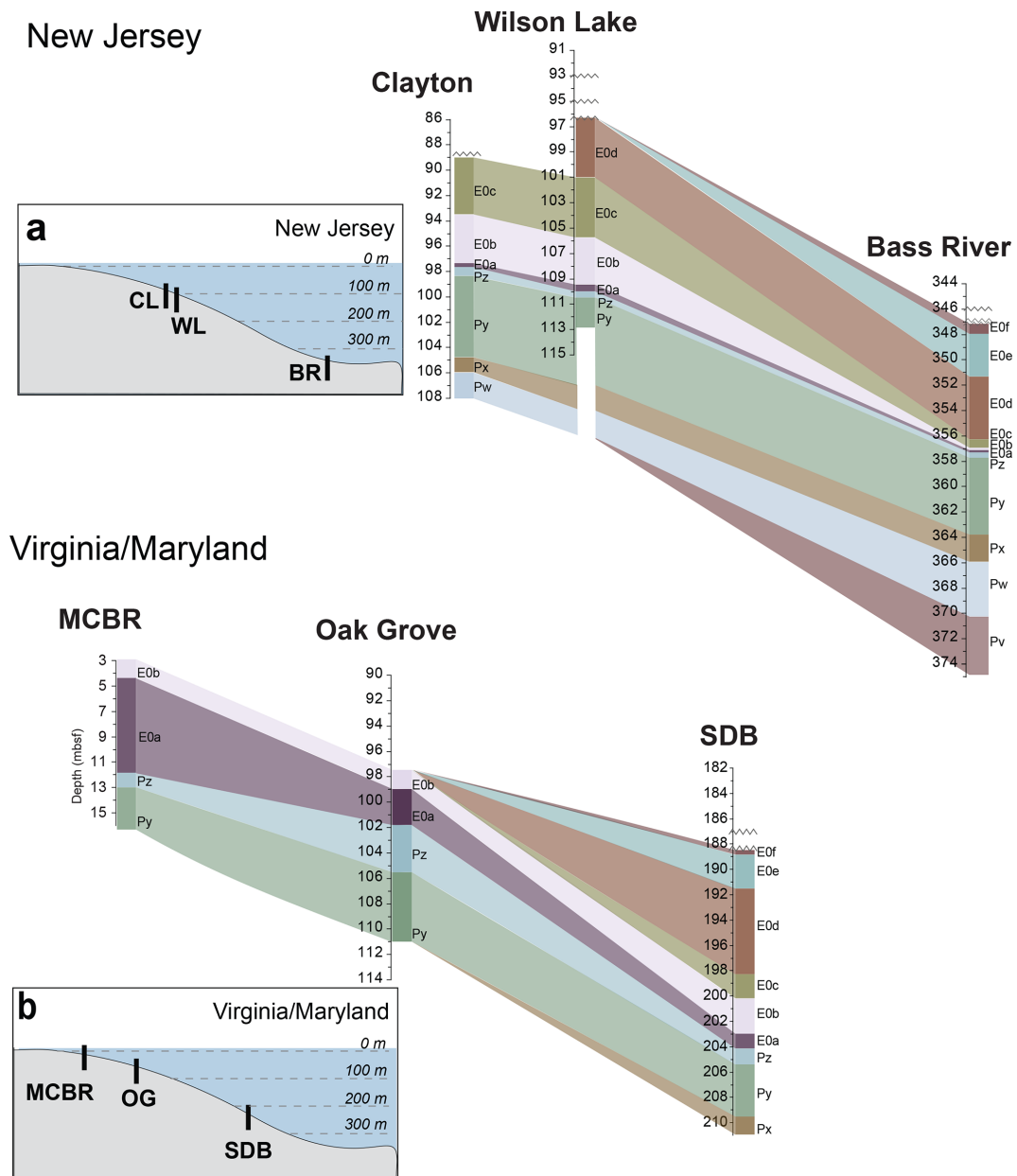


Figure 10. Thickness of ACP dinocyst zones (Pv to E0f) at six sites on the US Atlantic Coastal Plain. The top shows three sites located on the New Jersey Shelf: Clayton (CL), Wilson Lake (WL), and Bass River (BR). On the bottom, three sites from Virginia and Maryland are shown: Mattawoman Creek–Billingsley Road (MCBR), Oak Grove (OG), and South Dover Bridge (SDB). The relative proximity of these sites to the paleoshoreline is indicated in panels (a) (New Jersey sites) and (b) (Virginia/Maryland sites). Depths indicate the depth below sea level of the Marlboro Clay from Kopp et al. (2009). The exact water depths have not been constrained and may have varied substantially during the PETM. Nevertheless, these illustrate the inshore-to-offshore transect these sites are located on.

ages for the magnetic reversal and the boundary between zones NP8 and NP9, a sedimentation rate of 4.9 cm kyr^{-1} is calculated (Fig. S3), although we would like to point out that the precise age of the NP8/NP9 boundary is uncertain. If we extend that sedimentation rate further downcore, the lowest samples at Bass River at 374.61 m would be approximately 1.34 Ma older than the CIE onset. Within the PETM inter-

val, no age constraints are available, so we broadly constrain the duration and ages of the zones based on the assumption that the interval spanning the CIE from start to minimum values represents about 5 kyr, and we assume a duration of the CIE body of 100 kyr following Lyons et al. (2019), but note that this might well represent a low estimate, since the body likely represents much more time (Zeebe and Lourens,

2019). Based on the decrease in dinocyst $\delta^{13}\text{C}_{\text{dino}}$ in Wilson Lake (Fig. 7) and bulk $\delta^{13}\text{C}_{\text{org}}$ in SDB (Figs. 5, S3), we assume here that the CIE onset correlates to Zone E0a. We tentatively identify the CIE body at SDB from the boundary between dinocyst zones E0a/E0b at 202.98 m to the boundary between E0d/E0e at 191.45 m, based on the relatively stable negative $\delta^{13}\text{C}_{\text{carb}}$ values in these zones (Fig. S3). This is 0.95 m below the boundary between “CIE recovery phase 1 and 2” at 190.5 m (Röhl et al., 2007; Self-Trail et al., 2012). Following these assumptions, the calculated sedimentation rates during the CIE onset are 23.4 and 11.5 cm kyr^{-1} during the CIE body at SDB (Fig. S3), similar to the previously estimated sedimentation rate of 9.9 cm kyr^{-1} at SDB (Self-Trail et al., 2012). Interpolating these durations across the dinocyst zone boundaries provides some constraints on the duration of each zone and allow us to calculate average sedimentation rates per zone across the six studied sites on the ACP (Fig. S4). The average sedimentation rate per site per dinocyst zone is provided in Table 3. These data show a large variation in sedimentation rates, with the highest sedimentation rates recorded during Zone E0a (CIE onset) at MCBR (145 cm kyr^{-1}), Oak Grove (57 cm kyr^{-1}), and SDB (23.4 cm kyr^{-1}). Although the calculated sedimentation rates are highly dependent on assumptions, they do illustrate the progradation of the delta.

The zonation presents five zonal boundaries in the late Paleocene interval (from ~ 57.3 to ~ 56 Ma) and six zonal boundaries within the CIE of the PETM (~ 56 to ~ 55.85 Ma). Although not all zonal boundaries can be “dated” (thus durations are not determined in detail), this implies that our zonation yields an average time resolution of 10^5 years and 10^4 years for the late Paleocene interval and the PETM, respectively.

5 Concluding remarks

This study provides a highly resolved dinocyst zonation scheme of the latest Paleocene to early Eocene interval of key sections from the Atlantic Coastal Plain, calibrated against existing magnetostratigraphic, chemostratigraphic, and biostratigraphic data. This scheme, for the first time, allows high-resolution infra-PETM lithostratigraphic and chronostratigraphic correlation of sites across the Salisbury Embayment using a microfossil group that is continuously present at all sites. Moreover, our zonation scheme and associated dinocyst events create a robust basis for follow-up studies into a broader paleo-ecological reconstruction of environmental changes during the PETM at a high resolution. The correlation of sites allows a better understanding of local and regional signals both spatially and temporally. We show that organic microfossils, and particularly dinocysts, are useful for biostratigraphic and paleoenvironmental purposes in the ACP in previously drilled material and should be utilized in future drilling efforts.

6 Taxonomy

Four new species are formally described, and photographs, including holotypes and paratypes, are provided. A complete list of species with remarks and taxonomical and ecological grouping is provided. Photographs of relevant taxa and complexes are shown.

6.1 Systematic paleontology

Division Dinoflagellata (Bütschli, 1885) Fensome et al. (1993)

Class Dinophyceae Pascher (1914)

Subclass Peridiniphyceidae Fensome et al. (1993)

Order Gonyaulacales Taylor (1980)

Suborder Gonyaulacineae (autonym)

Family Gonyaulacaceae Lindeman (1928)

Subfamily Gonyaulacoideae Fensome et al. (1993)

Genus *Impagidinium* Stover and Evitt (1978)

Type: Cookson and Eisenack (1965a), pl. 12, figs. 5–6, as *Leptodinium dispersitum*

Impagidinium witmeri sp. nov.

Plate 1, figs. A–L

Synonym. “*Impagidinium speciosum*” Witmer, unpublished, PhD thesis 1987, Plate 11, figs. 1–8, p. 535.

Derivation of name. Named for Dr. Roger J. Witmer, in recognition of his achievements in marine palynology and organic geochemistry.

Diagnosis. An intermediate- to large-sized species of *Impagidinium* that is characterized by robust, suturocavate, denticulate, parasutural septa, of intermediate height, with the occasional development of rudimentary gonol processes.

Holotype. Plate 1, figs. A–C, SDB 204.84 m B19.4.

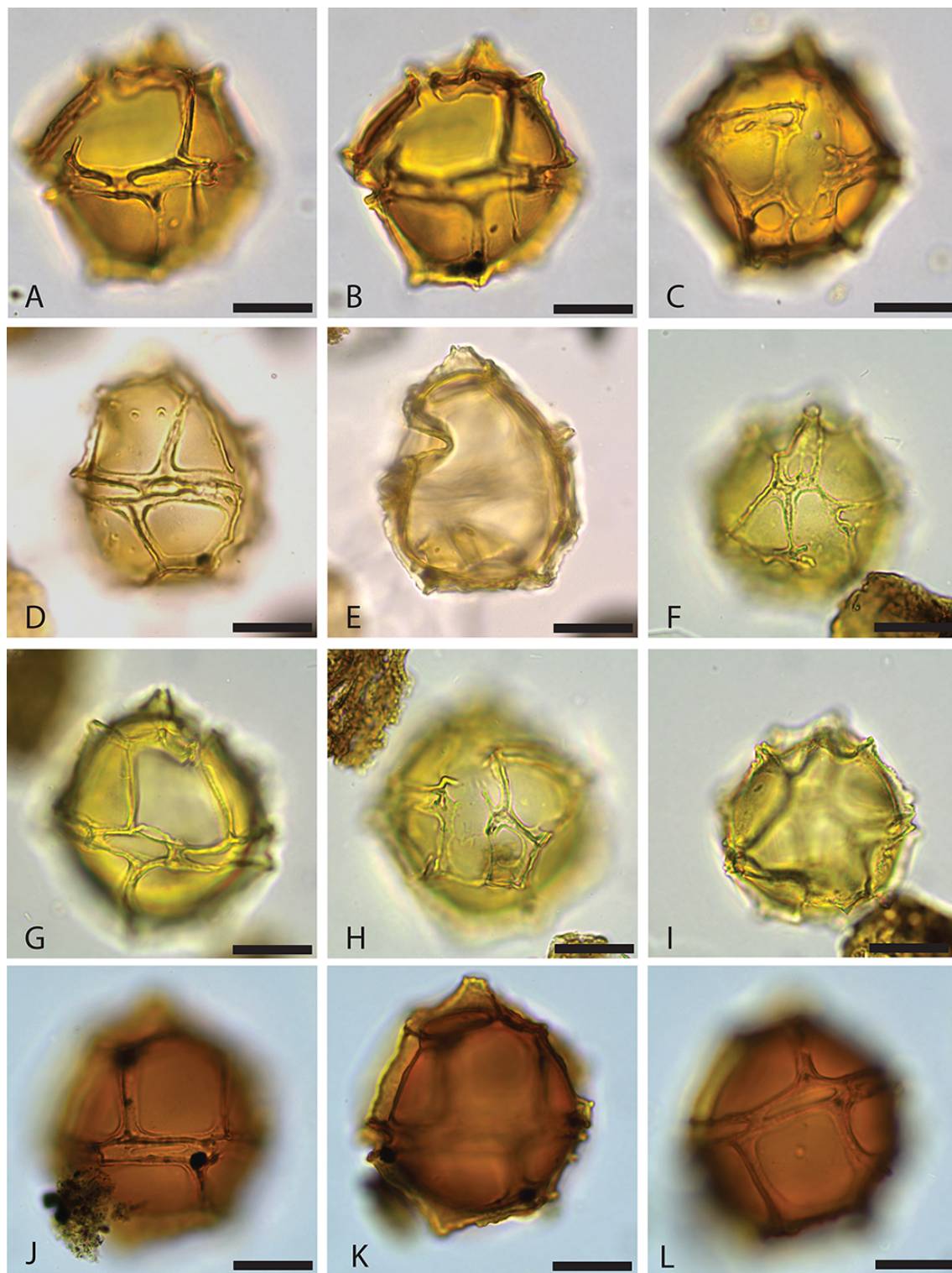
Paratypes. Paratype 1, Plate 1, figs. D–E, CL 98.62 m K48.1. Paratype 2, Plate 1, figs. F–I, MCBR1 15.40 m E42. Paratype 3, Plate 1, figs. G–H, MCBR1 15.40 m N38. Paratype 4, Plate 1, figs. J–L, SDB 204.84 m P39.

Material. South Dover Bridge (SDB) core, Talbot County, Maryland, USA.

Type locality and horizon. South Dover Bridge (SDB) core, latest Paleocene, 204.84 m.

Age. Latest Paleocene.

Description. Shape: Spherical to ellipsoidal. Wall relationships: Endophragm smooth (up to 2 μm thick), overlain by a faintly granulate periphragm (up to 1 μm thick). Periphragm closely appressed except for below the denticulate (para)sutural septa. Wall features: oval cysts characterized by rather robust (para)sutural septa. The apical



Scale bar = 25µm

Plate 1. *Impagidinium witmeri* sp. nov. (A–C) Holotype, SDB 204.84 m B19.4. (D–E) Paratype 1, CL 98.62 m K48.1. (F–I) Paratype 2, MCBR1 15.40 m E42. (G–H) Paratype 3, MCBR1 15.40 m N38. (J–L) Paratype 4, SDB 204.84 m P39. Scalebar = 25 µm.

Table 3. Calculated average net accumulation rates per ACP dinocyst zone per studied site in cm kyr^{−1}. Sites shown are Mattawoman Creek–Billingsley Road (MCBR), Oak Grove (OG), South Dover Bridge (SDB), Clayton (CL), Wilson Lake (WL), and Bass River (BR). Calculations for the late Paleocene zones Pv–Pz are based on the ages from Gradstein and Ogg (2020) of the C24r/C25n boundary and on Gradstein et al. (2012) for the NP8/NP9 boundary, all calculated for Bass River. Calculations for the PETM zones E0a–E0e are based on assumptions regarding the duration of the CIE onset and body phase in the SDB core. These were interpolated to provide some constraint on the duration of each zone and then applied to the other studied sites. These sedimentation rates give an average net accumulation rate per zone. For the calculations and assumptions used here, we refer to Nelissen et al. (2025) and Fig. S3.

	MCBR	Oak Grove	SDB	Clayton	Wilson Lake	Bass River
E0f			?			?
E0e			11.5			14.4
E0d			11.5		?	8.3
E0c		0	11.5	?	29.0	4.0
E0b	?	?	11.5	16.3	15.6	0.7
E0a	145.0	57.0	23.4	5.0	9.8	5.4
Pz	2.0	5.6	1.9	1.1	0.7	0.6
Py			0.4	0.6		0.6
Px				2.7		4.9
Pw						4.9

septa typically merge into a small apical horn-like protrusion. Processes: the (para)sutural septa give rise to rudimentary processes at gonial junctions. Paratabulation: indicated by (para)sutural septa, also clearly indicating an S-type (para)cingulum. (Para)cingular and sulcal plate sutures typically only faintly indicated. Archeopyle: indicated by the loss of 3'', operculum free. Paracingulum: S-type (para)cingulum. (Para)cingular and sulcal plate sutures typically only faintly indicated. Parasulcus: (Para)cingular and sulcal plate sutures typically only faintly indicated.

Dimensions. Holotype: endocyst 58 µm; pericyst 68 µm parasutural fold bases up to 9 µm across; parasutural fold heights up to 4 µm. Other types: Endocyst size 55–62 µm, pericyst size 61–73 µm, fold bases 5–10 µm and fold heights 3–5 µm (*n* = 6).

Stratigraphic range/occurrence. Latest Paleocene–earliest Eocene.

Remarks. This species differs from other *Impagidinium* species by its robust parasutural septa, with the tendency to develop suturocavation, akin to non-cavate species of *Pentadinium*. Roger Witmer first identified this taxon during his PhD studies (unpublished) (Witmer, 1987).

Genus *Nematosphaeropsis* Deflandre and Cookson (1955)

Type species *N. labyrinthus* Deflandre and Cookson (1955)

Nematosphaeropsis elongatus sp. nov.
Plate 2, figs. A–I.

Derivation of name. Latin word *elongatus*, in reference to the elongated shape of this species.

Diagnosis. An intermediate-sized, distinctly elongated species of *Nematosphaeropsis*.

Holotype. Plate 2, figs. A–C, SDB 204.05 m D24.4.

Paratypes. Paratype 1: Plate 2, figs. D–F, MCBR1 12.57 m V29.4. Paratype 2: Plate 2, figs. G–I, BR 357.85 m K39.

Material. South Dover Bridge (SDB) core, Talbot County, Maryland.

Type locality and horizon. South Dover Bridge (SDB) core, latest Paleocene, 204.05 m.

Age. Earliest Eocene.

Description. Shape: Elongate ellipsoidal. Wall relationships: Endophragm = smooth (up to 1 µm thick). Periphragm closely appressed except at the base of the processes. Wall features: Faint parasutural lines between base of processes. Processes: Gonial and intergonial and trifurcate processes with distal interconnecting trabeculae (up to 1 µm thick). Trabeculae may show ribbon-like connections. Some processes are not interconnected by trabeculae. Processes can be slightly thicker at the basis (up to 3 µm thick). Paratabulation: low, weakly developed parasutural ridges or lines. Archeopyle: Precingular (type P), operculum free. Paracingulum: Trabeculae indicate paracingulum. Parasulcus: not recognizable.

Dimensions. Holotype: endocyst width 28 µm, endocyst length 44 µm; total cyst length 71 µm, total cyst width 64 µm, length processes variable. Other types: endocyst width 27–29 µm, endocyst length 35–44 µm; total cyst length 57–71 µm, total cyst width 43–65 µm (*n* = 4).

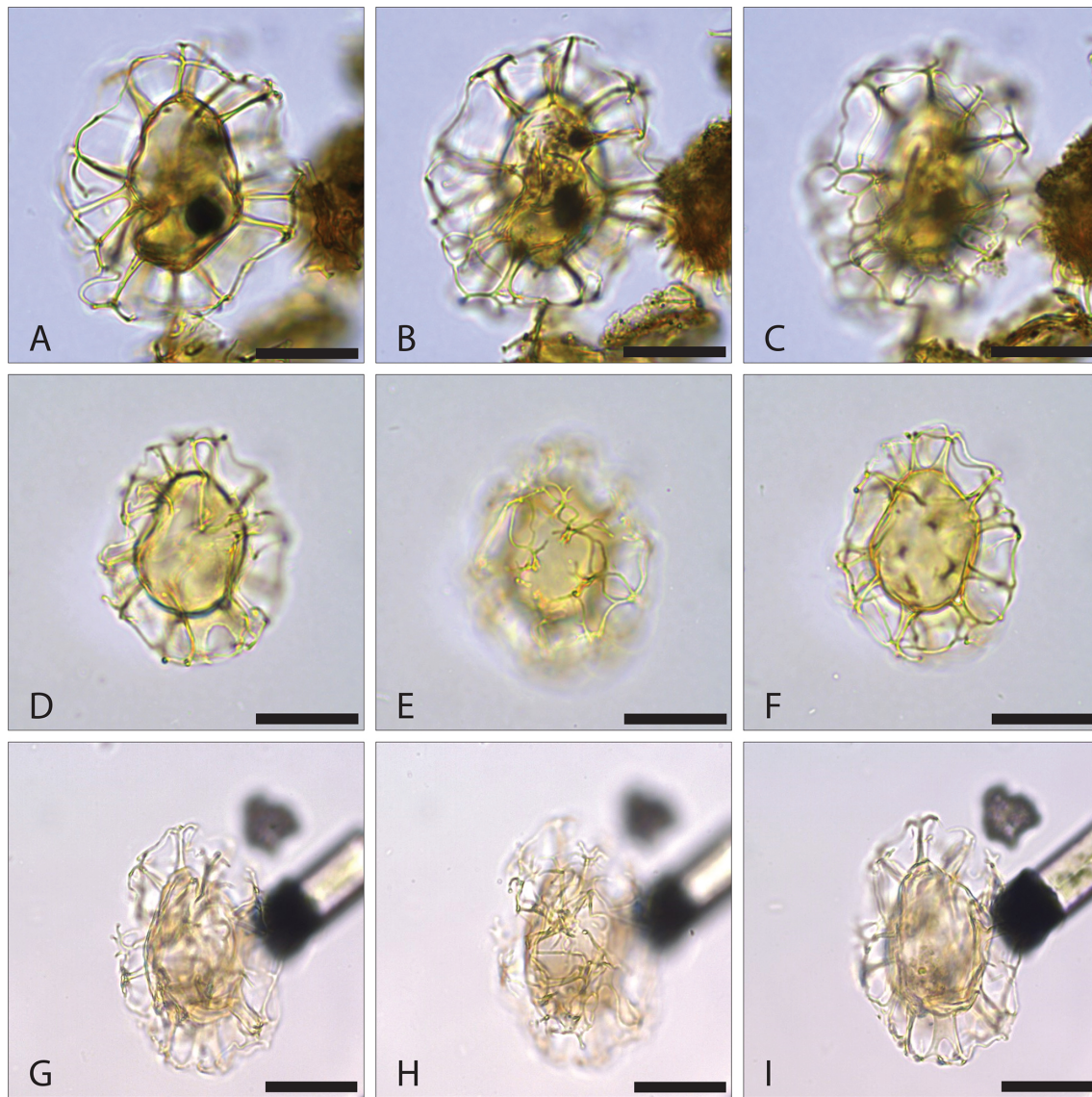
Stratigraphic range/occurrence. Latest Paleocene–earliest Eocene.

Remarks. This species differs from any other *Nematosphaeropsis* species by having an elongate ellipsoidal shape.

Genus *Cannosphaeropsis* Wetzel (1932)

Type species *Cannosphaeropsis utinensis* Wetzel (1932)

Cannosphaeropsis frielingii sp. nov.
Plate 3, figs. A–L.



Scale bar = 25µm

Plate 2. *Nemosphaeropsis elongatus* sp. nov. (A–C) Holotype, SDB 204.05 m D24.4. (D–F) Paratype 1, MCBR1 12.57 m V29.4. (G–I) Paratype 2, BR 357.85 K39. Scalebar = 25 µm.

Derivation of name. Named in honor of Dr. Joost Frieling in recognition of his achievements in marine palynology and work on the PETM at Utrecht University, at Oxford University, and soon at Ghent University.

Diagnosis. A species of *Cannosphaeropsis* with thick vesiculate trabeculae and gonal platforms.

Holotype. Plate 3, figs. A–C, SDB 204.51 m R33.4.

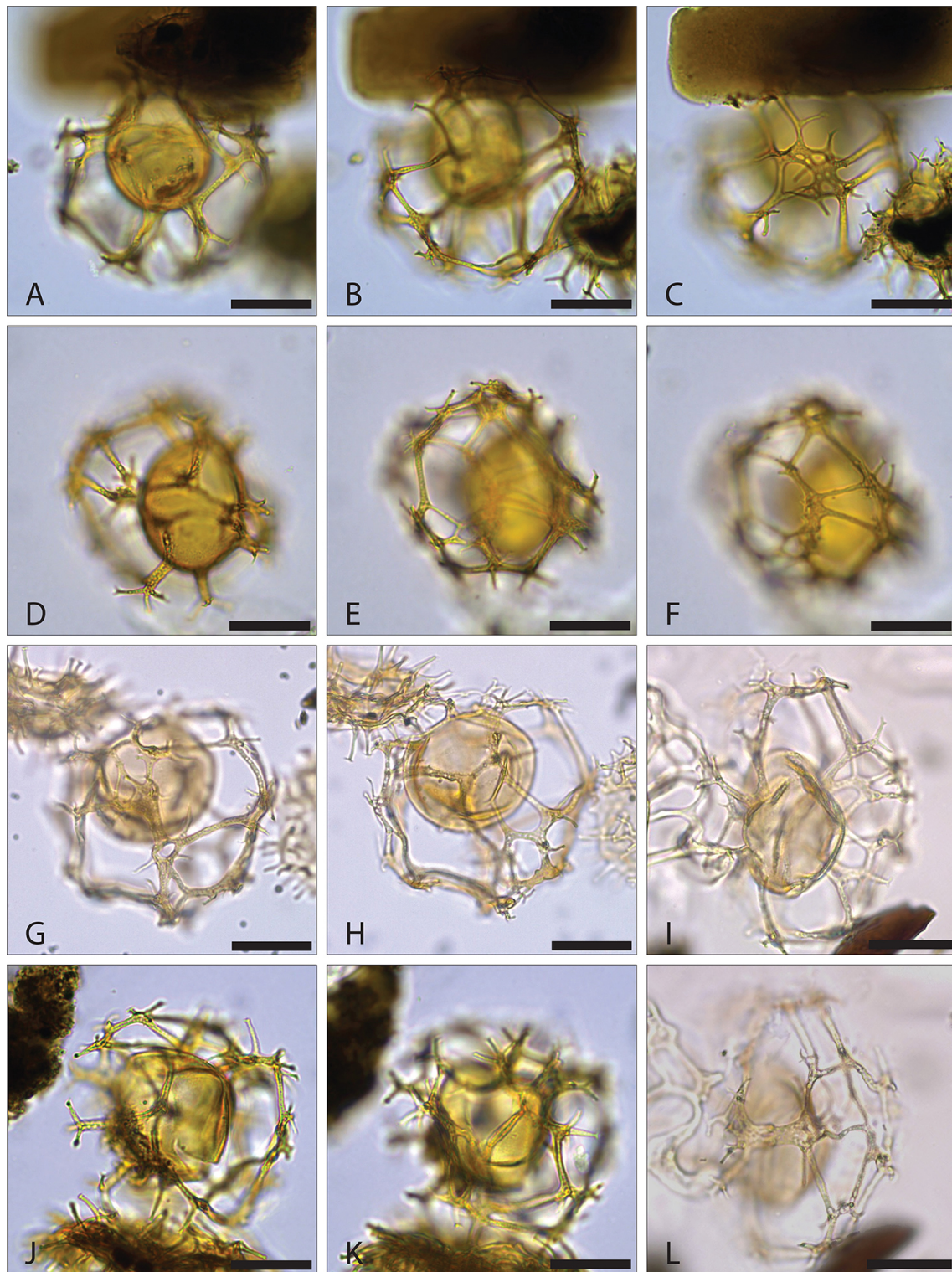
Paratypes. Paratype 1: Plate 3, figs. D–F, SDB 204.84 m R43. Paratype 2: Plate 3, figs. G–H, BR 357.39 m H36. Paratype 3: Plate 3, figs. I & L, CL 103.04 m M47. Paratype 4: Plate 3, figs. J–K, SDB 204.51 m K13.

Material. South Dover Bridge (SDB) core, Talbot County, Maryland, USA.

Type locality and horizon. South Dover Bridge (SDB) core, latest Paleocene, 204.51 m.

Age. Latest Paleocene.

Description. Shape: Cyst proximochorate to chorate. Central body subspherical to slightly elongate. Wall relationships: autophragm smooth to finely granulate, bearing processes connecting the autophragm to ectophragmal thick vesiculate trabeculae. Wall features: Ectophragmal network formed by single parasutural trabeculae that connect the distal ends of gonal processes. At gonal positions branches are present. Processes: The vesiculate trabeculae network is mostly oriented in dorsal direction with thick processes connecting this network to the autophragm. Ventral pro-



Scale bar = 25µm

Plate 3. *Cannosphaeropsis frielingii* sp. nov. (A–C) Holotype, SDB 204.51 m R33.4. (D–F) Paratype 1, SDB 204.84 m R43. (G–H) Paratype 2, BR 357.39 m H36. (I, L) Paratype 3, CL 103.04 m M47. (J–K) Paratype 4, SDB 204.51 m K13. Scalebar = 25 µm.

cesses are present, but these are shorter and do not connect to the trabeculae network. Processes are bi- or trifurcate. No trabecular spines midway between gonal positions indicated. “Gonal plates” are present at intersects between trabecula. Trabecula show thickening towards gonal platforms. Paratabulation: Difficult to determine, indicated by trabeculae only. Archeopyle: Precingular, Type P (3’), operculum free. Paracingulum: not well visible, can be indicated by network of trabeculae. Parasulcus: not well visible, can be indicated by parasutural trabeculae.

Dimensions: Holotype: endocyst width 33 µm; total cyst length 73 µm, length apical process 13 µm, thickness trabecula, 2 µm. Other types: endocyst width 33–43 µm; total cyst length 68–76 µm, length apical process 13–15 µm, thickness trabecula, 1–2 µm ($n = 5$).

Stratigraphic range/occurrence. Latest Paleocene.

Remarks. *Cannosphaeropsis frielingii* sp. nov. differs from the overall similar *Cannosphaeropsis utinensis* (Wetzel, 1932) in having alveolate trabecula containing vesicles and by lacking trabecular spines that are present in *C. utinensis*. The vesicles in *C. frielingii* are larger compared to the alveolate autophragm and/or trabecula in *Cannosphaeropsis passio* (de Verteil and Norris, 1996). Furthermore, the trabeculae are wider compared to *C. passio*, and no gonal platforms are present in *C. passio*. Similarly to *Cannosphaeropsis quattrocchia* (Guerstein et al., 2001), *C. frielingii* has “gonal platforms”. The difference between *C. quattrocchia* and *C. frielingii* is that *C. frielingii* has microperforate gonal platforms, which is not seen in *C. frielingii*. Furthermore, in *C. quattrocchia*, the trabeculae bear a thin crest that gives a fibrous appearance and is not alveolate. The size of structural voids and vesicles within various species within the genus *Cannosphaeropsis* has been used as a diagnostic trait. McLachlan et al. (2021) show that the degree of vesiculation varies within a group of 400 specimens in the species *Cannosphaeropsis franciscana* (Damassa, 1979) and assigned subspecies (McLachlan et al., 2021). Nevertheless, *Cannosphaeropsis frielingii* sp. nov. differs from other species within this genus based on other features than just the degree of vesiculation alone.

Subfamily Cribroperidinioideae Fensome et al. (1993)

Genus *Hystrichokolpoma* Klumpp (1953) emend. nov.

Type species *Hystrichokolpoma cinctum*, Klumpp, 1953 (pl. 17, figs. 3, 5a)

Emended diagnosis: The generic description of *Hystrichokolpoma* Klumpp 1953 is here emended to include species characterized by a distinct, robust, periphragmal membrane connecting the pre- and postcingular processes, overarching the cingular region (“cingular cavation”). The morphologically related genus *Cousteaudinium* de Verteil and Norris, 1996 is distinctly circumcavate.

Full emendation: Species within the genus *Hystrichokolpoma* possess a gonyaulacacean, sexiform tabulation

with dextral torsion. The cysts bear large, distally open penitabular processes situated on the apical, precingular, postcingular, and antapical plates. Processes on the paracingulum and parasulcus are markedly narrower, are often elongate, and may be distally open or closed. Here, we expand on the latter by including species in which the pre- and postcingular processes are connected with a periphragmal membrane overarching the cingular region. As a result of this overarching membrane in the cingular region, the cingular and sulcal processes become less visible and appear absent in some individuals. The archeopyle is apical, typically formed by the loss of a single plate.

Remarks. The morphologically related genus *Oligokolpoma* (Fensome et al., 2009) differs from *Hystrichokolpoma* emend. nov. by lacking any reflection of the cingular and sulcal plates.

Hystrichokolpoma heroldiae sp. nov.

Plate 4, figs. A–L

Cyst Type 1 (Steeman et al., 2020) Plate 3, figs. 5–11.

Derivation of name. This is named in honor of the memory of Lotte Herold, a dear friend and an inspiration to the lead author in both work and personal life. Additionally, the name also relates to the Latin *hērōs*, meaning a hero, here referring to the “superhero” cape-like feature this species has, which is a result of the distinct connection of the pre- and postcingular plates.

Diagnosis. A large, distinctive species of *Hystrichokolpoma* with interconnected pre- and postcingular processes, overarching the paracingulum.

Holotype. Plate 3, figs. A–C, SDB 204.26 m E8.

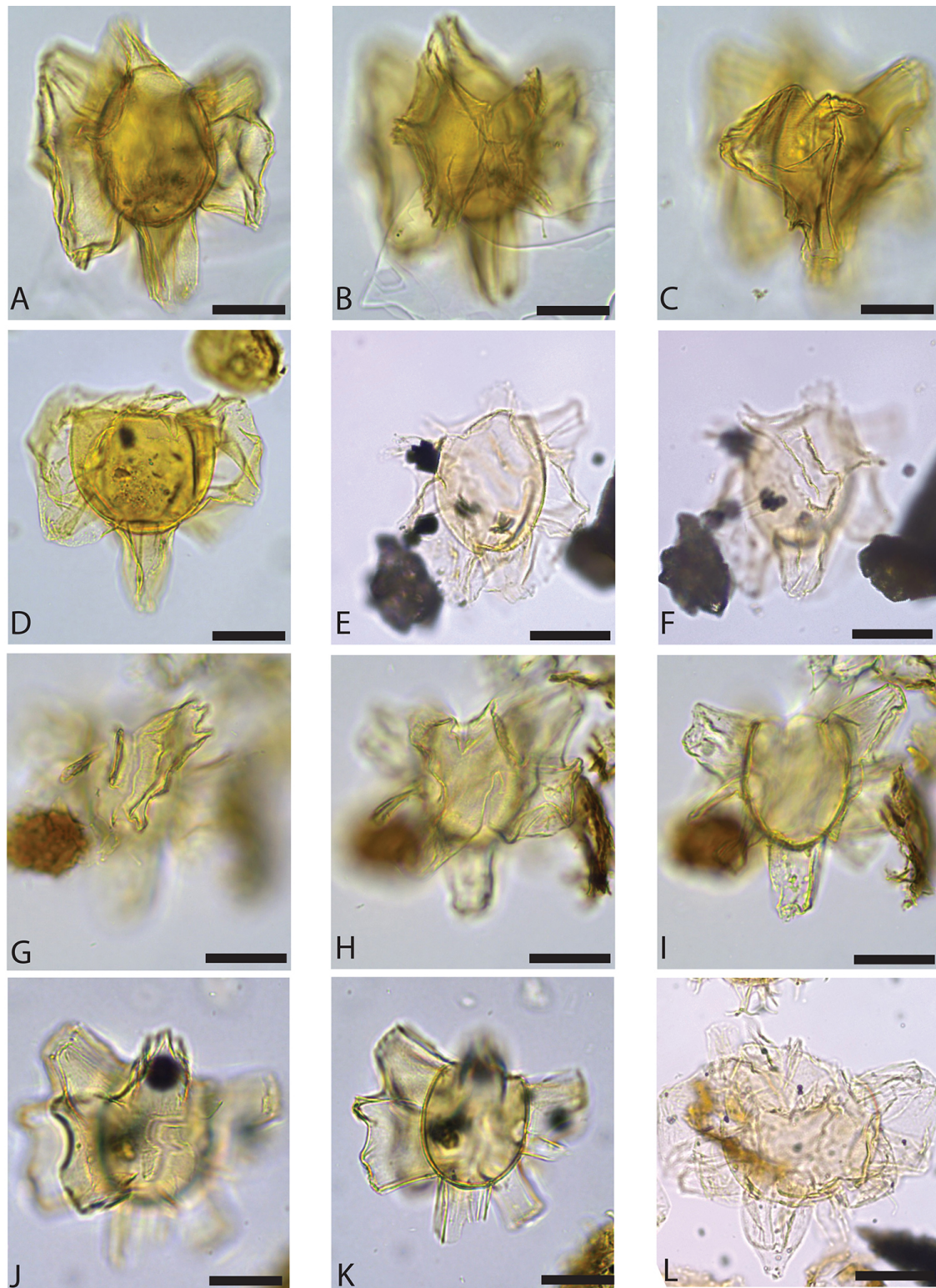
Paratypes. Paratype 1: Plate 4, fig. D, SDB 202.86 m C40.2. Paratype 2: Plate 4, figs. E–F, WL 108.69 m N56.4. Paratype 3: Plate 4, figs. G–I, MCBR1 13.92 m K27.1. Paratype 4: Plate 4, figs. J & K, MCBR1 12.77 m D19. Paratype 5: Plate 4, fig. L, BR 357.21 m H31.3.

Material. South Dover Bridge (SDB) core, Talbot County, Maryland, USA.

Type locality and horizon. The South Dover Bridge (SDB) core, latest Paleocene, 204.05 m.

Age. Earliest Eocene.

Description. Shape: Body subspherical. Wall relationships: Endophragm and periphragm appressed between processes. Wall features: Parasutural areas between expanded processes well expressed by periphragmal thickenings. Wall smooth to finely striate with some individuals showing some granulation. Endophragm smooth 1–2 µm thick. Processes: Large, intratabular processes, large closed cylindrical shape, showing longitudinal folds. The slender cingular processes can be faintly expressed, but, in most individuals, these processes have become part of the periphragm that connects the pre- and postcingular processes. Antapical process is not connected to the other processes. Paratabulation: Antapical plate expressed by a separate process, and other tabulation is



Scale bar = 25μm

Plate 4. *Hystrichokolpoma heroldiae* sp. nov. (A–C) Holotype, SDB 204.26 m E8. (D) Paratype 1, SDB 202.86 m C40.2. (E–F) Paratype 2, WL 108.69 m N56.4. (G–I) Paratype 3, MCBR1 13.92 m K27.1. (J–K) Paratype 4, MCBR1 12.77 m D19. (L) Paratype 5, BR 357.21 m H31.3. Scalebar = 25 μm.

expressed by groups of processes. Archeopyle: Apical, Type tA, operculum free. Paracingulum: Can be indicated by slender cingular processes that are in most cases distally connected to the pre- and postcingular plates, which makes the paracingulum less visible. Parasulcus: can be indicated by intratabular, distally connected processes.

Dimensions. Holotype: endocyst width 42 µm; pericyst width 68 µm, length antapical process 30 µm, width antapical process, 20 µm. Paratypes: endocyst width 33–47 µm; pericyst width 59–85 µm, length antapical process 16–30 µm, width antapical process, 14–21 µm ($n = 6$).

Stratigraphic range/occurrence. Latest Paleocene–earliest Eocene.

Remarks. This species of *Hystrichokolpoma* differs from any other species in having distinct connected pre- and postcingular processes. Steeman et al. (2020) recognized this taxon in the upper Paleocene–lower Eocene in Angola and called it Cyst Type 1.

6.2 Photoplates of new species and species of stratigraphic importance

Codes in plate captions represent the site locations with depth of the sample and associated England finder coordinates. All samples, depths, and dinocyst abundances can be found in Nelissen et al. (2025).

6.3 Annotated species list

In this subsection, we show which species and groups we included in the zonation scheme (raw data file included in Nelissen et al., 2025) and how the naming and grouping of these taxa compares to previous studies. The taxonomical/paleo-ecological groups are indicated in parentheses.

Adnatosphaeridium multispinosum. Plate 7, figs. A–C.

Adnatosphaeridium robustum. Plate 7, figs. D–F.

Alisocysta spp. Plate 8, figs. J–L.

Apectodinium augustum. Plate 7, figs. G–I.

Apectodinium spp. (pars.). Including all species within the genus *Apectodinium*, except for *Apectodinium augustum*.

Areoligeraceans. Remarks: we lumped all encountered species from the morphologically similar Areoligeracean genera *Areoligera* and *Glaphyrocysta*.

Areoligera volata. Plate 9, fig. A.

Batiacaspheera sp. A. Plate 5, figs. A–F. Remarks: An intermediate- to large-sized species of *Batiacaspheera*, characterized by a thin endophragm and a thicker, typically regularly reticulated (“pitted”) periphragm, with a large, distinctly “zig-zag”-styled archeopyle. Witmer (1987) described this species, but his work remains unpublished.

Batiacaspheera sp. B. Plate 8, figs. A–F. Remarks: An intermediate- to small-sized species of *Batiacaspheera*,

characterized by a thin endophragm and thicker, irregularly reticulated periphragm.

Cannosphaeropsis frielingii sp. nov. Plate 3, figs. A–L.

This species was not recorded previously.

Cordosphaeridium fibrospinosum cpx. Plate 8, figs. G–I. Includes all species of *Cordosphaeridium* that have one process per plate and fibrous processes. Species include *Cordosphaeridium inodes*, *Cordosphaeridium fibrospinosum*, *Cordosphaeridium gracile*, and other similar morphotypes, with *C. fibrospinosum* as central taxon. Note: this complex is different compared to the *Cordosphaeridium fibrospinosum* cpx from previous studies including *Fibrocysta*, *Ifecysta*, *Muratodinium*, and other genera (Brinkhuis and Schiøler, 1996; Sluijs and Brinkhuis, 2009).

Elytrocysta spp. Remarks: in Sluijs and Brinkhuis (2009), dinocysts from this genus were identified as *Membranospheera* spp.

Eocladopyxis peniculata. Plate 6, figs. J–L.

Eocladopyxis sp. A. Plate 6, figs. A–I. Remarks: Subspherical cyst with numerous randomly distributed processes, lacking the distinctive sutures from *Eocladopyxis peniculata*.

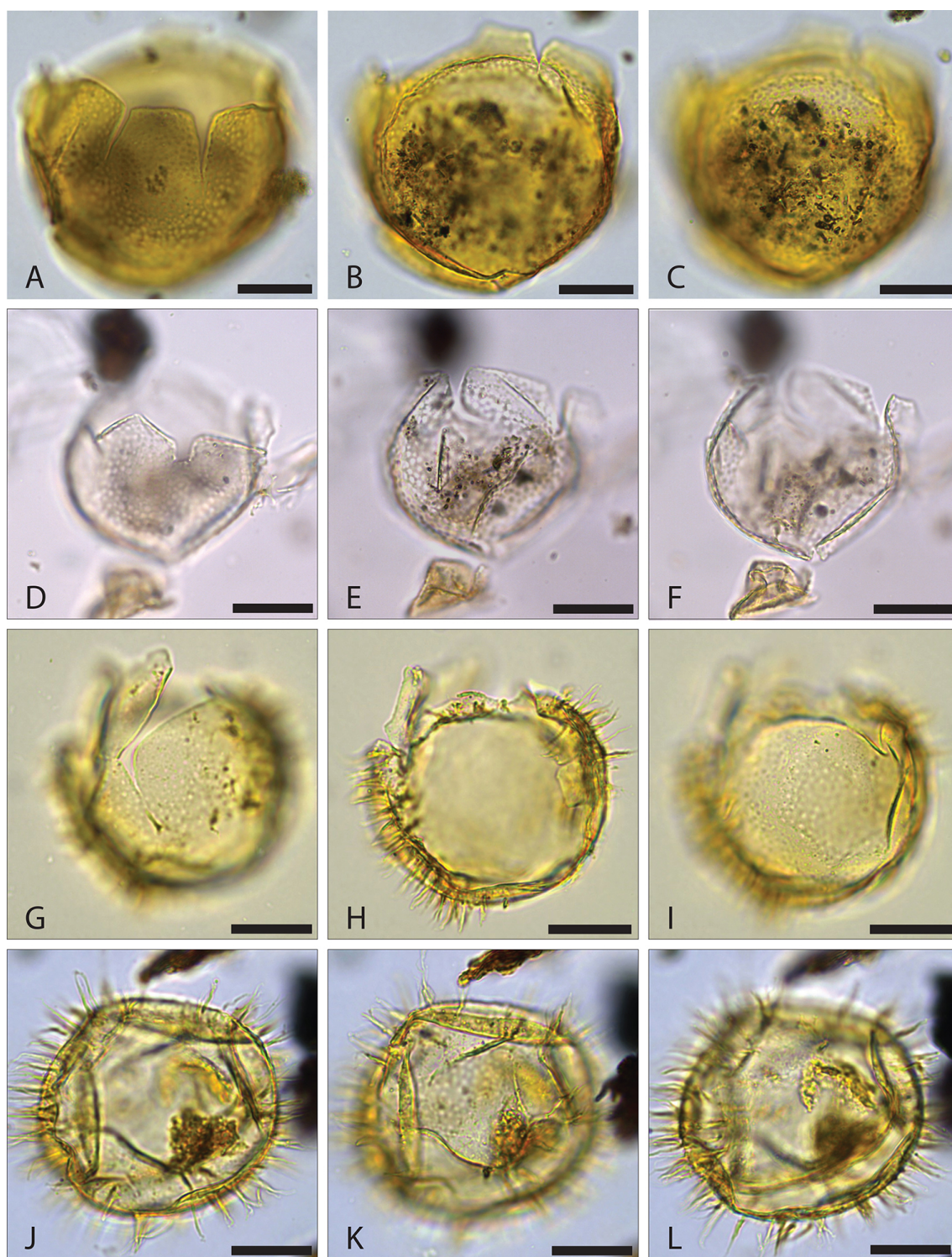
Florentinia reichartii.

Hystrichokolpoma heroldiae sp. nov. Plate 4, figs. A–L.

Hystrichosphaeridium tubiferum cpx. This complex includes *Hystrichosphaeridium tubiferum* and similar species that show varying process lengths and widths and variations in distal terminations, e.g., *Hystrichosphaeridium truswelliae*, which has distally closed processes with a thin membrane.

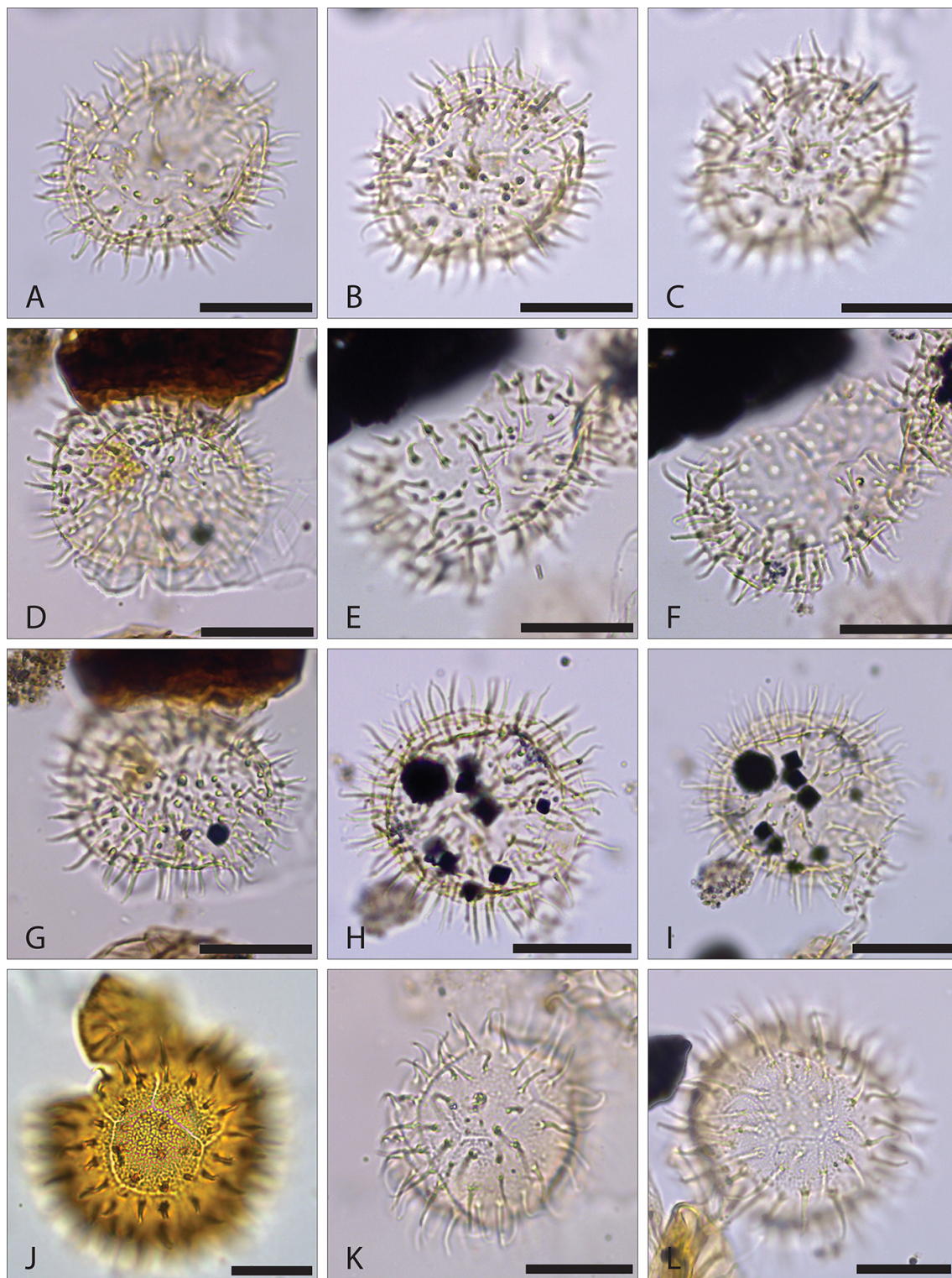
Ifecysta pachyderma cpx. Plate 9, figs. B–F. Remarks: this complex includes a variety of *Ifecysta* species, including individuals with an (ant)apical protrusion or apical horn (Plate 9, figs. B–C). Some individuals can be more elongate or rounded (Plate 9, fig. D), which we all assign to this complex. Moreover, the length of the penitabular processes may vary with some specimens expressing very short processes, becoming nearly “process-free” (see Plate 9, fig. E). Paratabulation can be expressed by penitabular processes or platform-like complexes, but, in some individuals, the fibrous process network surrounds the entire cyst and paratabulation is less clearly indicated. Also note that, in Sluijs and Brinkhuis, 2009, taxa we include in this complex were assigned to *Lanternosphaeridium lanosum*. In Witmer (1987), such specimens were allocated to “*Turbiosphaera rotunda*” and “*Turbiosphaera paratabulata*”. Here, we place all of these in the *Ifecysta pachyderma* complex.

Impagidinium witmeri sp. nov. Plate 1, figs. A–L. In Witmer (1987), this species was not formally described, but the name used in this unpublished PhD thesis is “*Impagidinium speciosum*”.



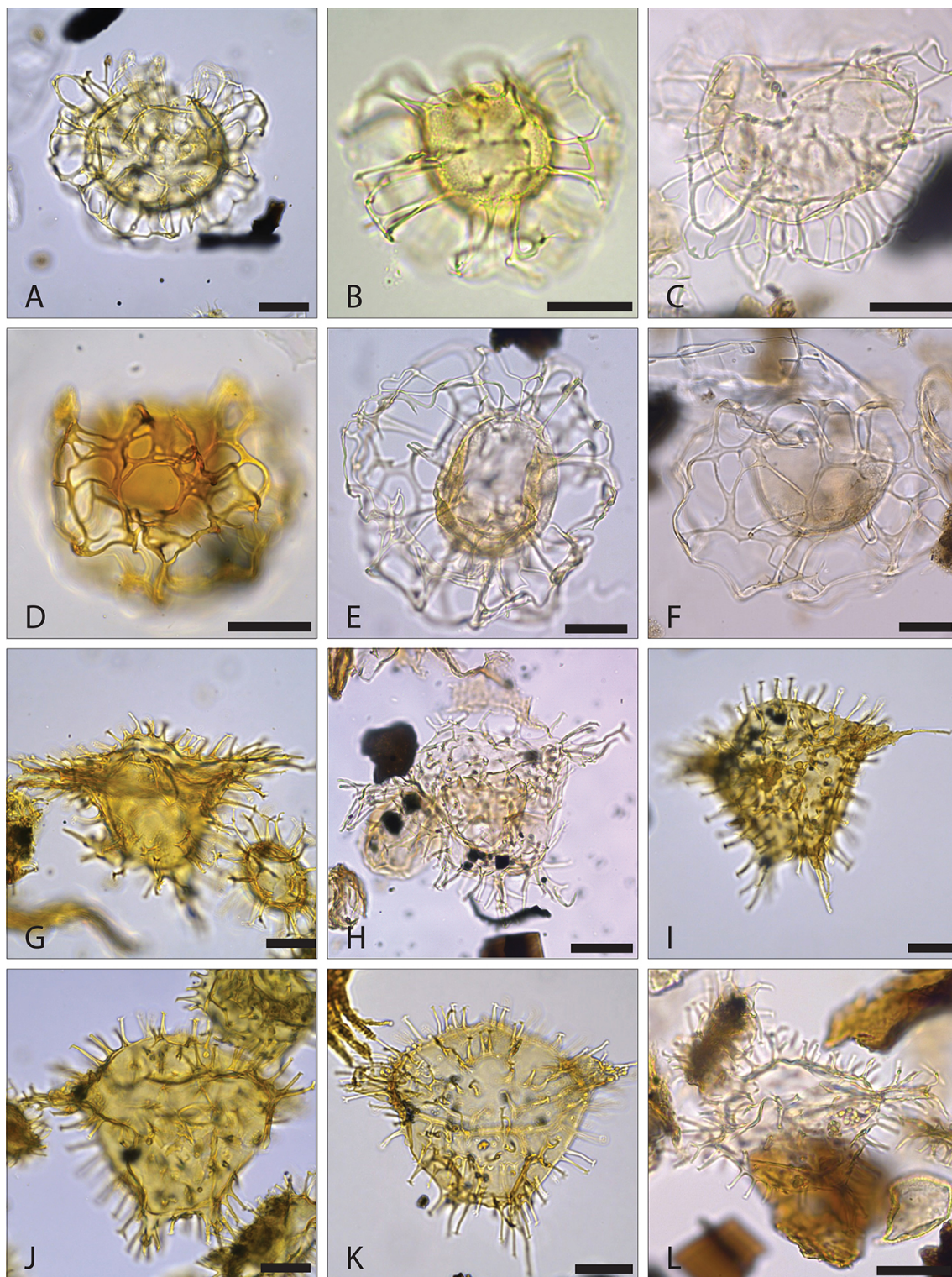
Scale bar = 25μm

Plate 5. *Batiacasphaera* sp. A (A–C) SDB 203.62 m Q10.1, (D–F) CL 99.38 m H53.3. *Kallosphaeridium orchiesense* (G–I) MCBR2 5.42 m E23.2, (J–L) MCBR2 5.42 m M36.3. Scalebar = 25 μm.



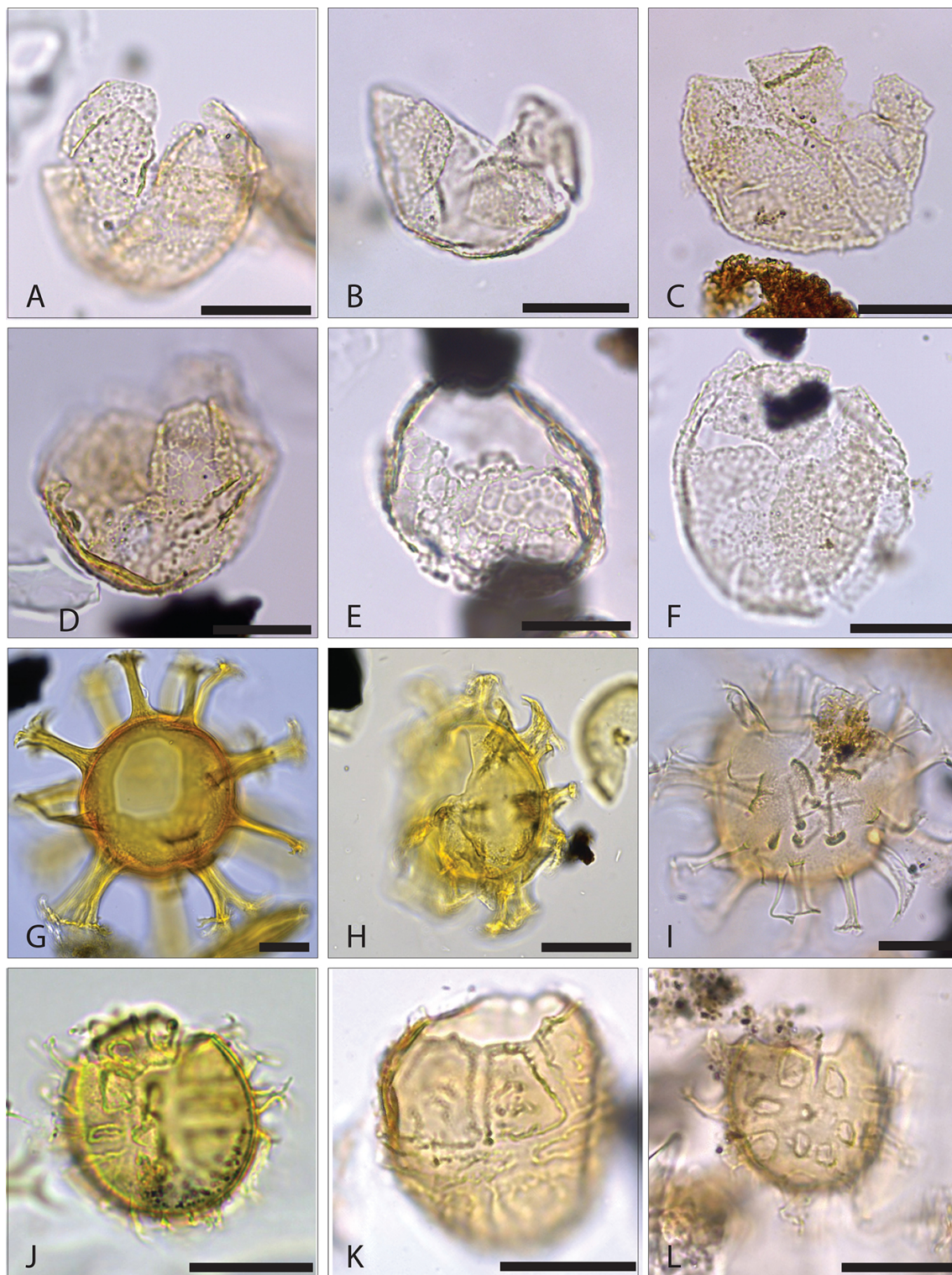
Scale bar = 25µm

Plate 6. *Eocladopyxis* sp. A (A) SDB 202.10 m X28, (D, G) CL 95.72 m H45.4, (E–F) CL 95.72 m M42.3. *Eocladopyxis peniculata* (J) SDB 208.04 m L32, (K) CL 100.05 m E55, (L) WL 110.61 m N62.1. Scalebar = 25 µm.



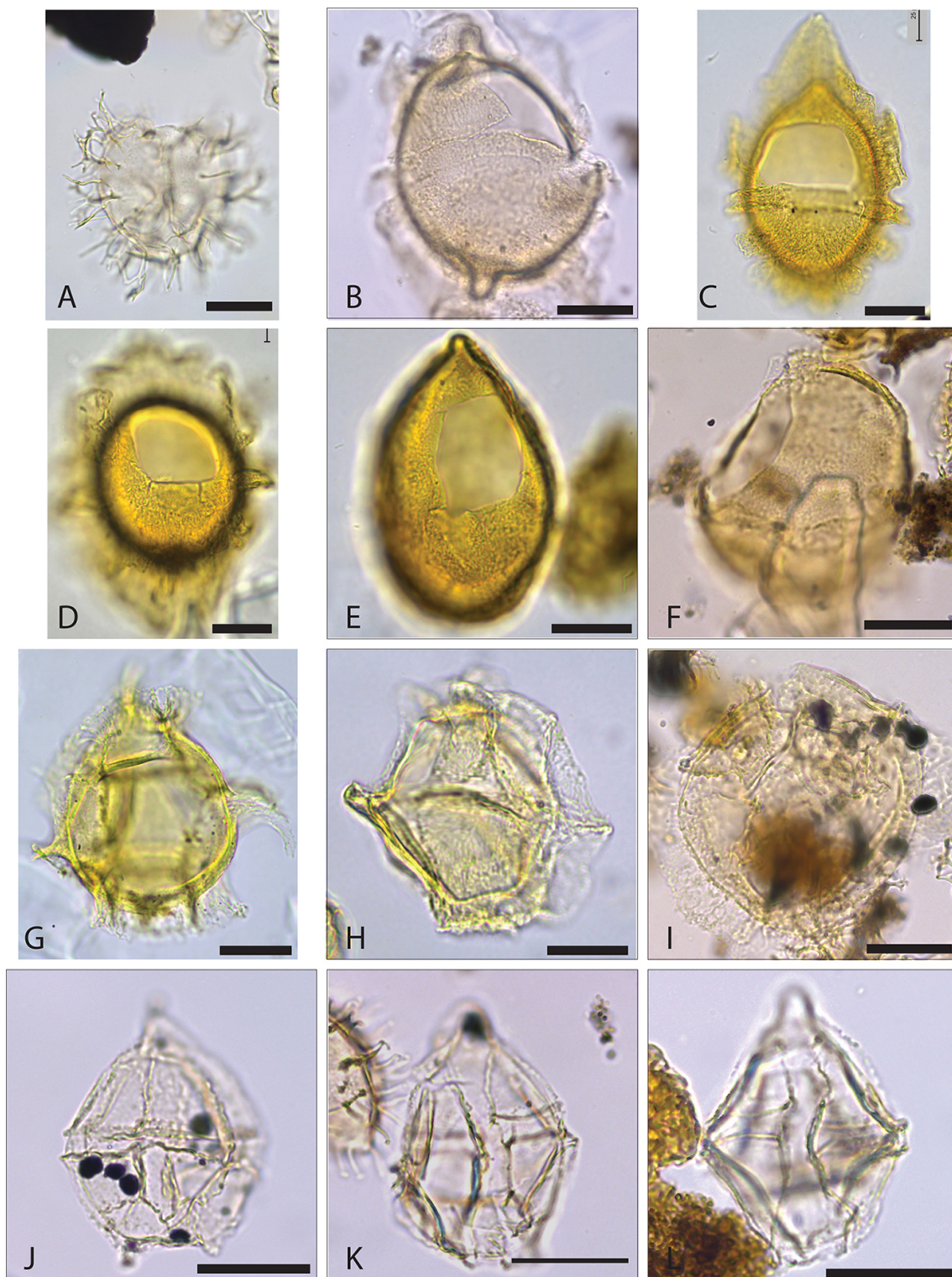
Scale bar = 25µm

Plate 7. *Adnatosphaeridium multispinosum* (A) SDB 200.57 m Q25.4, (B) MCBR2 4.62 m D35, (C) CL 94.05 m S46. *Adnatosphaeridium robustum* (D) SDB 208.04 m Q9.4, (E) BR 361.72 m S46.3, (F) CL 101.51 m H42. *Apectodinium augustum* (G) SDB 203.62 m R11, (H) BR 357.21 m T39.3, (I) MCBR2 5.02 m D43.3. *Apectodinium hyperacanthum* (J) SDB 204.05 m B31.3, (K) MCBR2 11.77 m N41. *Apectodinium* cf. *augustum* (L) WL 110.08 m G44. Scalebar = 25 µm.



Scale bar = 25µm

Plate 8. *Batiacasphaera* sp. B (A) SDB 198.74 m O2, (B) CL 89.32 m S40.2, (C) BR 356.45 m K43. *Batiacasphaera* sp. C (D) SDB 198.74 m J21, (E) CL 89.32 m S41.3, (F) BR 356.45 m E38. *Cordosphaeridium fibrospinosum* cpx (G) SDB 207.13 m C40, (H) MCBR1 15.40 m E42.3, (I) CL 89.32 m Q39.3. *Alisocysta* cpx (J) SDB 209.11 m P19.3, (K) BR 369.95 m E40, (L) CL 107.3 m M53. Scalebar = 25 µm.



Scale bar = 25μm

Plate 9. *Areoligera volata* (A) BR 371.29 m H41.3. Representatives of the *Ifecysta pachyderma* cpx, (B) CL 99.68 m D47.4, (C) MCBR1 12.77 m U33, (D) SDB 210.02 m F18, (E) MCBR1 12.77 m Q12, (F) CL 96.39 m O54. *Muratodinium fimbriatum* cpx (G) SDB 202.1 m J37, (H) MCBR2 12.15 m Z43.2, (I) CL 96.39 m K54.3. *Phthanoperidinium crenulatum* (J) SDB 197.88 m H9.3, (K) CL 89.32 m S40.2, (L) BR 356.45 m F41.2. Scalebar = 25 μm.

Kallosphaeridium spp. Plate 5, figs. G–I. Remarks: includes a wide variety of different morphotypes with a reduced number of processes as shown in Plate 4, figs. G–I. The wall structure closely resembles that of *Batiacaspheera* sp. A.

Muratodinium fimbriatum. Plate 9, figs. G–I.

Nematosphaeropsis elongatus sp. nov. Plate 2, figs. A–I. Remarks: We consider this species conspecific with specimens Witmer (1987) called “*Nematosphaeropsis* cf. *pertusa*”.

Operculodinium spp.

Phthanoperidinium crenulatum. Plate 9, figs. J–L. This species was not recognized in the unpublished PhD thesis of Witmer (1987).

Senegalinium cpx. Remarks: this includes all specimens assignable to the genera *Senegalinium*, *Lentinia*, and *Deflandrea*. Note: in Sluijs and Brinkhuis (2009), *Phthanoperidinium crenulatum* was also grouped within their *Senegalinium* cpx. However, due to the stratigraphic importance of *Phthanoperidinium crenulatum*, here we choose not to include this species within that complex.

Spiniferites cpx. Remarks: this includes all specimens assignable to the genera *Spiniferites*, *Achomosphaera*, and *Hafniasphaera*.

Appendix A

Listed below are all species discussed in this article with their original description.

Adnatosphaeridium multispinosum Williams and Downie (1966)

Adnatosphaeridium robustum Morgenroth (1966)

Alisocysta heilmannii Casas-Gallego et al. (2021)

Alisocysta margarita Harland (1979a)

Apectodinium augustum Harland (1979b)

Apectodinium homomorphum Deflandre and Cookson (1955)

Apectodinium hyperacanthum (Cookson and Eisenack, 1965b)

Areoligera volata Drugg (1965)

Cannosphaeropsis franciscana Damassa (1979)

Cannosphaeropsis frielingii sp. nov.

Cannosphaeropsis passio de Verteil and Norris (1996)

Cannosphaeropsis quattrocchia Guerstein et al. (2001)

Cannosphaeropsis utinensis Wetzel (1932)

Cordosphaeridium fibrospinosum Davey et al. (1966)

Cordosphaeridium gracile Eisenack (1954)

Cordosphaeridium inodes Klumpp (1953)

Deflandrea oebisfeldensis Alberti (1959)

Eocladopyxis peniculata Morgenroth (1966)

Florentinia reichartii Sluijs and Brinkhuis (2009)

Hystriocholpoma cinctum Klumpp (1953)

Hystriocholpoma heroldiae sp. nov.

Hystriocholpoma truswelliae Wrenn and Hart (1988)

Hystriocholpoma tubiferum Ehrenberg (1837)

Ifecysta pachyderma Jan du Chêne and Adediran (1985)

Impagidinium witmeri sp. nov.

Kallosphaeridium orchiesense De Coninck (1975)

Leptodinium dispertitum Cookson and Eisenack (1965a)

Muratodinium fimbriatum Cookson and Eisenack (1967)

Nematosphaeropsis elongatus sp. nov.

Nematosphaeropsis labyrinthus Deflandre and Cookson (1955)

Phthanoperidinium crenulatum De Coninck (1975).

Wetzeliiella articulata Eisenack (1938)

Data availability. Data are available at <https://doi.org/10.5281/zenodo.17473795> (Nelissen et al., 2025).

Sample availability. Samples are stored at Utrecht University at the department of Marine Palynology and Paleoceanography (MPP). The slides containing the holotypes and paratypes described in this article can be found for Bass River (LPP 863, slide box 017.834), Wilson Lake (LPP 864, slide box 017.388), South Dover Bridge and Mattawoman Creek–Billingsley Road (LPP 1224, slide box 017.387), and Clayton (LPP 094, slide box 004.595).

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Author contributions. Conceptualization: MN, HB, AS, and DW. Counting: MN, HB, and AS. Supervision: HB and AS. Data analysis: MN, HB, AS, and DW. Writing (original draft): MN. Writing (review and editing): MN, HB, AS, and DW.

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