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A dynamic climate and ecosystem state during the Paleocene-Eocene Thermal Maximum: inferences from dinoflagellate cyst assemblages on the New Jersey Shelf

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Abstract. Late Paleocene and Early Eocene climates and ecosystems underwent significant change during several transient global warming phases, associated with rapidly increasing atmospheric carbon concentrations, of which the Paleocene-Eocene Thermal Maximum (PETM; ~55.5 Ma) is best studied. While biotic response to the PETM as a whole (~170 kyrs) has been relatively well documented, variations *during* the PETM have been neglected. Here we present organic dinoflagellate cyst (dinocyst) distribution patterns across two stratigraphically expanded PETM sections from the New Jersey Shelf, Bass River and Wilson Lake. Many previously studied sites show a uniform abundance of the thermophilic and presumably heterotrophic taxon *Apectodinium* that spans the entire carbon isotope excursion (CIE) of the PETM. In contrast, the New Jersey sections show large variations in abundances of many taxa during the PETM, including the new species *Florentinia reichartii* that we formally propose. We infer paleoecological preferences of taxa that show temporal abundance peaks, both qualitative and absolute quantitative, from empirical as well as statistical information, i.e., principle (PCA) and canonical correspondence analyses (CCA). In the CCAs, we combine the dinocyst data with previously published environmental proxy data from these locations, such as TEX_{86} paleothermometry, magnetic susceptibility and sedimentary size fraction. The combined information supports previous inferences that sea level rose during the PETM, but also indicates a (regional) increase in fresh-water runoff that started ~10 kyr after the onset of the CIE, and perhaps precession-paced cycles in sea surface productivity. The highly variable dinocyst assemblages of the PETM contrast with rather stable Upper Paleocene assemblages, which suggests that carbon input caused a dynamic climate state, at least regionally.

1 Introduction

Now that almost everyone expects a certain amount of global warming by the end of the century (IPCC, 2007), interest to climate change as a whole is increasing. Global and regional climate models expect an increase in year-to-year variability of weather resulting from increasing CO_2 concentrations (e.g., Diffenbaugh et al., 2008). If so, one may expect increasing variability in climate over the coming centuries, millennia and even longer time scales, because carbon concentrations in the atmosphere are expected to remain high for several hundreds of thousands of years (Archer, 2005; Archer et al., 2009). One way to assess climate dynamics in a rapidly warming world is to perform high-resolution paleoenvironmental reconstructions on high-accumulation rate sediment sections deposited during a past analogue, such as the Paleocene-Eocene Thermal Maximum (PETM).

The PETM represents a ~170 kyr (Röhl et al., 2007; Abdul Aziz et al., 2008) long episode of extreme global greenhouse warmth ~55.5 Million years ago (Ma), superimposed on the already warm Late Paleocene and Early Eocene (Bowen et al., 2006; Sluijs et al., 2007a). The onset of the PETM is marked by a pronounced negative stable carbon

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isotope (δ^{13}C) excursion (CIE), documented in marine and terrestrial sedimentary components (Kennett and Stott, 1991; Koch et al., 1992; Schouten et al., 2007) and an additional global warming of ~5–9°C (Kennett and Stott, 1991; Zachos et al., 2003; Sluijs et al., 2006). The CIE is widely taken to evidence the injection of large amounts of ^{13}C-depleted carbon in the shape of CH_4 and/or CO_2 into the ocean-atmosphere system (Dickens et al., 1995, 1997). This addition of 'light' carbon is generally thought to lie at the root of this episode of extreme global warmth (Higgins and Schrag, 2006; Pagani et al., 2006), or to represent a positive feedback to warming, for example through the melting of submarine methane hydrates (Dickens et al., 1995; Sluijs et al., 2007b).

Although warming and perturbations in the hydrological cycle during the PETM as a whole is relatively well documented, not much is known about climate changes *during* the PETM. Generally, biotic and geochemical records suggest a relatively uniform, warm climate state over the span of the PETM. At least partially, this is due to many studies using extremely condensed deep-sea sediment sections, where bioturbation has potentially blurred signals and carbonate dissolution reduced temporal resolution, particularly for the onset of the event (Zachos et al., 2005). Expanded sections show much more detail; for example, continental sections comprised of stacked paleosols such as those in the Bighorn Basin, Wyoming, USA, have high accumulation rates and have revealed wet and dry phases (Bowen et al., 2004; Wing et al., 2005; Kraus and Riggins, 2007), as well as precession-forced variations in hydrology (Abdul Aziz et al., 2008) within the PETM.

In the marine realm, notably oil exploration and production companies have retrieved many high accumulation rate PETM sections from the continental shelves. Both from internal company reports, as well as the comparatively few marginal marine sections from which biogeological data are publically available it has become clear that among morphologically recognizable remains of eukaryotic planktonic biota, the dinoflagellates exhibit the most dramatic response across the PETM (Sluijs et al., 2007a). This is most notably shown by the quasi-globally recorded acme of the organic cysts (or dinocysts) of the thermophilous, and possibly heterotrophic taxon *Apectodinium* (Bujak and Brinkhuis, 1998; Crouch et al., 2003a; Crouch et al., 2001; Egger et al., 2003). Recent studies have focussed on high-accumulation rate, expanded marginal marine PETM cores from New Jersey, USA, named "Wilson Lake" (Gibbs et al., 2006; Zachos et al., 2006) and "Bass River" (Cramer et al., 1999), drilled by the United States Geological Survey (USGS) and the Ocean Drilling Program (ODP), respectively (Fig. 1). These studies showed that the onset of the *Apectodinium* acme represents the earliest sign of anomalous PETM-related environmental change, since it occurred several kyrs prior to the onset of warming and the subsequent initiation of the CIE (Sluijs et al., 2007b).

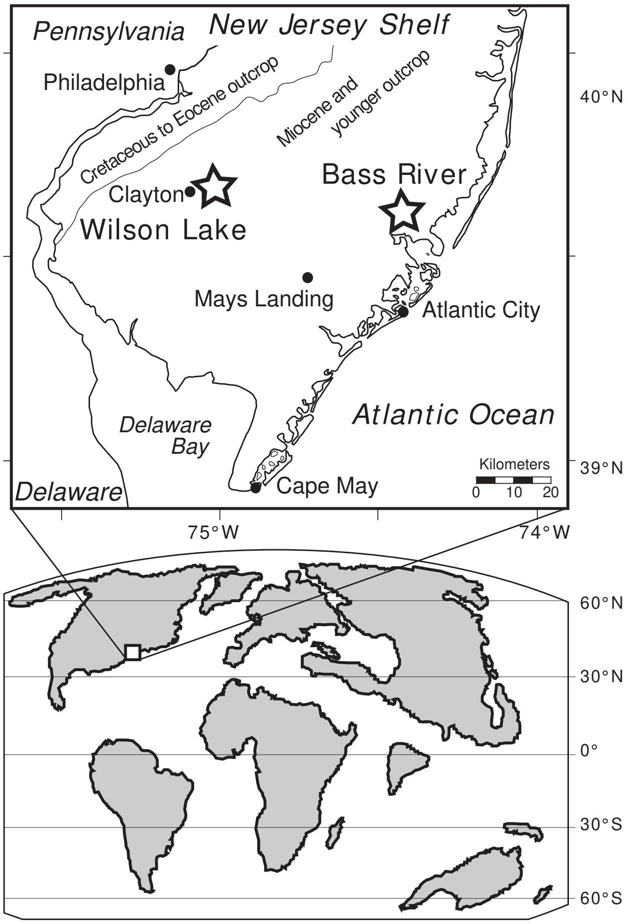

Fig. 1. Locations of the Wilson Lake and Bass River cores. Modified from Miller (1997) and Scotese (1992) for the top and bottom parts, respectively.

Since sediment accumulation rates were ~10 cm/kyr across the PETM on the New Jersey Shelf, on average, these sections are potentially well suited to assess infra-PETM climate dynamics. Here we provide a paleoecological evaluation of the PETM by using dinocyst distribution patterns set against the background of the combined multidisciplinary New Jersey paleoenvironmental datasets related to sea surface temperature (planktonic foraminifer δ^{18}O, TEX_{86}), energy level of the sedimentary environment (bulk sediment grain size), productivity (calcareous nannofossils) and river supply of terrigenous matter (Branched and Isoprenoid Tetraether (BIT) index, and clay flux data). With this approach, we aim to detect environmental trends *within* the PETM to eventually contribute to the understanding of processes that underly this event, and the effects of rapid global warming and exogenic carbon release during greenhouse conditions.

2 Material and methods

2.1 Material

The Bass River core (39°36′42″ N, 74°26′12″ W) was drilled in Bass River State Forest, New Jersey, during ODP Leg 174AX in 1996 (Miller et al., 1998). The Wilson Lake core (39°39′ N, 75°03′ W) was drilled by the USGS in 2000 and is located approximately 30 km west of Bass River. Wilson Lake was, hence, located closer to the paleoshoreline than Bass River. Previously published lithological and micropaleontological information indicates that the New Jersey sites were located on the shelf during the PETM (Gibson et al., 1993, 2000). Uppermost Paleocene sediments of the Vincetown Formation at both sites are relatively condensed (average sedimentation rates of $\sim$1 cm kyr^{-1}) and consist of glauconite-bearing siltstones, interpreted as a transgressive systems tract (Liu et al., 1997; Cramer et al., 1999) (Figs. 2, 3). The PETM was previously identified at both sites, based on the CIE in calcite and dinocyst δ^{13}C records (Cramer et al., 1999). Based on these records, the onset of the CIE is at 357.3 meters below surface (mbs) at Bass River (Fig. 2). In the δ^{13}C record measured on bulk carbonate (BC) at Wilson Lake, the base of the CIE is not as clearly marked as at Bass River, primarily due to the absence of carbonate between $\sim$109.3 and $\sim$109.8 mbs (Fig. 3). The δ^{13}C record measured on dinocysts (DINO) shows background late Palaeocene values up to $\sim$110.0 mbs. At this level the transition to true CIE values starts, coinciding with a negative step in the $\delta^{13}\mathrm{C}_{\mathrm{BC}}$ record, together implying the base of the CIE to be at this level (Sluijs et al., 2007b). The onset of the CIEs marks the transition to the Manasquan Formation, and the entire CIE is rich in clay, particularly kaolinite, and devoid of any siliciclastic coarse fraction (Cramer et al., 1999). The CIEs comprise very expanded deposits that exhibit sedimentation rates of approximately 8–10 cm kyr^{-1} (Gibbs et al., 2006; Sluijs et al., 2007b; John et al., 2008). The upper part of the CIE is truncated by a sequence boundary at both sites, and sediments overlying this interval are at least 2 Myr younger than the PETM (Cramer et al., 1999).

2.2 Methods

Processing and analyses

Palynological processing was performed using standard methods described in Sluijs et al. (2003). Briefly, $\sim$10 g of freeze-dried sample, spiked with a known amount of *Lycopodium* spores, was treated with 30% HCl and twice with 38% HF for carbonate and silicate removal, respectively. Residues were sieved using a 15-μm nylon mesh, and subsequently mounted on microscope slides and analyzed under 500x magnification. Raw dinocyst data are available in the supplement, see: http://www.biogeosciences.net/6/1755/2009/bg-6-1755-2009-supplement.zip. All slides, including type materials, are lodged in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, The Netherlands.

Dinoflagellate cyst ecology and grouping of taxa

Less than 20% of living dinoflagellate species produce "fossilizable" organic walled cysts, or "dinocysts" (Fensome et al., 1996a). It is generally assumed that most of these fossil organic dinocysts represent the hypnozygotic stage of a dinoflagellate species. Organic cysts of dinoflagellates can be traced back to the motile stage (theca) through laboratory incubation experiments (e.g., Rochon et al., 2009). Increasingly, it is made clear that at least several Recent dinoflagellate species may produce various cyst "morphotypes" depending on the physicochemical parameters of the water mass in which the theca develops or because of other, unknown ecological and/or biological, incl. genetic aspects (Ellegaard, 2000; Hallett, 1999). In the absence of fossilized genetic materials and/or relevant DNA/RNA studies, paleontologists have based dinocyst taxonomy on even the smallest of morphological details observed in/on fossil remains. Unfortunately, seen in the light of the incubation experiments, it is notoriously difficult, if not impossible, to determine the true biological and/or ecological relevance of such details. Yet, in order to extract meaningful paleoecological information from fossil dinoflagellate remains, it is vital to establish whether recorded specimens represent relatively consistent biological or even ecological entities or not. Here, in order to at least assess *some* possible ecological relationships between apparently changing physicochemical parameters and dinocyst paleoecology we take an approach that is founded on largely empirically based grouping of morphologically closely related forms. These taxa may either be strictly, or loosely defined accepted "species", groups of "species" within genera, genera themselves, or even groups of genera (cf., Brinkhuis, 1994; Pross and Brinkhuis, 2005; Sluijs et al., 2005). Next, we assume that any given high relative and/or high absolute abundance of these taxa per unit time reflects (sub) optimal environmental conditions and/or wider tolerance towards certain environmental conditions for such taxa. For example, a monotypic assemblage is taken to indicate that only that specific taxon was able to cope with apparently restricted marine conditions.

For practical purposes, we follow the nomenclature cited in Fensome and Williams (2004). In the taxonomic section, we present the rationale for the established "eco" taxa employed herein.

Statistical analyses

For paleoenvironmental analyses we carry out correspondence analyses similar to those presented in Pross and Schmiedl (2002) and Dale et al. (2005). Principle component (PCA) and canonical correspondence analyses (CCA)

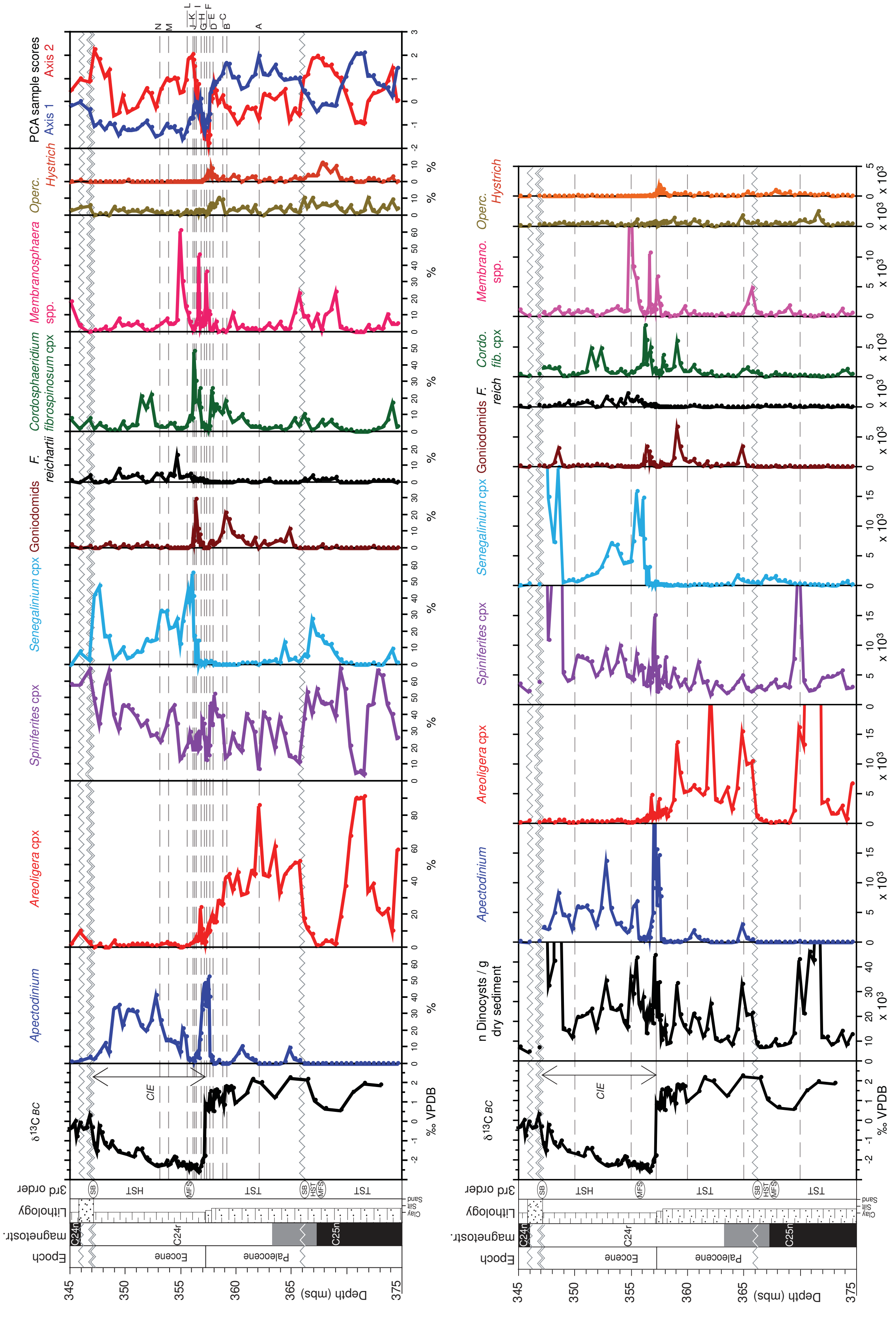

Fig. 2. Dinocyst distribution across the Late Paleocene – Early Eocene at Bass River. **(A)** Relative abundances (percentages). Letters refer to dinocyst events listed in Table 1. **(B)** Absolute quantitative results.

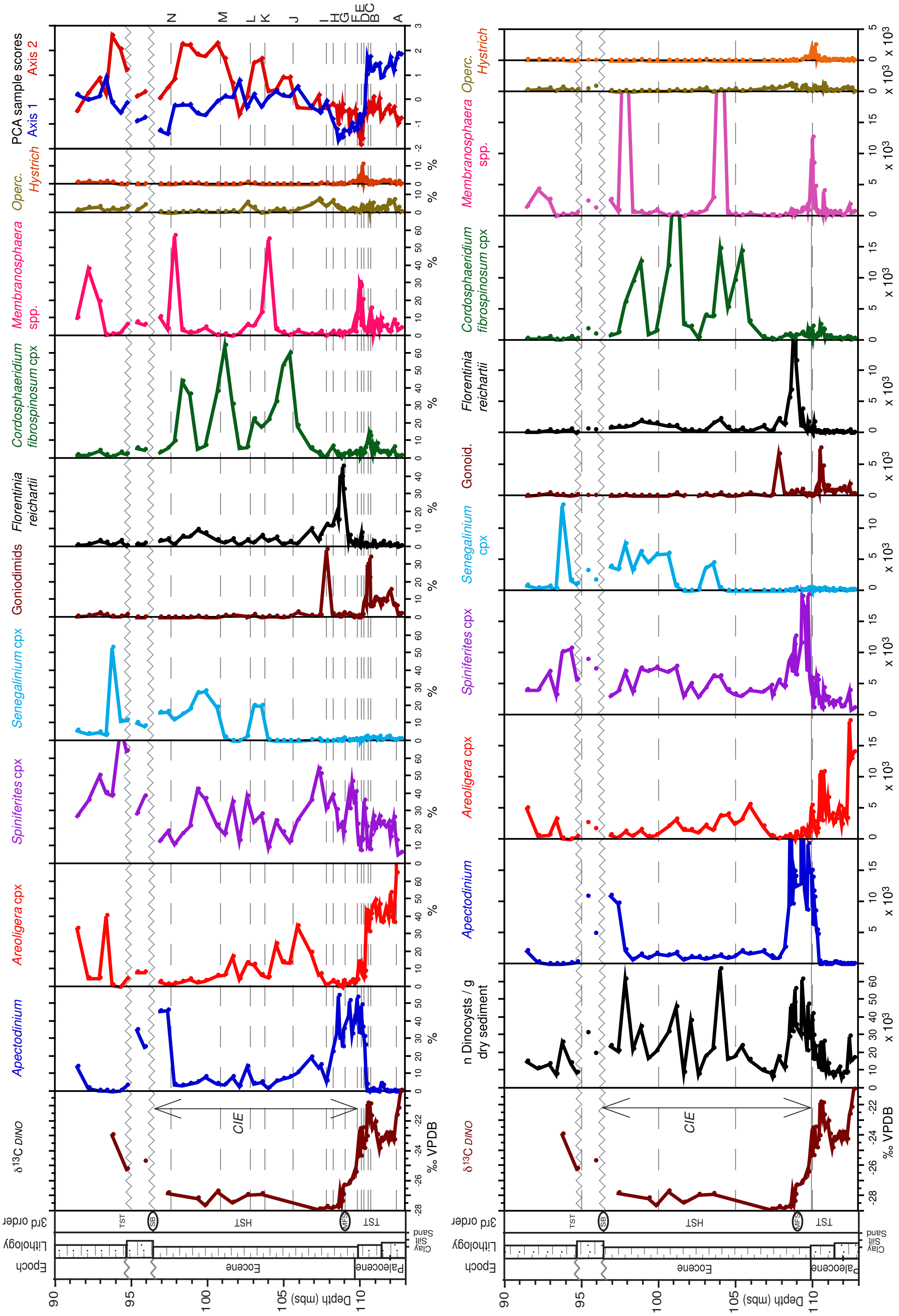

Fig. 3. Dinocyst distribution across the Late Paleocene – Early Eocene at Wilson Lake. **(A)** Relative abundances (percentages). Letters refer to dinocyst events listed in Table 1. **(B)** Absolute quantitative results.

were done using the software package Canoco (ter Braak and Smilauer, 2002). With the CCAs we aim to assess correspondence of dinocyst taxa with the environmental parameters sea surface temperature (TEX_{86}; (Sluijs et al., 2007b; Zachos et al., 2006), energy level of the environment ($>63\,\mu$m sediment fraction; (John et al., 2008), input of terrestrial organic matter (BIT; Sluijs et al., 2008a) and the abundance of metals (MS) in the sediment. This will be done to gain better insight in the paleoecological preferences of the dinoflagellates.

3 Results

3.1 Dinocyst distribution patterns

Dinocyst assemblages are very similar in both relative and absolute abundances between Bass River and Wilson Lake, and generally comprise taxa commonly recorded in mid-latitude marginal marine lower Paleogene sediments (Figs. 2, 3 and supplement: http://www.biogeosciences.net/6/1755/2009/bg-6-1755-2009-supplement.zip). Late Paleocene assemblages are either dominated by representatives of the typically open marine *Spiniferites* complex, or by members of the *Areoligera* complex (Figs. 2, 3). We have recorded transient abundances of representatives of the family Goniodomaceae, particularly *Eocladopyxis* spp., but also *Heteraulacacysta* spp. and *Polysphaeridium* spp. These are widely considered to be characteristic of restricted marine, usually lagoonal, settings with generally high, but also (seasonally) variable salinities in the Quaternary (Reichart et al., 2004) and the Paleogene (Brinkhuis, 1994). Approximately 5 kyrs prior to the onset of the CIE, specimens assignable to *Apectodinium* spp. become dominant (Sluijs et al., 2007b). Particularly within the PETM, representatives of a suite of morphologically closely related peridinioid genera are abundant (particularly those assignable to *Senegalinium* and *Phthanoperidinium*), a group that in general tolerated very low surface water salinities (Brinkhuis et al., 2006; Röhl et al., 2004; Sluijs et al., 2006, 2007b, 2008b), and likely preferred high nutrient and/or food supply (e.g., Dale and Fjellså, 1994; Sluijs et al., 2005). Additional locally common to abundant taxa include *Cordosphaeridium* spp., *Membranosphaera* spp., *Hystrichosphaeridium tubiferum*, *Operculodinium* spp., and a new species of *Florentinia*.

3.2 Site-to-site correlation

Prior to the PETM, assemblages both at Wilson Lake and Bass River are dominated by representatives of *Areoligera*, but diversity increases within the PETM. Because the sites are only ∼30 km apart, changes in dinocyst assemblages on these timescales should be concomitant between these sites if they represent regional rather than local changes in environment. Therefore, the various shifts allows a much more detailed correlation of dinocyst-defined events than can be achieved by carbon isotope stratigraphy (Table 1). Even though some of these correlations are tentative, they are stratigraphically consistent and indicate that the dinocyst assemblage changes reflect environmental change on a regional scale. According to this correlation, events D through K occur within 2 meters at Bass River but span ∼6 m at Wilson Lake, indicating condensation at Bass River relative to Wilson Lake during the time of deposition (Fig. 4). Because the sequence of events is the same for both sites across the onset of the PETM, it is likely that both sites are complete in this interval and there is no sign of a hiatus at Bass River as was hypothesized by John et al. (2008). Moreover, at Wilson Lake, the 2 Myr hiatus occurs approximately 1 m above event N, while the PETM continues for another 6 m at Bass River. This implies that more of the PETM is present at Bass River than at Wilson Lake.

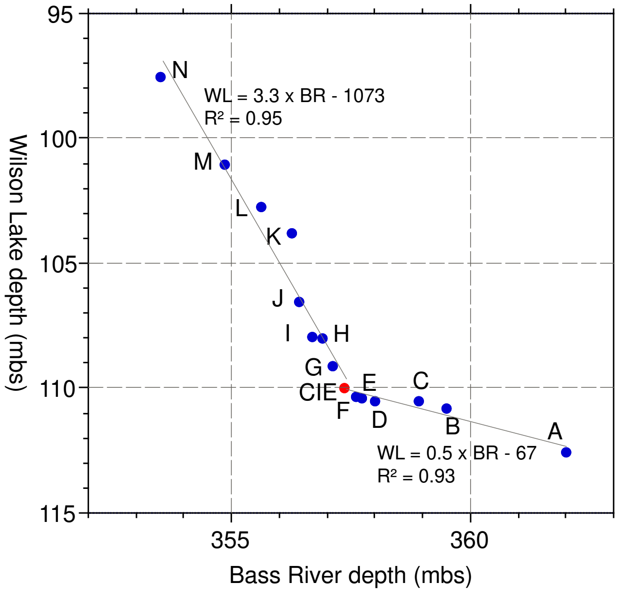

Fig. 4. Depth-depth plot based on dinocyst events (Table 1) indicating relative sedimentation rates between Wilson Lake and Bass River.

3.3 Statistical analyses

The similarity in dinocyst assemblages between Wilson Lake and Bass River is confirmed by the PCA analyses on relative abundances (Fig. 5a). For both sites the PCAs clearly separate the *Areoligera*, *Apectodinium* and *Senegalinium* complexes along axes 1 and 2. Also most other taxa mutually plot in similar directions, e.g., Goniodomids and *Operculodinium* plot in a similar direction as *Areoligera*. For further comparison between the sites, we carried out a PCA combining the Wilson Lake and Bass River data (Fig. 5b) and included the sample scores of Axis 1 and Axis 2 in Figs. 2a and 3a. The patterns in this PCA are similar to the PCAs of the individual sites.

Table 1. Dinocyst events recognized at Bass River and Wilson Lake.

Event	Description	Remarks	Onset Bass River (mbs)	Termination Bass River (mbs)	Onset Wilson Lake (mbs)	Termination Wilson Lake (mbs)
A	sharp decrease (>70% −40%) in the abundance of *Areoligera*		362.00		112.55	
B	short-lived acme of Goniodomid taxa		359.50	359.00	110.80	110.60
C	second decrease in *Areoligera* abundance		358.90		110.50	
D	short-lived abundance of *Hystrichosphaeridium*		358.00	357.40	110.50	110.00
E	the onset of the *Apectodinium* acme		357.70		110.40	
F	abundance of *Membranosphaera*	tentative correlation	357.60	357.30	110.30	109.90
CIE			357.35		110.00	
G	abundance of *Florentinia reichartii*	tentative correlation, not truly unambiguous at Bass River	357.10		109.10	108.30
H	rapid decrease in *Apectodinium* abundance		356.90		108.00	
I	short-lived acme of Goniodomid taxa		356.67	356.35	107.90	
J	abundance of *Cordosphaeridium*	tentative correlation	356.40	356.15	106.50	103.00
K	onset of abundant *Senegalinium* cpx (low salinity-tolerant)		356.25		103.80	
L	pulse in *Apectodinium* abundance	tentative correlation, not truly unambiguous at Wilson Lake	355.60	355.10	102.70	102.60
M	second increase in *Senegalinium* cpx (low salinity-tolerant)		354.85		101.00	
N	increase in *Apectodinium* abundance		353.50		97.50	

CCA analyses also show congruent patterns between Wilson Lake and Bass River (Fig. 6). At both sites, *Areoligera* and *H. tubiferum* (although abundances are relatively low in the assemblages for the latter) plot along wt% >63 μm fraction. At Bass River, the low-salinity-tolerant group plots very close to magnetic susceptibility. *Apectodinium* generally plots in the same direction as TEX_{86}, although the correlation is not very firm.

4 Discussion

4.1 *Apectodinium* paleoecology

The biotic response of dinocysts to the PETM is particularly interesting because it includes a quasi-global acme of *Apectodinium* spp., thereby comprising usually >40% of the dinocyst assemblage (Heilmann-Clausen, 1985; Powell et al., 1996; Bujak and Brinkhuis, 1998; Heilmann-Clausen and Egger, 2000). Such a global, synchronous acme is unique in the dinocyst fossil record spanning the late Triassic to the Recent.

4.1.1 Temperature

In the CCAs, *Apectodinium* correlates best, although still weakly, with temperature. It plots in different directions to the low-salinity-tolerant group, and the inner neritic *Areoligera* complex. The taxon *Apectodinium* originated close to the Danian-Selandian boundary (Brinkhuis et al., 1994), and abundant occurrences remained largely restricted to low latitudes throughout the Palaeocene (Bujak and Brinkhuis, 1998). It has been hypothesized that temperate to polar sea surface temperatures increased to allow poleward migration of *Apectodinium* during the PETM (Bujak and Brinkhuis, 1998; Crouch et al., 2001; Sluijs et al., 2006). However, recently it was shown that temperatures in mid-latitude regions, incl. New Jersey, were probably already high enough during the Late Paleocene to allow for abundant *Apectodinium* (Zachos et al., 2006; Sluijs et al., 2007b). This indicates

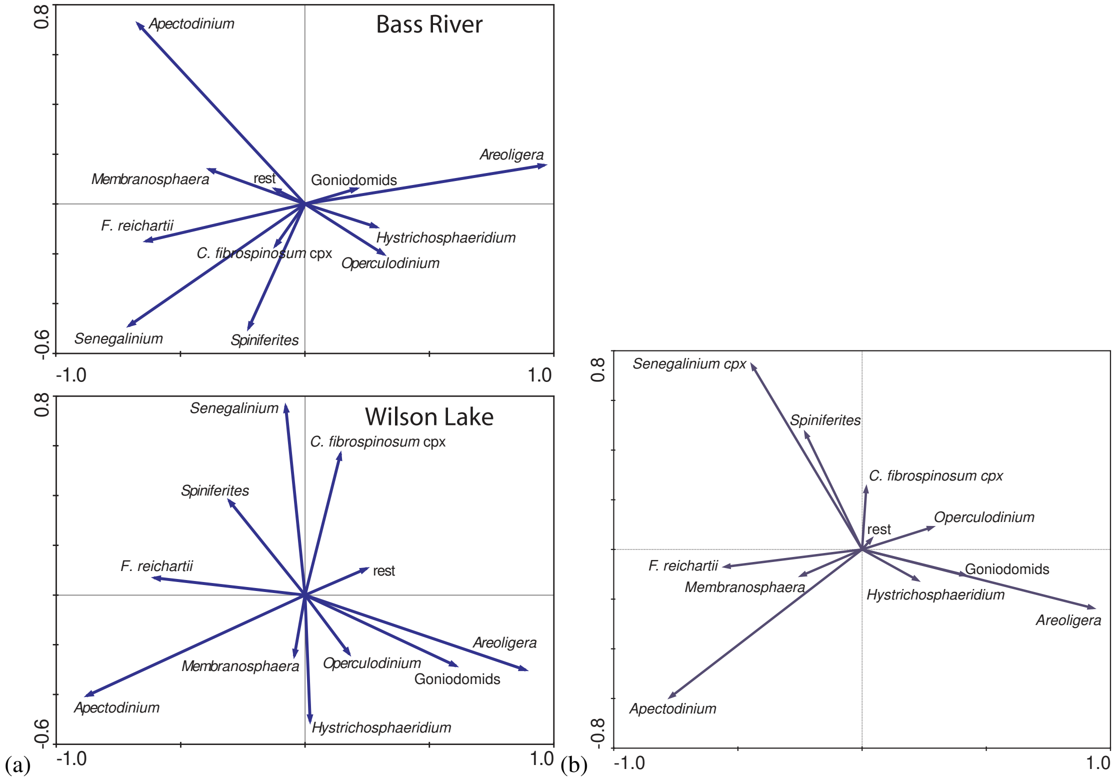

Fig. 5. Principle Component Analysis scatter plots. **(A)** Bass River and Wilson Lake; **(B)** combined Bass River and Wilson Lake.

that factors other than temperature prevented mid-latitude abundances of this taxon at that time (Sluijs et al., 2007b). Moreover, the onset of the *Apectodinium* acme in New Jersey occurred prior to the onset of the rise in mean annual temperature (MAT), suggesting that (an) additional environmental factor(s) triggered the acme in this region (Sluijs et al., 2007b). However, many dinoflagellates bloom in a particular season (e.g., Dale, 2001), implying that proliferation of *Apectodinium* may have been initiated by environmental change (such as warming or stratification) of one critical season, thereby not significantly influencing MAT. In effect, there is the option that the apparently massive abundance actually only reflects 2–3 anomalous weeks per year (Fensome et al., 1996b).

4.1.2 Salinity

Most representatives of *Apectodinium* were likely also euryhaline, although truly brackish conditions were perhaps not optimal (Sluijs et al., 2007b, 2008b). While in mid-latitude regions *Apectodinium* contributes at least 40% of the assemblage for much of the PETM (Figs. 2, 3) (Heilmann-Clausen, 1985; Powell et al., 1996; Bujak and Brinkhuis, 1998; Heilmann-Clausen and Egger, 2000), *Apectodinium* abundances only reach to ~20% in the Arctic, where typical low-salinity-tolerant dinocysts remain dominant (Sluijs et al., 2008b). Similar trends are recorded at Bass River and Wilson Lake, where *Apectodinium* spp. became outnumbered by typical low salinity-tolerant dinocysts during phases of the PETM (Figs. 2, 3). Moreover, *Apectodinium* spp. do not plot closely to the low-salinity-tolerant dinocysts in the PCA. This indicates that while *Apectodinium* was reasonably successful at relatively low salinities, such as in the Arctic during the PETM (Sluijs et al., 2008b), other taxa were able to dominate dinocyst assemblages under such ecological conditions.

4.1.3 Heterotrophy

Several authors have suggested that the dinoflagellates that formed *Apectodinium* cysts may have been heterotrophic and fed on organic detritus or other plankton (Bujak and Brinkhuis, 1998; Crouch et al., 2001, 2003b; Sluijs et al., 2005, 2007b). This suggestion was primarily based on the fact that *Apectodinium* exhibits some similarities in the plate organization, a critical tool in taxonomical classification, with extant heterotrophic dinoflagellates (Evitt, 1985; Lentin and Vozzhennikova, 1989; Fensome et al., 1996b). Discussion also exists on whether *Apectodinium* and its family Wetzeliellioidae are related to the Recent, mainly diatom feeding (Buskey, 1997) genus *Protoperidinium*.

At both Wilson Lake and Bass River we have recorded many *Apectodinium* specimens that have the typical brown color usually observed in cysts of Recent members of

Protoperidinium (Plate 1I–L). This implies that, along with some systematic resemblances, the *Apectodinium* cyst wall materials are very similar to *Protoperidinium* cysts. Hence, although morphological differences remain between Recent cysts of heterotrophic dinoflagellates and *Apectodinium*, this could be taken as an additional line of evidence that *Apectodinium* was a heterotrophic dinoflagellate.

The question whether *Apectodinium* was heterotrophic or not is critical, because the nutrient load of an ecosystem is usually well reflected in the abundance of heterotrophs versus autotrophs. Nutrient-rich conditions are required to sustain abundant heterotrophs in an ecosystem because of the loss of energy in subsequent stages of the food chain. Its presumed heterotrophic lifestyle implies that *Apectodinium*, similar to Recent *Protoperidinium*, was dependent on the availability of prey (perhaps diatoms, or other [even zoo-] plankton) that are, in turn, dependent on nutrient availability (particularly nitrogen and phosphorus). Hence, if it was heterotrophic, the global nature of the *Apectodinium* acme during the PETM (Sluijs et al., 2007a) suggests that shallow seas around the globe exhibited a strong increase in nutrient availability, or some food source (Powell et al., 1996; Bujak and Brinkhuis, 1998; Crouch et al., 2001, 2003a; Crouch and Brinkhuis, 2005; Sluijs et al., 2005). Locally, elevated near-coast productivity at the PETM has been suggested to explain benthic foraminiferal and calcareous nannofossil assemblage changes as well as organic-rich sediments in marginal marine realms (e.g., Thomas and Shackleton, 1996; Speijer and Schmitz, 1998; Gavrilov et al., 2003; Gibbs et al., 2006; Sluijs et al., 2006, 2008b; see overview in Sluijs et al., 2007a).

The mechanism behind global eutrophication of at least shallow seas is as yet unclear. It has been suggested that the global warming associated with the PETM triggered intensification of weathering, the hydrological cycle and run off in many regions around the world (Robert and Kennett, 1994; Ravizza et al., 2001; Schmitz et al., 2001; Crouch et al., 2003b; Hollis et al., 2005; Giusberti et al., 2007; Nicolo et al., 2007; Sluijs et al., 2007b). The increase in clay supply to the New Jersey shelf (and many other regions; see Sluijs et al. (2008a) for an overview) supports such a scenario. However, the low amount of terrestrial palynomorphs throughout the section hampers the evaluation of changes in the flux of terrestrial material on the New Jersey Shelf. An alternative mechanism of eutrophication is related to hurricanes. Modeling studies have suggested intensification of storms in an extreme greenhouse world (Emanuel, 2005; Emanuel et al., 2004; Sriver and Huber, 2007). If more intense storms occurred during the PETM compared to background conditions, they should have caused mixing of deeper nutrient-rich waters into the photic zone on a regional scale thereby promoting primary production.

Because the fossil record probably only represents a very small percentage of the surface water assemblages, it is hard to reconstruct a relatively complete food web for the PETM. Therefore it is equally difficult to identify the exact food source of *Apectodinium* and to unequivocally show it was auto- or heterotrophic. Regardless of these unanswered questions on its nature, the acme directly implies that the food source of *Apectodinium* was globally very abundant in shallow marine settings. If it was heterotrophic, the acme implies that the global marginal marine ocean became enriched in nutrients and food.

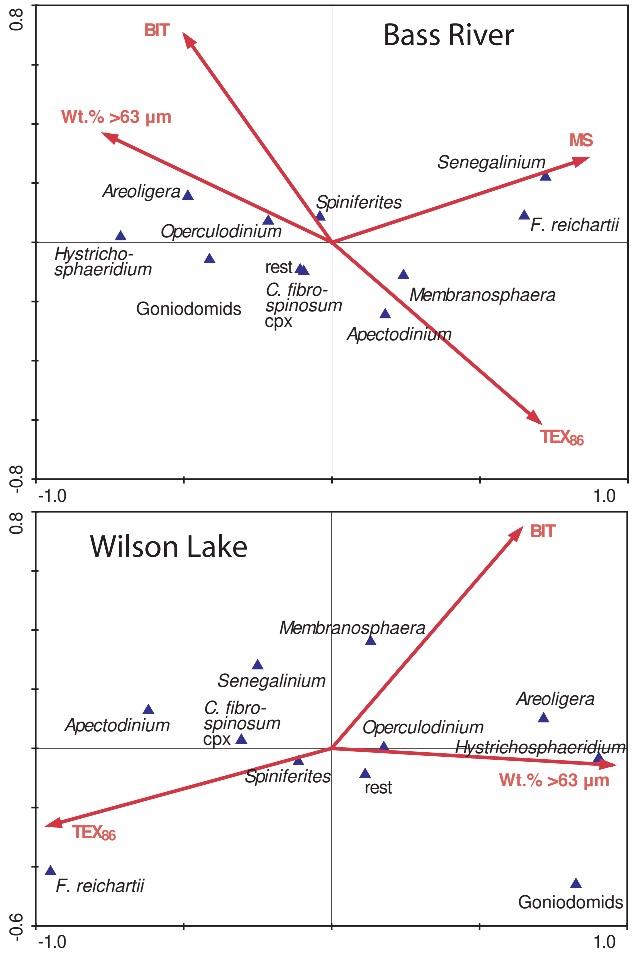

Fig. 6. Canonical Correspondence Analysis scatter plots.

4.1.4 Which other critical factor?

A baseline requirement for the distribution of *Apectodinium* appears to have been high temperatures. *Apectodinium* acmes have been recorded from upper Paleocene deposits in the Tethyan Ocean (Powell et al., 1996; Bujak and Brinkhuis, 1998; Iakovleva et al., 2001), suggesting that conditions there were episodically and locally similar to those on a global scale during the PETM (Crouch et al., 2003a). Similar to other mid-latitude regions, *Apectodinium* was already present on the New Jersey Shelf at least since Chron C25n times (Fig. 2); yet, in contrast to low-latitude sites (Iakovleva et al., 2001) no pre-PETM acmes have been reported from such regions. Moreover, food availability and salinity, and/or stratification seem important. Although these parameters were likely important for the distribution of *Apectodinium*, it appears that even a combination of these factors was likely not truly unique in the early Paleogene at mid latitudes. This suggests that some critical other environmental factor(s) that stimulated massive *Apectodinium* production has not yet been identified. Somehow, however, this unidentified factor was related to the PETM. Whichever combination of surface water parameters caused the global acme of *Apectodinium*, it is consistently associated with the PETM and appears to signify a harbinger to global warming and carbon injection as the acme started just prior to the PETM warming and the CIE in mid-latitude areas (Sluijs et al., 2007b).

4.2 *Areoligera* and transgression

Much empirical evidence suggests that a dominance of the *Areoligera* complex indicates inner neritic, high energy environments (Brinkhuis, 1994; Pross and Brinkhuis, 2005), while the *Spiniferites* complex is mostly recorded from neritic deposits with increasing relative abundances at outer neritic localities (Brinkhuis, 1994; Pross and Brinkhuis, 2005). This evidence was previously used to infer a late Paleocene transgression in New Jersey by applying the ratio between *Spiniferites* and *Areoligera* abundances (Sluijs et al., 2008a). In the CCA analyses (Fig. 6), *Areoligera* shows a significant correlation with the wt% coarse fraction of the sediment, which had been previously been used to identify a phase of transgression (Liu et al., 1997; Cramer et al., 1999). *Spiniferites* does not correlate to any proxy data in the CCAs, supporting the inference that they inhabited all areas on the shelf during the Paleogene, much like today (Wall et al., 1977). In New Jersey, and also in other regions, abundant *Areoligera* appears consistently related to third order transgressive systems tracts in sequence stratigraphic terms, and thus sea level rise in neritic settings (e.g., Crouch and Brinkhuis, 2005; Iakovleva et al., 2001; Sluijs et al., 2008a).

Hence, in a manner similar to the *Spiniferites/Aeroligera* ratio (Sluijs et al., 2008a), the sample scores for Axis 1 of the PCA at Bass River and Wilson Lake should in part reflect sea level (Fig. 2). The recorded trends are consistent with a transgression during the PETM, a phenomenon recorded on a global scale (Sluijs et al., 2008a).

4.3 Fresh water forcing

Axis 2 in all PCAs is dominated by the abundances of the low-salinity-tolerant group, making it an indicator for low salinity. In the CCA, the low-salinity-tolerant group corresponds closely to magnetic susceptibility (MS) of the sediment at Bass River. The MS values are dominantly controlled by abundances of biogenic magnetic particles, produced by bacteria (Kopp et al., 2007; Lippert and Zachos, 2007). These bacteria thrive in a particular niche, as they require low oxygen concentrations and a high supply of iron (Fe^{2+}). However, conditions were not euxinic because free sulfide dissolves bacterial magnetite (Canfield and Berner, 1987; Dickens, 2008). These specific requirements suggest that high fluxes of organic carbon to the sea floor to supply the Fe^{2+}, but the magnetic grains were not subject to sulfidic conditions because the sediments were deposited on top of oxygenated uppermost Paleocene sediments (Dickens, 2008). This scenario requires a significant increase in runoff and production rates (Lippert and Zachos, 2007), which is consistent with the vast increase in clay sedimentation (Cramer et al., 1999; John et al., 2008) as well as with the strong positive correlation between MS and the *Senegalinium* complex, which not only suggests low salinities, but also high food/nutrient supply (Sluijs et al., 2007b).

This supports previous inferences (Brinkhuis et al., 2006; Sluijs et al., 2006, 2007b, 2008b) that many hexaperidinioids, particularly *Senegalinium* and *Phthanoperidinium*, but also *Deflandrea*, *Cerodinium, Spinidinium* and related genera (Sluijs et al., 2009), were indeed tolerant of low salinities and flourished best during episodes of abundant nutrients/food (e.g., Dale and Fjellså, 1994; Firth, 1996; see overview in Sluijs et al., 2005). Abundances of the *Senegalinium* complex suggest that increased fresh water forcing started some time (perhaps 10 kyr, if the cycles in *Apectodinium* (Fig. 2) are precession-related (Sluijs et al., 2007b), see below) after the onset of the CIE, consistent with a humid climate state at least during the first ∼100 kyr of the PETM (e.g., Bowen et al., 2004).

5 A variable climate state during the PETM?

Although high abundances of *Apectodinium* and the *Senegalinium* complex occur across portions of the New Jersey PETM sections, abundances clearly vary significantly during the PETM. Short-lived acmes of *Hystrichosphaeridium*, *Eocladopyxis* spp., *Cordosphaeridium fibrospinosum*, *Membranosphaera* spp. and the new species *Florentinia reichartii* occur throughout the PETM at both Bass River and Wilson Lake both in the relative and absolute quantitative records (Figs. 2 and 3). Such variation is absent in the sediments deposited during the ∼1 Ma prior to the PETM. It is unlikely that the record is affected by preferential oxidation of some (peridinioid) taxa, as these are present throughout the record and well preserved. In part, in may be related to winnowing, indicated by the general low abundance of clay and the coarse nature of the sediments, which would concentrate the relatively large taxon *Areoligera* and reduce abundances of smaller taxa, particularly *Senegalinium* spp., *Phthanoperidinium* spp. and *Membranosphaera* spp. However, the absence of temporal abundances of other typically large taxa, such as specimens of *Cordosphaeridium* and

Hystrichosphaeridium, as recorded within the PETM, suggests more stable conditions prior to than during the event.

The cyclic abundances of *Apectodinium* as recorded within the PETM at Bass River, both as a percentage of the assemblage and numbers per gram sediment, has been suggested to be associated to the precession cycle (Sluijs et al., 2007b). Regardless of the forcing mechanism, maxima in *Apectodinium* co-occur with maxima in the number of total dinocysts per gram sediment. The cyclic behaviour of total dinocysts and *Apectodinium* per gram, while absolute abundances of most other taxa remain constant, strongly suggests nutrient/food supply as a cause rather than variations in siliciclastic sediment supply. Assuming constant preservation, which is likely considering persistent suboxic seafloor conditions (Dickens, 2008; Kopp et al., 2007; Lippert and Zachos, 2007), varying nutrient/food abundances controlled the cycles in *Apectodinium*, consistent with a heterotrophic lifestyle of this taxon.

Peak abundances of representatives of *Eocladopyxis*, a genus within the family Goniodomaceae that in the Recent is usually associated with low latitude hyposaline or hypersaline lagoonal settings (Bradford and Wall, 1984; Wall et al., 1977), are recorded just prior to and immediately after the onset of the PETM at both Bass River and Wilson Lake (Figs. 2, 3). Perhaps these taxa were transported down the shelf from lagoonal settings, but persistent low abundances of terrestrial organic matter (palynomorphs or biomarkers) invoke another mechanism. Perhaps the establishment of a hot and dry season increased sea surface salinities. In this light, high abundances of the related taxon *Polysphaeridium zoharyi*, recorded in the central Arabian Sea following North Atlantic Heinrich events (Reichart et al., 2004), are interesting. These abundances were explained by a mechanism of regional warming in winter, preventing a saline surface layer to overturn, causing a "hyperstratified" situation with lagoonal-type conditions in the open ocean (Reichart et al., 2004). Analogously, the establishment of seasonal hyperstratification, with hypersaline and warm surface waters, could explain temporal *Eocladopyxis* abundances on the New Jersey shelf.

Abundances of *Cordosphaeridium fibrospinosum* and (a large group of) related taxa often informally referred to by several authors as the *C. fibrospinosum* complex of morphologically highly variable taxa (see taxonomic section) occur abundantly during intervals within the PETM at Bass River and Wilson Lake. Although this complex as a whole has become extinct, it was cosmopolitan and several taxa within this group have been associated with stratified and even brackish conditions (e.g., Pross, 2001; Houben, 2008). *Hystrichosphaeridium* is also temporally abundant and our CCA analyses plot this species together with *Areoligera* towards wt% coarse fraction, suggesting it thrived in relatively high-energy environments. Only little paleoecological information is available for *Membranosphaera*, although it seems most abundant in higher latitudes (sometimes called *Elytrocysta* in Southern Ocean sections (e.g., Brinkhuis et al., 2003; Sluijs et al., 2003), and tolerated relatively low salinities (Sluijs et al., 2008b). Even less information is available for the new species *Florentinia reichartii* apart from that we have recorded it in marginal marine upper Paleocene – lower Eocene sediments in the Gulf of Mexico and the southwest Pacific we are currently studying (personal observation).

6 Synthesis/concluding remarks

Our findings prompt a picture of high environmental variability during the PETM at the New Jersey Shelf, likely related to at least regional climatic variability. Our results strongly suggest that the bulk of the variation we note is due to regional precipitation and runoff fluctuations, rather than the overall warm temperature. Such fluctuations may have led to strong, coupled stratification and salinity changes that may have guided the subsequent abundances of, for example, the *Senegalinium, Membranosphaera*, and goniodomid groups, *Hystrichosphaeridium* and *F. reichartii.* The hydrological cycle during the "ultra greenhouse" was apparently highly unstable, at least on a regional scale and on Milankovitch time scales. In this light, it is also remarkable that the relative and absolute abundance of sporomorphs from terrestrial higher plants is low during the PETM in New Jersey. Other mid latitude sites across this time interval around the world yield sometimes extremely abundant pollen and spores (e.g., Crouch et al., 2003b; Harrington, 2003; Steurbaut et al., 2003). One speculation concerning this aspect is that the hydrological or temperature regime of the region was so extreme that no stable vegetation could be established during this time.

This study also indicates the necessity of analyzing more chronostratigraphically well calibrated, high accumulation, marine and terrestrial PETM sites from around the world, principally to determine if the New Jersey climatic variability during the PETM was a regional or a larger scale phenomena.

7 Taxonomy

7.1 Systematic paleontology

Division Dinoflagellata (Bütschli, 1885) Fensome et al. (1993)
Class Dinophyceae Pascher (1914)
Subclass Peridiniphycidae Fensome et al. (1993)
Order Gonyaulacales Taylor (1980)
Family Gonyaulaceae Lindemann (1928)
Subfamily Cribroperidinioideae Fensome et al. (1993)
Florentinia reichartii sp. nov.
Plate 3F–L, Plate 4A–C

Derivation of name: named for Gert-Jan Reichart, geochemist at Utrecht University, in recognition of his pioneer integrated geochemical and palynological studies.

Holotype: Plate 4A–C. Specimen with numerous hollow processes, an antapical horn (4A), and an archeopyle involving precingular plate 3" (4A–B) plus all apical plates (see sulcal notch, Plate 4C); paratypes: Plate 3F–G, 3H–I, 3J, 3K–L.

Diagnosis: a small species of *Florentina* with distally closed, hollow, long cone-shaped processes and a short, blunt antapical horn.

Description: small, chorate gonyaulacean cyst, characterized by a small antapical horn, and an archeopyle that involves all apical and sometimes precingular plates. Operculum usually free, but may be partially attached. Central body is psilate and almost transparent. Processes are long, approximately (or sometimes more than) half the size of the main body, are hollow and distally-closed and non-tabular. Some processes may fuse in proximity of the central body. The antapical horn is relatively short, approximately as wide as long, and often barely visible. The archeopyle can only rarely be positively identified as type tA, and may additionally involve plate 4", with a usually detached operculum. Tabulation is barely discernable, either by some degree of clustering of groups of processes, the archeopyle or the antapical horn reflecting 6'"', which often constitutes the only consistent marker for orientation.

Discussion: *Florentinia reichartii* can be easily confused with *Lingulodinium machaerophorum* or *Diphyes* spp. during microscope analyses, but these are both usually larger and have precingular archeopyles, while *L. machaerophorum* also lacks an antapical horn. *F. reichartii* is much smaller than most other species within the genus, and its antapical horn is small relative to the size of the central body. Within the genus *Florentinia*, it bears closest resemblance to the much larger *F. ferox*, because processes may also fuse in proximity of the central body to create process-complexes. However, *F. ferox* has more proximally united processes that reflect tabulation, rather than clustered individual processes.

Dimensions: Holotype: 23×28 μm. Range: length 20(23)25 μm, breadth 23(24)28 μm. Specimens measured 10.

Stratigraphic occurrence: latest Paleocene and earliest Eocene on the New Jersey Shelf (upper Vincetown and Manasquan formations, this paper), northern plain of the Gulf of Mexico (Alabama, Missisippi, personal observation), East Tasman Plateau (Ocean Drilling Program Leg 189, personal observation).

7.2 List of encountered dinocyst species and complexes

The generic allocation of taxa follows that cited in Fensome and Williams (2004) unless stated otherwise. Along with *Florentinia reichartii* sp. nov., some new taxa have been recorded and are discussed below, and will be formally described elsewhere. Notes on certain taxa are also provided. Illustrated taxa are followed by plate references in brackets.

Achilleodinium biformoides (1A-B)
Achomosphaera alcicornum (1C)
Achomosphaera crassipellis
Adnatosphaeridium multispinosum
Adnatosphaeridium robustum (1D–F; 9A)
Alisocysta sp. 2 of Heilmann-Clausen (1985)
Apectodinium augustum (1I)
Apectodinium homomorphum Remarks: variation with very long processes abundant (1J; 9B–C)
Apectodinium parvum (1K)
Apectodinium quinquelatum Remarks: variation with very long processes abundant (1L)
Apteodinium spp.
Areoligera coronata
Areoligera senonensis
Areoligera complex. This complex includes the morphologically closely related, dorsal-ventrally compressed gonyaulacoid genera *Areoligera, Glaphyrocysta* and *Adnatosphaeridium* (9D)
Batiacasphaera compta
Batiacasphaera spp. (pars). Other species of *Batiacasphaera*
Calligodinium aceras
Cerebrocysta spp. (9E)
Cerodinium denticulatum
Cerodinium depressum
Cerodinium speciosa
Cerodinium wardenense
Cladopyxidium saeptum (2A)
Cordosphaeridium fibrospinosum (2B–E; 9F–G)
Cordosphaeridium fibrospinosum complex. Several authors (e.g., Brinkhuis and Schiøler, 1996) have discussed the morphologically closely related genera *Apteodinium*, *Cordosphaeridium, Damassadinium, Fibrocysta*, *Kenleya*. *Lanternosphaeridium*, *Muratodinium*, *Thalassiphora*, and *Turbiosphaera*, and even others. The "plasticity" in specimens assignable to this group is extremely large and virtually any morphological intermediate between several types of genera may be readily identified in Late Palaeocene and Early Eocene assemblages. Following Brinkhuis and Schioler (1996), we have chosen *C. fibrospinosum* as a central taxon in this group. Ongoing studies (e.g., Houben, 2008), indicate that many of the morphological manifestations recorded within this complex may in fact represent a single biological species, yet with different morphological end-members through geological time.
Cordosphaeridium miminum
Cribroperidinium sp. A. An unusual, very large ($\sim$100 μm), thin-walled species of *Cribroperidinium*. Questionably assigned because the tabulation is only discernible at cingulum and through the 4" archeopyle; operculum detached. (2H)
Cribroperidinium spp. (pars.). Other species of *Cribroperidinium*
Damassadinium spp. Part of the *C. fibrospinosum* complex
Dapsilidinium spp.
Deflandrea oebisfeldensis (2I)
Deflandrea phosphoritica

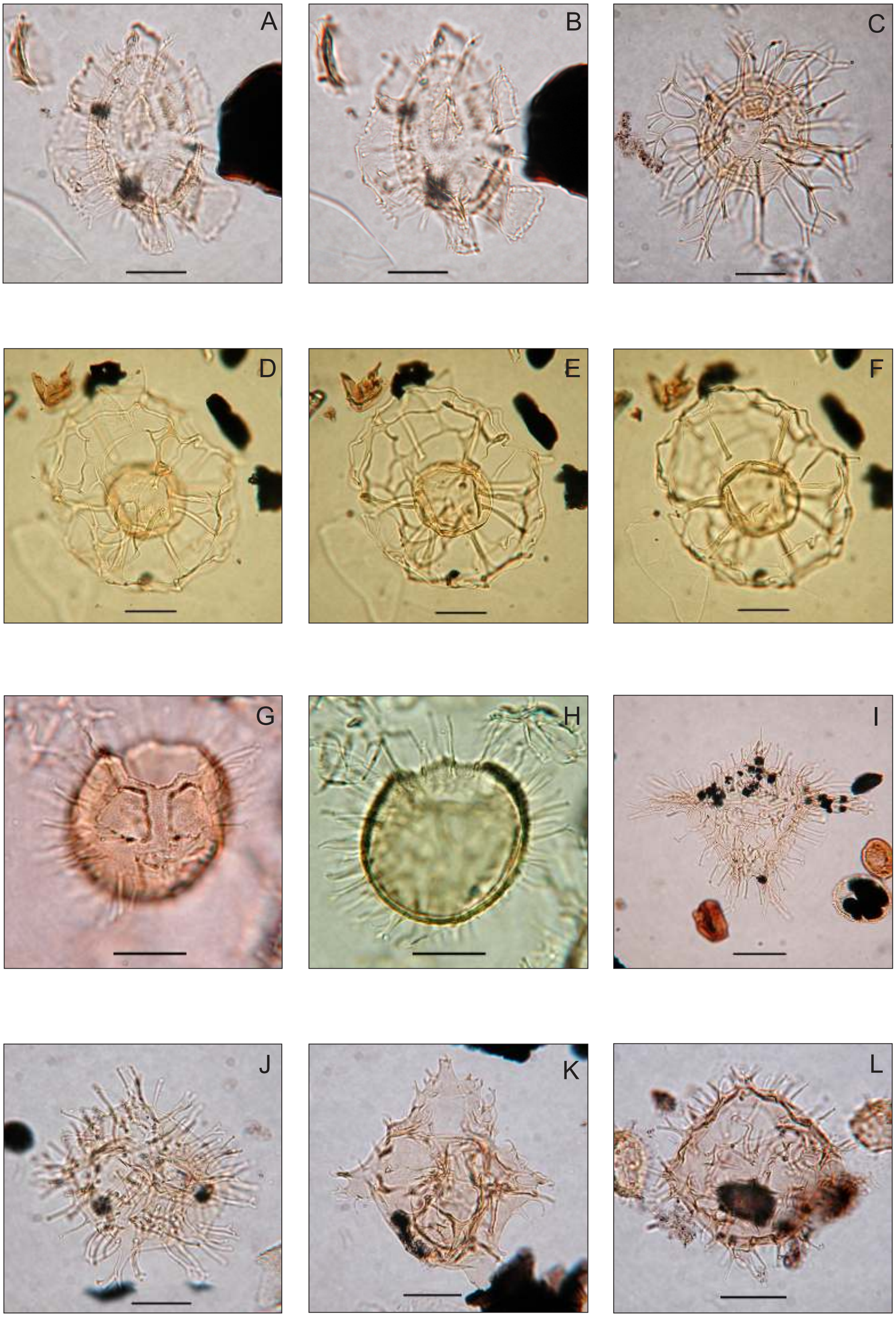

Plate 1. **(A–B)**, *Achilleodinium biformoides* (Bass River, 357.76 mbs, #1, England Finder coordinates: M61-2); **(C)**, *Achomosphaera alcicornu* (Bass River, 360.20 mbs, #1, P59-1); **(D–F)**, *Adnatosphaeridium robustum* (Bass River, 358.12 mbs, #1, N56-2); **(G–H)**, *Alisocysta* sp. 2 of Heilmann-Clausen (1985) (Wilson Lake, 110.0 mbs, #1, U45-1); **(I)**, *Apectodinium augustum* (Wilson Lake, 107.40 mbs, #1, O59-1); **(J)**, *Apectodinium homomorphum* (Bass River, 353.25 mbs, #1, L59-4); **(K)**, *Apectodinium parvum* (Bass River, 354.41 mbs, #1, N63-3); **(L)**, *Apectodinium quinquelatum* (Wilson Lake, 91.51 mbs, #1, M56-3). Scale bar=20 μm.

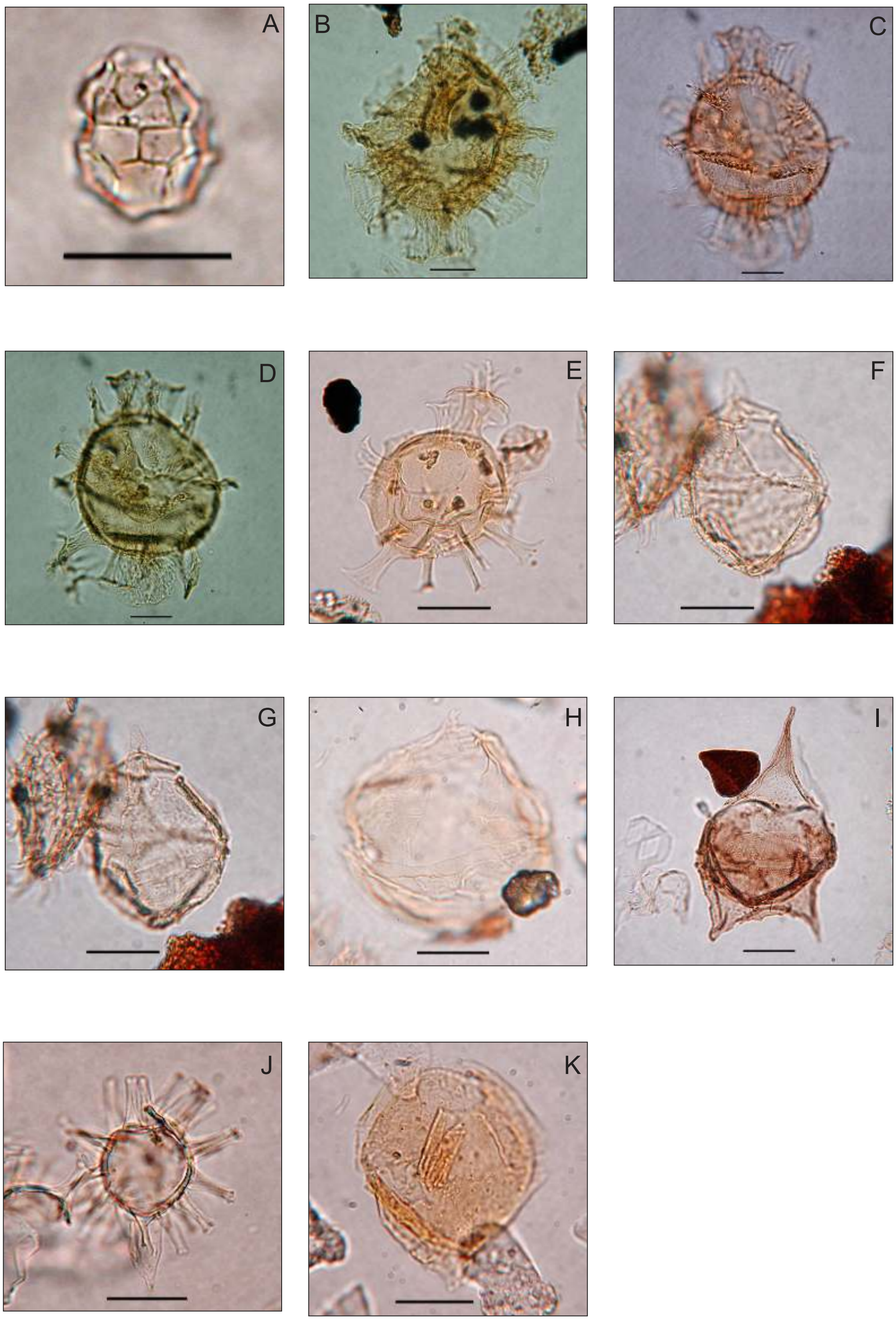

Plate 2. **(A)**, *Cladopyxidium saeptum* (Wilson Lake, 112.76 mbs, #1, England Finder coordinates: R44-3); **(B)**, *Cordosphaeridium fibrospinosum* complex. Morphotype intermediate between *C. fibrospinosum* and *Damassadinium* spp. (Bass River, 366.20 mbs, #1, L59-3); **(C–D)**, *Cordosphaeridium fibrospinosum* complex. Morphotype intermediate between *C. fibrospinosum* and *Turbiosphaera* spp. (Bass River, 396.95 mbs, #1, M62-1); **(E)**, *Cordosphaeridium fibrospinosum* (Bass River, 356.69 mbs, #1, M62-1); **(F–G)**, *Cribroperidinium* spp. (Bass River, 357.30 mbs, #1, Q52-1); **(H)**, *Cribroperidinium* sp. A. (Bass River, 347.13 mbs, #1, L64-2); **(I)**, *Deflandrea oebisfeldensis* (Bass River, 374.19 mbs, #1, H55-1); **(J)**, *Diphyes colligerum* (Wilson Lake, 112.76 mbs, #1, D53-3); **(K)**, *Dracodinium pachyderma* (Bass River, 345.93 mbs, #1, G60-4). Scale bar=20 μm.

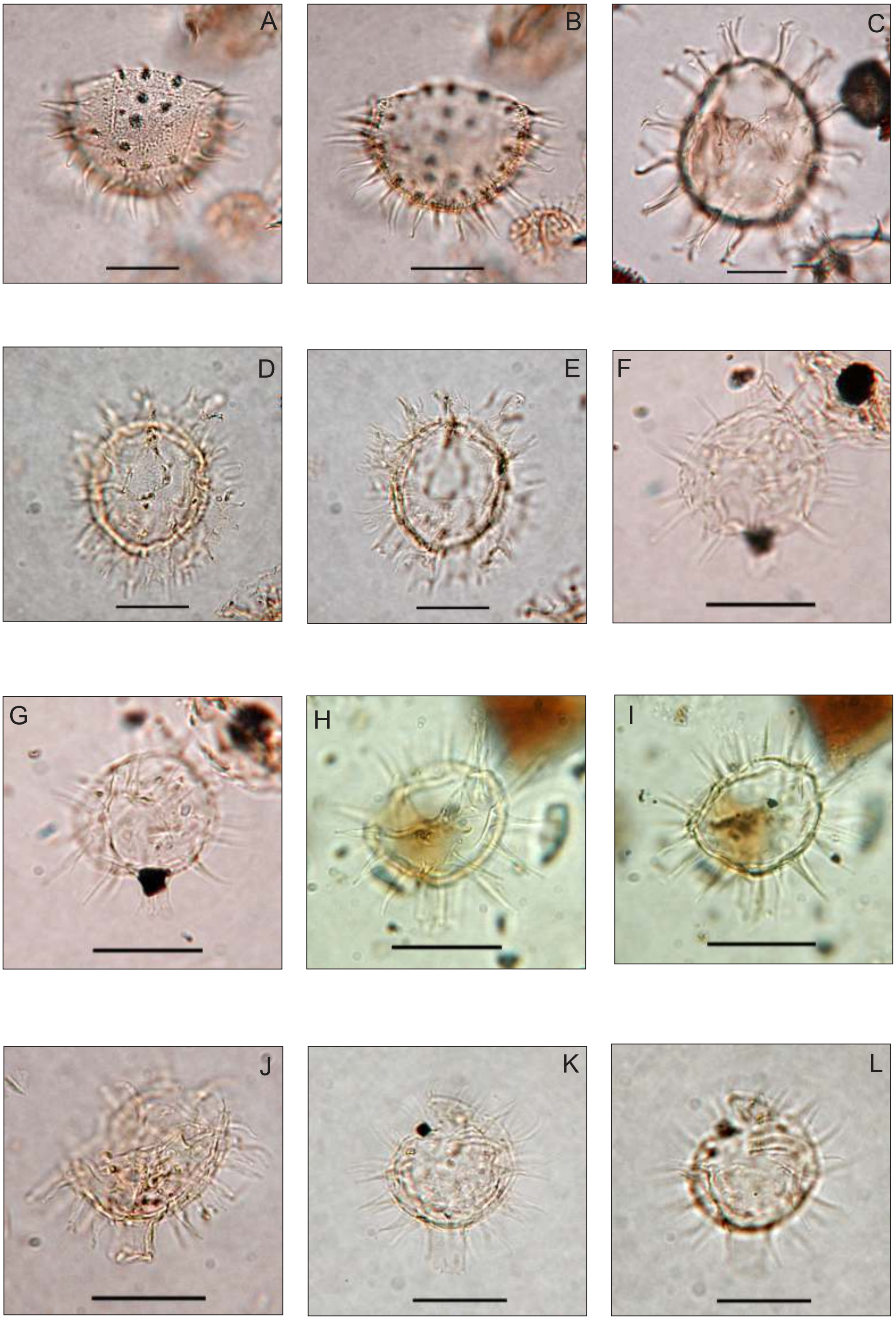

Plate 3. **(A–B)**, *Eocladopyxis peniculata* (Wilson Lake, 112.76 mbs, England Finder coordinates: O48-3); **(C)**, *Fibrocysta* spp. (Wilson Lake, 110.14 mbs, L45-2); **(D–E)**, *Florentinia ferox* (Bass River, 357.76 mbs, L62-1); **(F–L)**, *Florentinia reichartii* sp. nov. (F–G, paratype, Wilson Lake, 104.07 mbs, #1, N56-1; H-I, paratype, Wilson Lake, 111.97 mbs, #1, O57-1; J, paratype, Bass River, 349.04 mbs, #1, L52-2; K–L, paratype, Bass River, 351.08 mbs, #1, M49-2). Scale bar=20 μm.

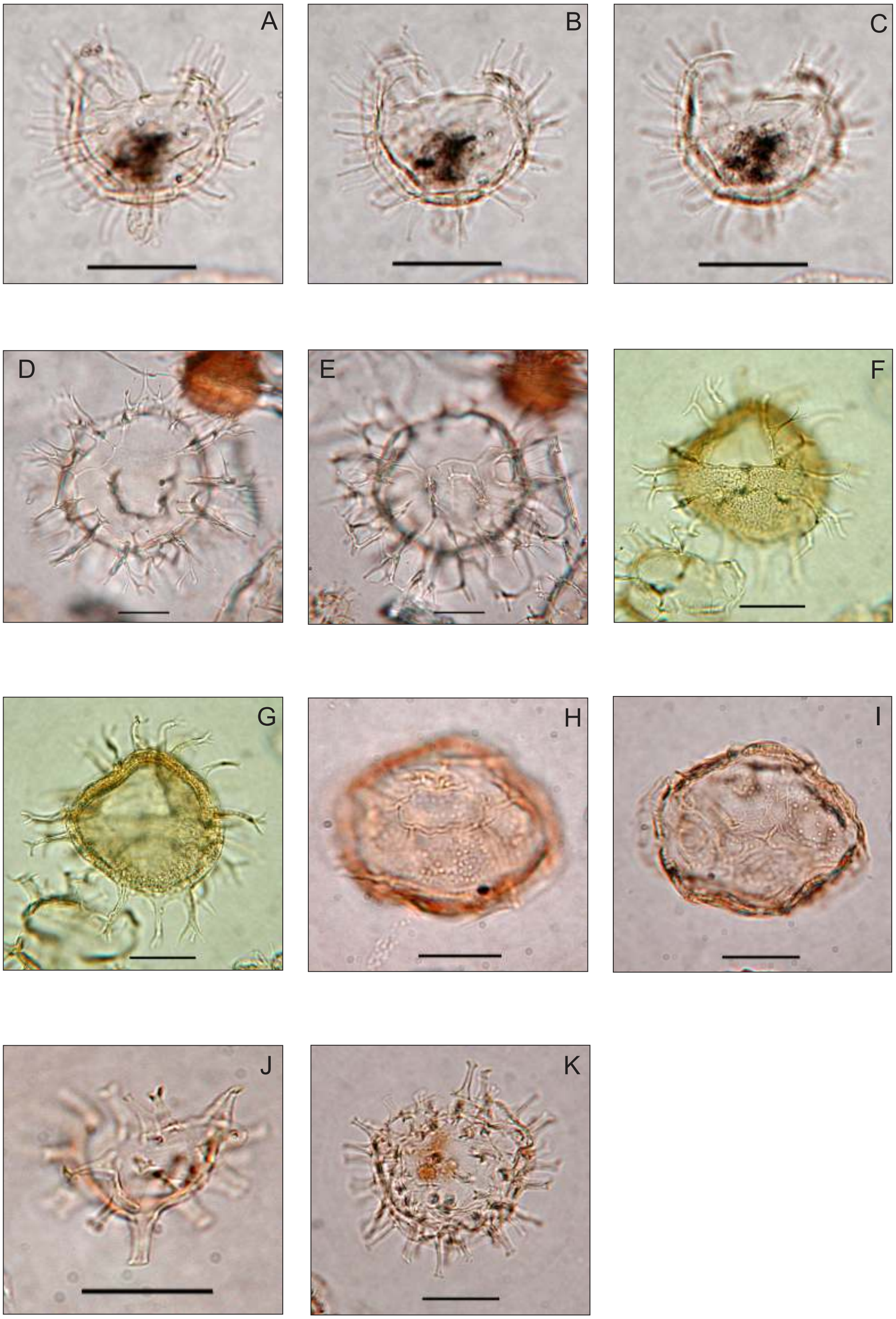

Plate 4. **(A–C)**, *Florentinia reichartii* sp. nov. Holotype (Bass River, 355.26 mbs, #1, England Finder coordinates: N52-2); **(D–E)**, *Glaphyrocysta volata* (Wilson Lake, 112.76 mbs, #1, M49-1); **(F–G)**, *Hafniasphaera septata* (Wilson Lake, 110.14 mbs, #2, L45-1); **(H–I)**, *Heteraulacacysta* spp. (Wilson Lake, 110.73 mbs, #1, M56-4); **(J–K)**, *Homotryblium* spp. (J, Bass River, 349.44 mbs, #1, K50-3; K, Bass River, 351.08 mbs, #1, L49-3). Scale bar=20 μm.

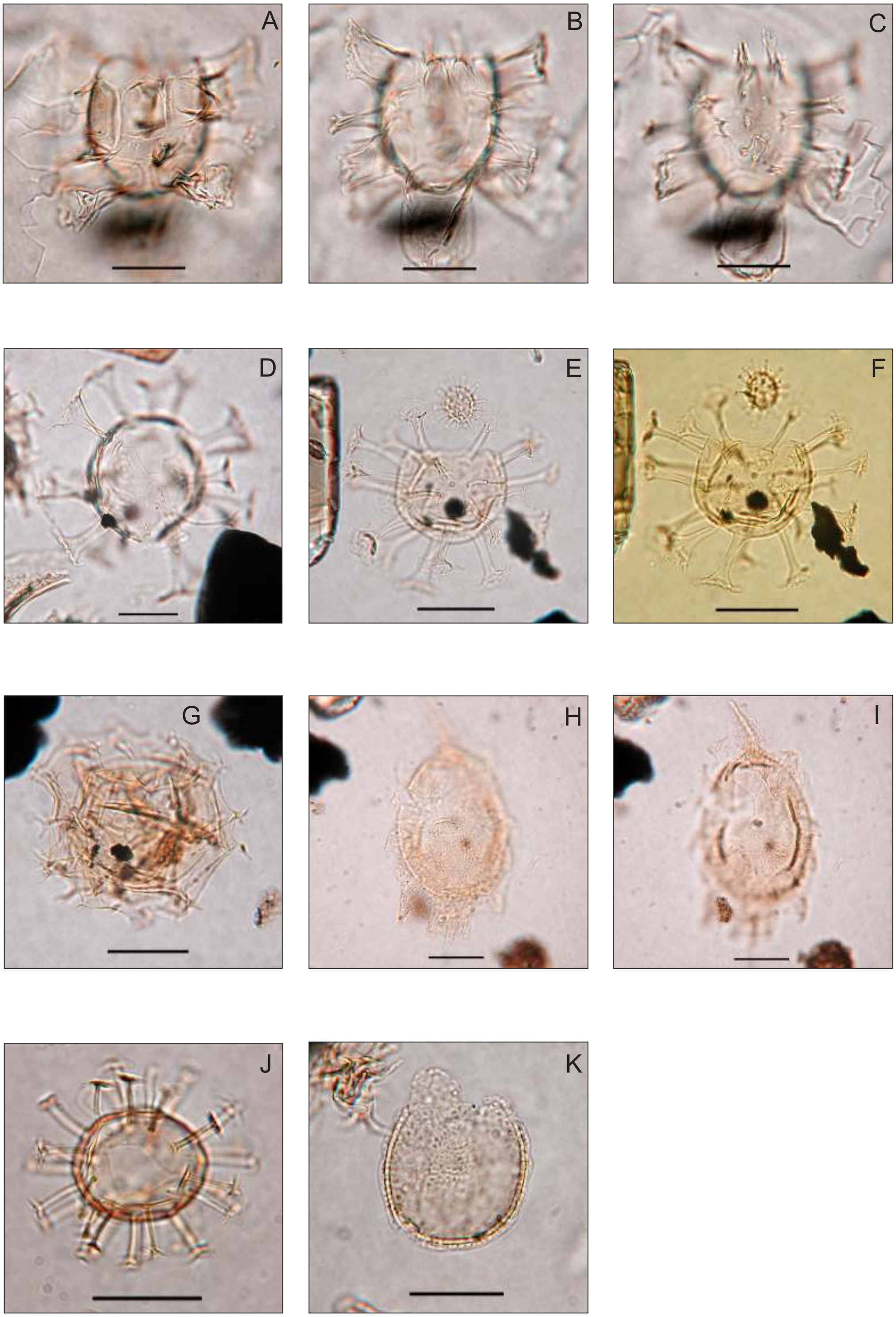

Plate 5. **(A–C)**, *Hystrichokolpoma salacia* (Wilson Lake, 112.76 mbs, #1, England Finder coordinates: O48-4); **(D–F)**, *Hystrichosphaeridium truswelliae* (D, Wilson Lake, 110.14, #1, G59-3; (E–F), Bass River, 357.76 mbs, #1, O62-1); **(G)**, *Hystrichostrogylon* spp. (Bass River, 356.69 mbs, #1, M58-1); **(H–I)**, *Lanternosphaeridium lanosum* (Bass River, 349.44 mbs, #1, O53-3); **(J)**, *Melitasphaeridium pseudorecurvatum* (Wilson Lake, 110.06 mbs, #1, N52-1), **(K)**, *Membranosphaera* spp. (Wilson Lake, 110.14 mbs, J53-4). Scale bar=20 μm.

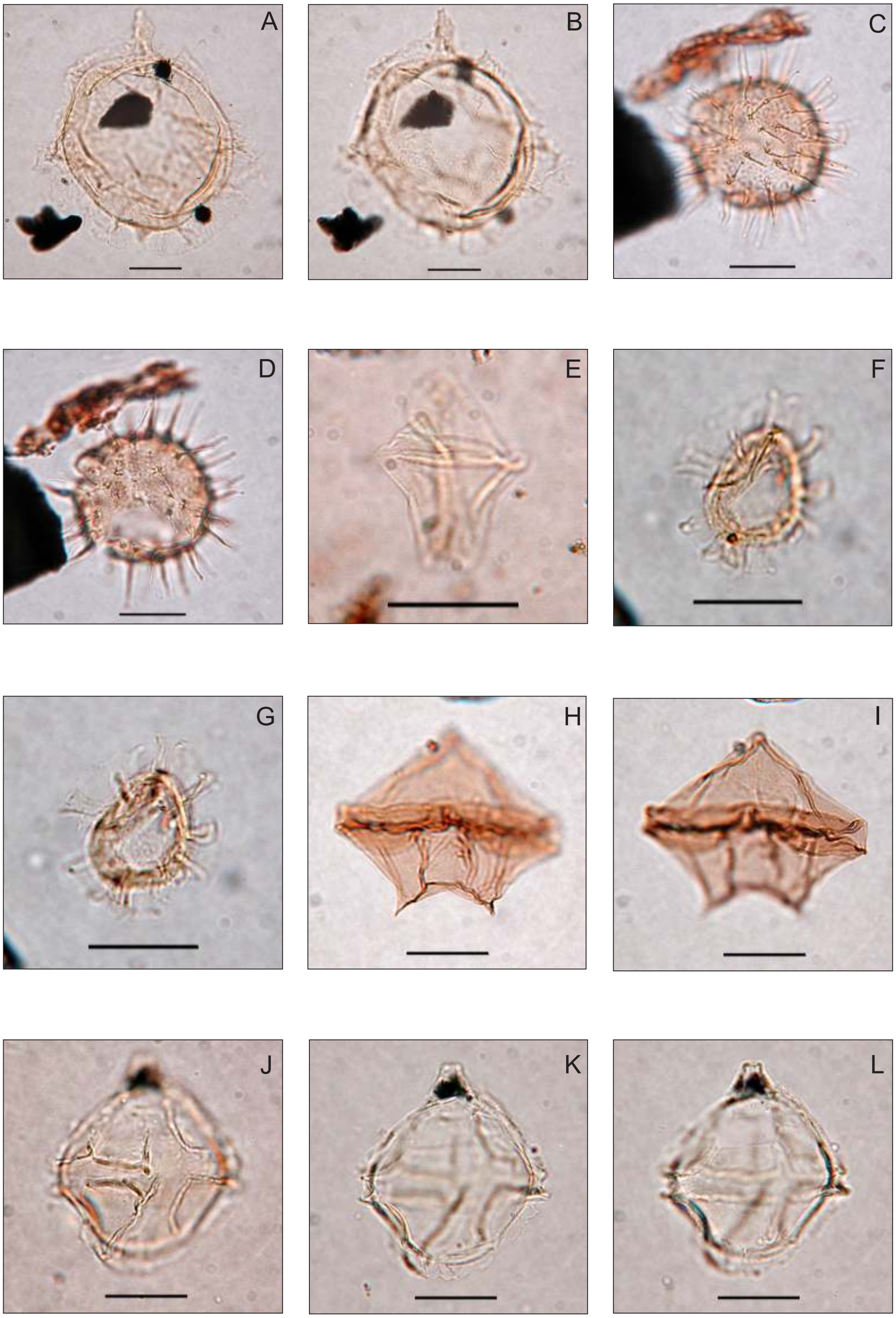

Plate 6. **(A–B)**, *Muratodinium fimbriatum* (Bass River, 354.41 mbs, #1, England Finder coordinates: N63-3); **(C–D)**, *Operculodinium* spp. (Bass River, 359.77 mbs, #1, N61-1); **(E)**, *Paleotetradinium minisculum* (Wilson Lake, 111.97 mbs, #1, N52-3); **(F–G)**, *Paucisphaeridium* spp. (Bass River, 357.76 mbs, L56-4); **(H–I)**, *Phelodinium magnificum* (Bass River, 356.69 mbs, #1, S60-3); **(J–L)**, *Phthanoperidinium crenulatum* (Wilson Lake, 95.96 mbs, #1, J44-4). Scale bar=20 μm.

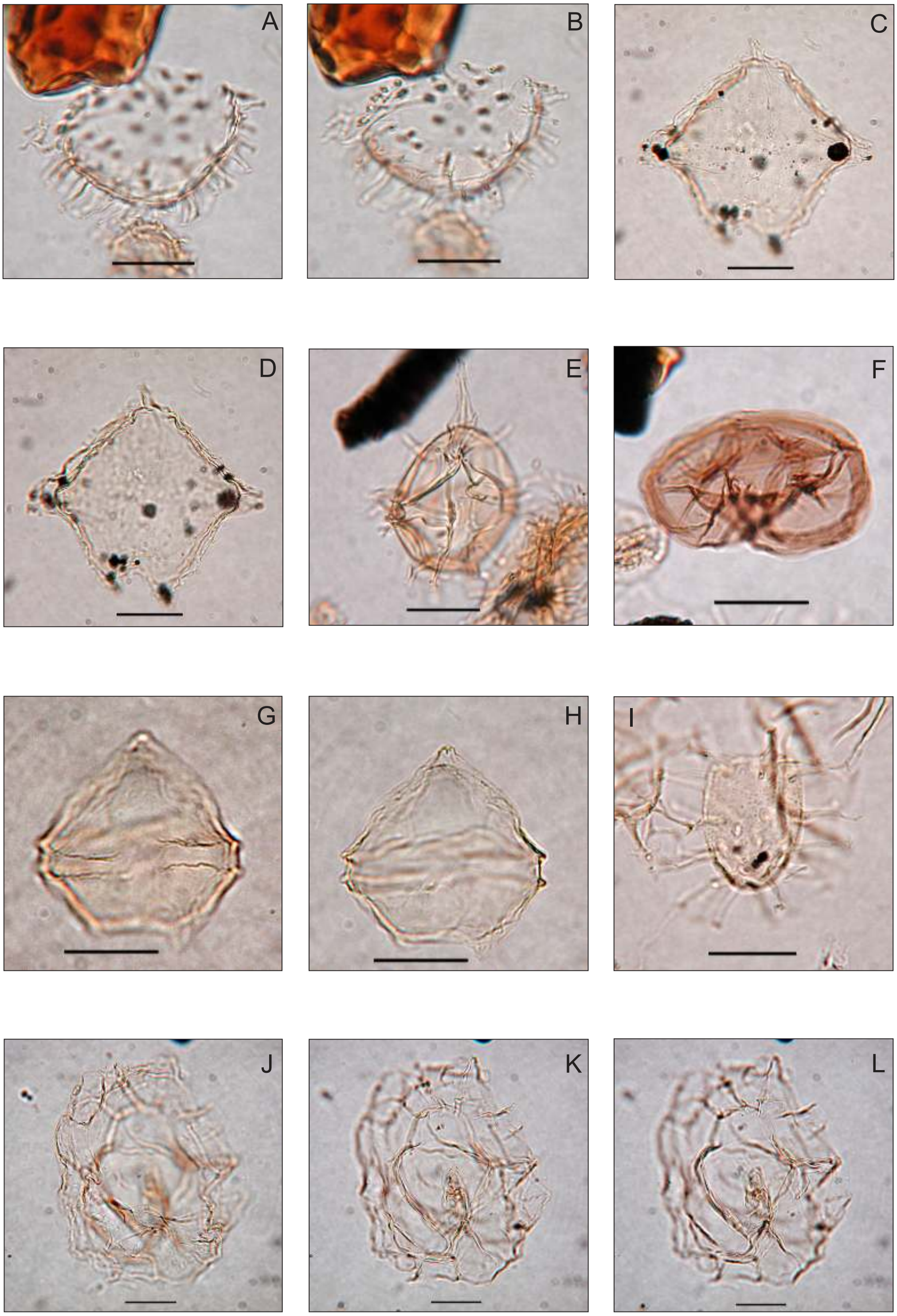

Plate 7. **(A–B)**, *Polysphaeridium zoharii* (Bass River, 361.05 mbs, #1, England Finder coordinates: N19-1); **(C–D)**, *Rhombodinium* spp. (Wilson Lake, 109.42 mbs, #1, L45-2); **(E)**, *Rottnestia borrusica* (Bass River, 354.41 mbs, #1, N58-4); **(F)**, *Selenopemphix nephroides* (Bass River, 356.69 mbs, #1, R61-4); **(G–H)**, *Senegalinium* spp. (Wilson Lake, 94.40 mbs, #1, T57-3); **(I)**, *Tanyosphaeridium* spp. (Bass River, 350.66 mbs, #1, N44-4); **(J–L)**, *Thalassiphora delicata* (Bass River, 373.76 mbs, #1, K60-2). Scale bar=20 μm.

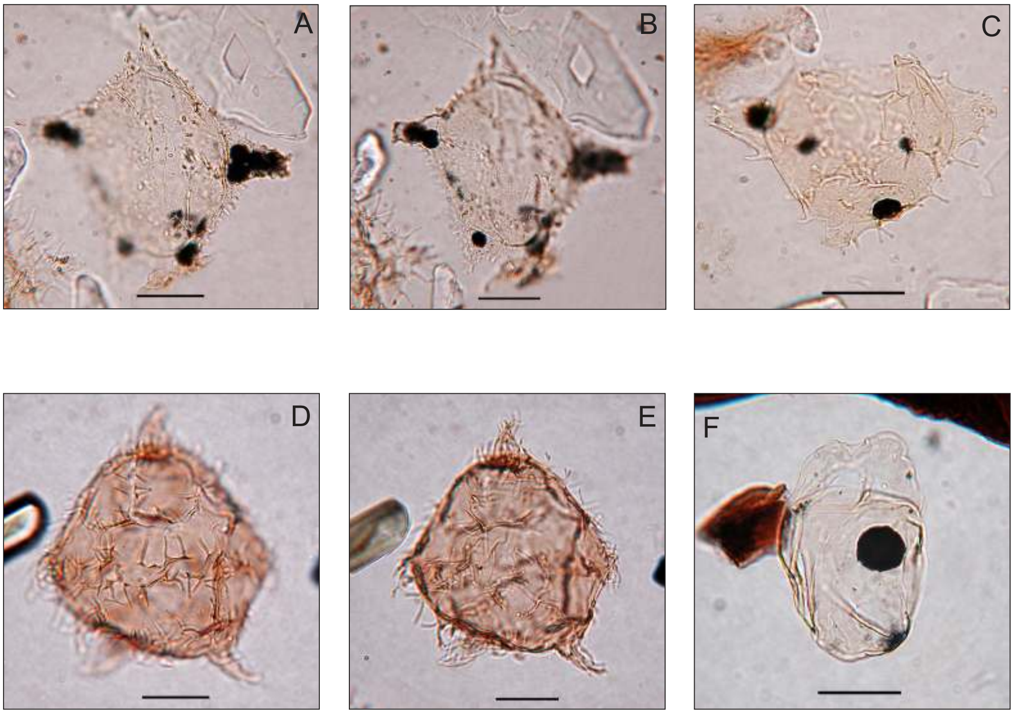

Plate 8. **(A–B)**, *Wetzeliella articulata* (Bass River, 346.82 mbs, #1; England Finder coordinates: N58-3); **(C)**, *Wetzeliella – Dracodinium varielongitudum* (Bass River, 345.96 mbs, #1; L66-4); **(D–E)**, *Wilsonidium tesselatum* (Bass River, 357.39 mbs, #1, J54-4); **(F)**, *Nelsoniella* spp. (potentially reworked; Bass River, 366.93 mbs, #1, M60-3). Scale bar=20 μm.

Diphyes colligerum (2J; 9H)

Dracodinium pachydermum (2K)

Dracodinium varielongitudum (8C)

Eocladopyxis peniculata (3A–B; 9I–L)

Eocladopyxis? sp. A. A proximate goniodomid, questionably assigned to *Eocladopyxis*

Fibrocysta axialis (10A) Part of the *C. fibrospinosum* complex

Fibrocysta bipolaris Part of the *C. fibrospinosum* complex

Fibrocysta sp. A. A species of *Fibrocysta* with numerous slender processes. Part of the *C. fibrospinosum* complex

Fibrocysta spp. (pars). All other taxa assignable to *Fibrocysta* (3C) Part of the *C. fibrospinosum* complex

Florentinia ferox (3D–E)

Florentinia reichartii sp. nov. (3D–L; 4A–C; 10B–E)

Glaphyrocysta ordinata

Glaphyrocysta pastielsii/exuberans

Glaphyrocysta reticulata

Glaphyrocysta volata (3D–E; 10F–G)

Hafniasphaera septata (3F–G)

Heteraulacacysta spp. (3H–I)

Homotryblium spp. (3J–K)

Horologiniella spp.

Hystrichokolpoma salacia (5A–C)

Hystrichokolpoma spp. (pars)

Hystrichosphaeridium truswelliae Remarks: first record outside Southern Ocean. (5D–F; 10H–I)

Hystrichosphaeridium tubiferum

Hystrichostrogylon spp. (5G)

Impagidinium californiense

Impagidinium sp. cf. I. sp. B Crouch and Hollis (1996)

Impagidinium sp. cf. *sphaericum*

Impagidinium spp. (pars)

Kallosphaeridium brevibarbatum

Kenleya spp.

Lanternosphaeridium lanosum (5H–I; 10J). Part of the *C. fibrospinosum* complex

Lejeunecysta spp.

Leptodinium spp.

Lingulodinium machaerophorum

Melitasphaeridium pseudorecurvatum

Membranosphaera spp. Remarks: tabulation sometimes discernable in the distribution of process ornamentation (5K; 10K)

Microdinium ornatum

Muratodinium fimbriatum (6A–B; 10L). Part of the *C. fibrospinosum* complex

Nelsoniella (potentially reworked; 8F)

Nematosphaeropsis spp.

Operculodinium severinii

Operculodinium cf. *O. israelianum.*

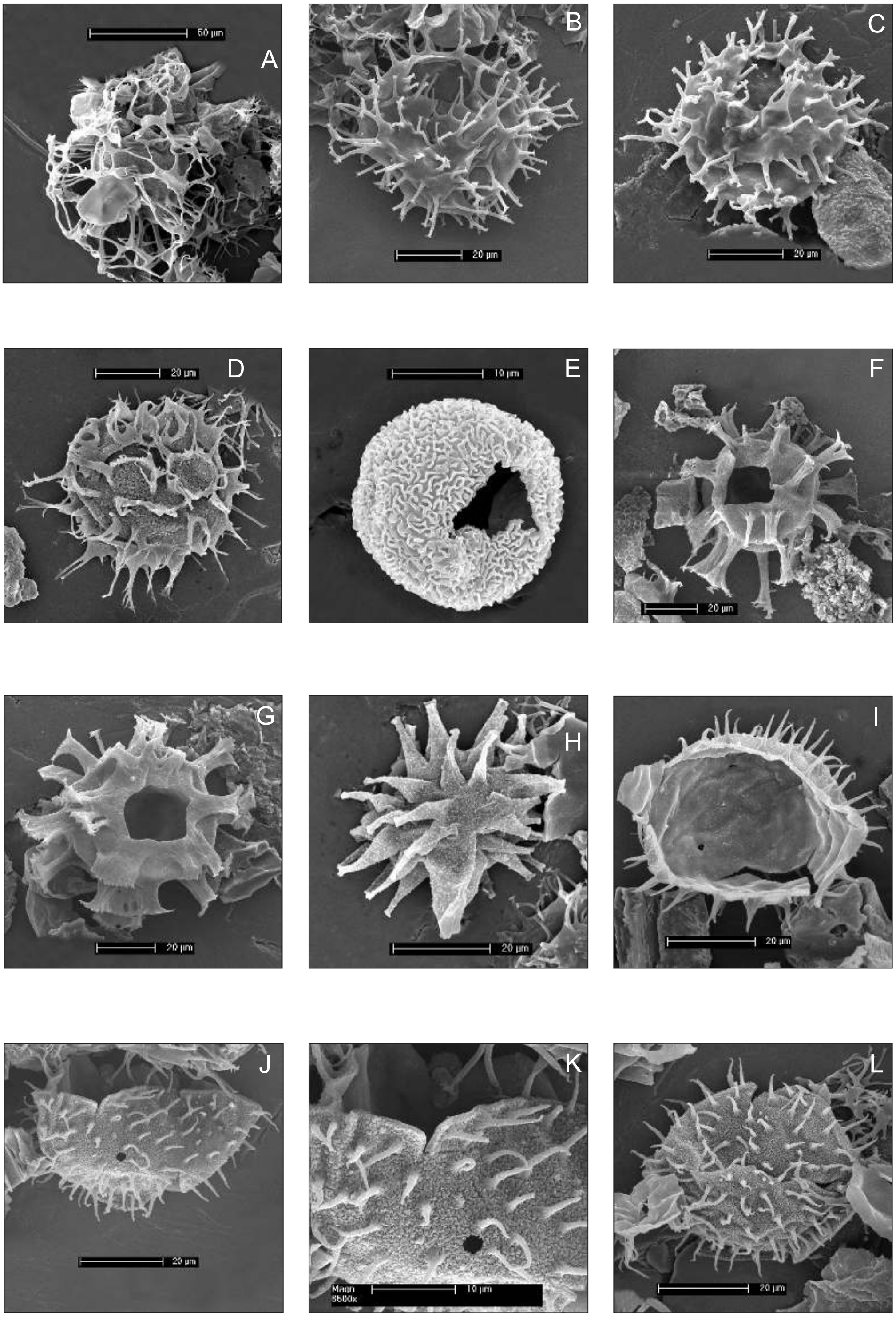

Plate 9. **(A)**, *Adnatosphaeridium robustum* (Bass River, 364.89 mbs); **(B–C)**, *Apectodinium homomorphum* (Bass River, 357.39 mbs); **(D)**, *Areoligera* spp. (Bass River, 355.93 mbs); **(E)**, *Cerebrocysta* spp. (Bass River, 355.93 mbs); **(F–G)**, *Cordosphaeridium fibrospinosum* (F, Bass River 356.93 mbs; (G), Bass River, 355.93 mbs); **(H)**, *Diphyes colligerum* (Bass River, 357.39 mbs); **(I–L)**, *Eocladopyxis peniculata* (Bass River, 364.89 mbs; (K) is a detail of (J) to indicate sutures).

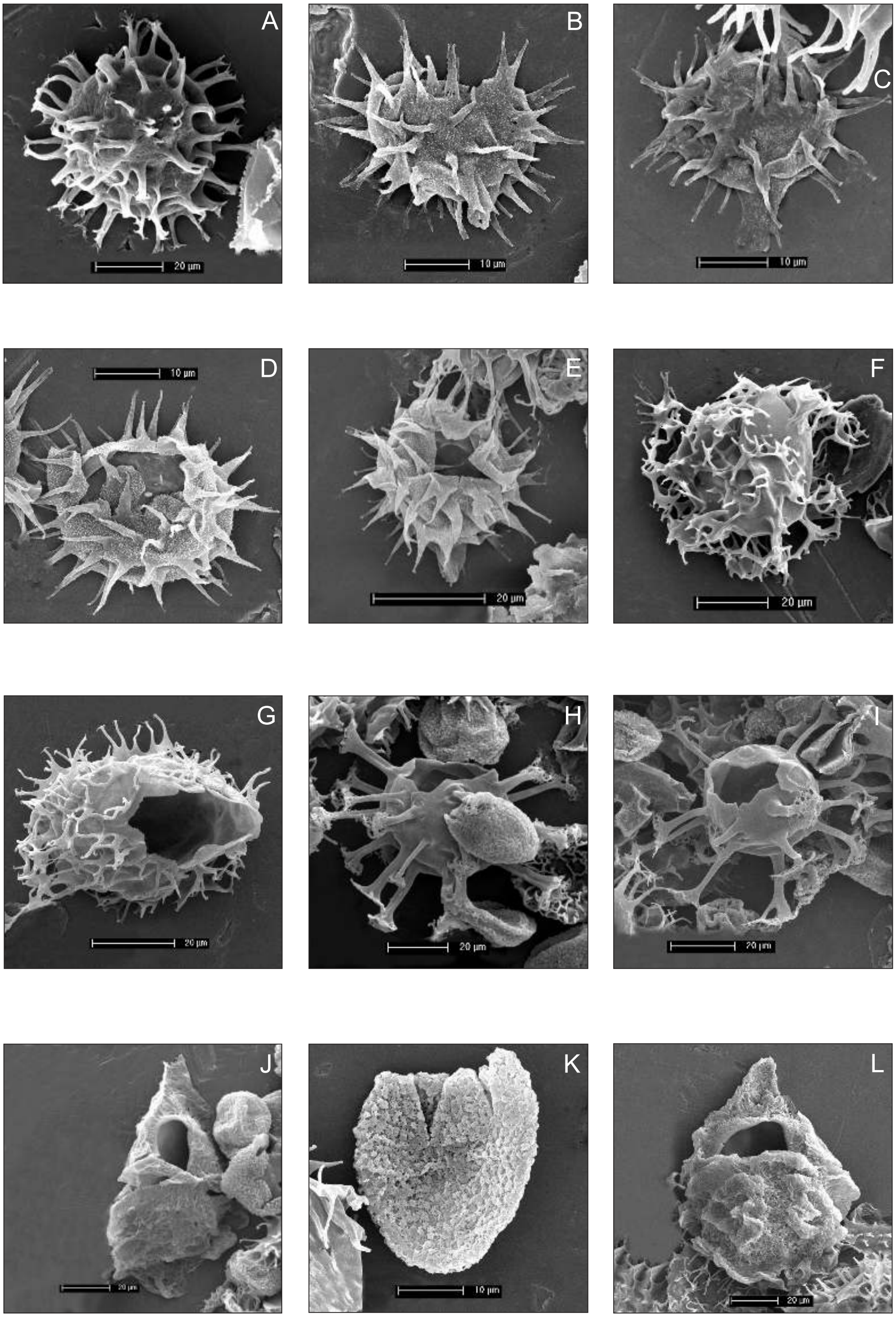

Plate 10. (A), *Fibrocysta axialis* (Bass River, 356.93 mbs); **(B–E)**, *Florentinia reichartii* sp. nov. (B–D, Bass River, 356.93; (E), 355.93 mbs); **(F–G)**, *Glaphyrocysta volata* (Bass River, 364.89 mbs); **(H–I)**, *Hystrichosphaeridium truswelliae* (Bass River, 357.39 mbs); **(J)**, *Lanternosphaeridium lanosum* (Bass River, 357.39 mbs); **(K)**, *Membranosphaera* spp. (Bass River 357.39 mbs); **(L)**, *Muratodinium fimbriatum* (Bass River, 357.39 mbs).

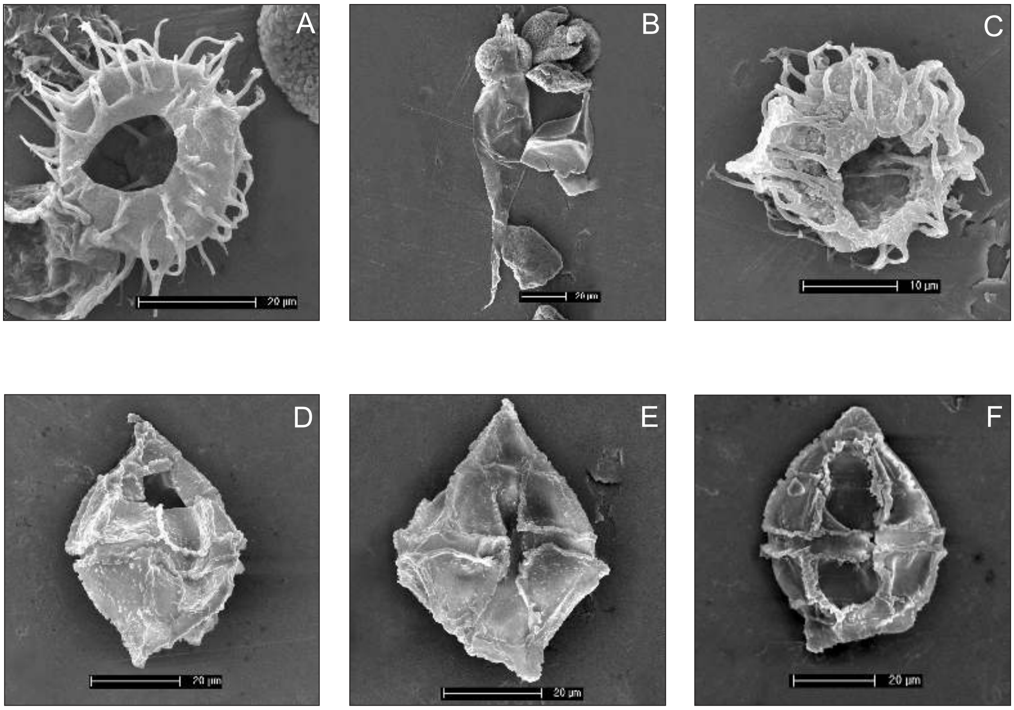

Plate 11. **(A)**, *Operculodinium* spp. (Bass River, 357.39 mbs); **(B)**, *Palaeocystodinium* spp. (Bass River, 357.39 mbs); **(C)**, *Paucisphaeridium* spp. (Bass River 364.89 mbs); **(D–F)**, *Phthanoperidinium crenulatum* (Bass River 356.93 mbs).

Operculodinium spp. (pars) (6C–D; 11A)
Paleocystodinium lidiae
Paleocystodinium spp (pars) (11B)
Paleotetradinium minisculum (6E)
Paucisphaeridium inversibuccinum
Paucisphaeridium spp. (pars) (6F–G; 11C)
Phelodinium magnificum (6H–I)
Phthanoperidinium crenulatum (6J–L; 11D–F)
Phthanoperidium spp. (pars)
Polysphaeridium zoharyi (7A–B)
Rhombodinium spp. (7C–D)
Rottnestia borussica (7E)
Selenopemphix nephroides (7F)
Senegalinium spp. (7G–H)
Senegalinium complex. Includes all peridinioid taxa with a 6-sided second intercalary plate; here comprising *Alterbidinium* spp., *Cerodinium* spp., *Deflandrea* spp., *Phthanoperidinium* spp., and *Senegalinium* spp.
Spiniferites pseudofurcatus
Spiniferites ramosus
Spiniferites spp. (pars)
Tanyosphaeridium spp. (7I)
Thalassiphora delicata (7J–L)
Thalassiphora pelagica. Part of the *C. fibrospinosum* complex
Turbiosphaera spp. Part of the *C. fibrospinosum* complex
Wetzeliella articulata (8A–B)
Wetzeliella meckelfeldensis
Wilsonidium tesselatum (8D–E)

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