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Palynology and Paleoclimatology of the Chicxulub Impact Crater in the Early Paleogene

Vann Smith

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PALYNOLOGY AND PALEOCLIMATOLOGY OF THE CHICXULUB IMPACT CRATER IN THE EARLY PALEOGENE

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
Requirements for the degree of
Doctor of Philosophy

in

The Department of Geology and Geophysics

by
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B.S. Louisiana State University
M.S. Tulane University
August 2020

I dedicate this dissertation to my wife, Stephanie, our children, Felix and Iris, and my parents, Fain and Robert. I couldn't have done it without you.

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	iii
LIST OF PLATES	vi
ABSTRACT.....	vii
CHAPTER 1. INTRODUCTION	1
CHAPTER 2. PALEOCENE-EOCENE MIOPORES FROM THE CHICXULUB IMPACT CRATER, MEXICO. PART 1: SPORES AND GYMNOSPERM POLLEN.....	3
2.1. Introduction.....	3
2.2. Materials and methods	5
2.3. Morphology, nomenclature, and botanical affinities	5
2.4. Systematic paleontology	6
2.5. Conclusions.....	28
2.6. Plates to Chapter 2	30
CHAPTER 3. PALEOCENE-EOCENE PALYNOMORPHS FROM THE CHICXULUB IMPACT CRATER, MEXICO. PART 2: ANGIOSPERM POLLEN	38
3.1. Introduction.....	38
3.2. Methods.....	38
3.3. Morphology, systematic nomenclature, and paleoecological interpretation	39
3.4. Systematic paleontology	41
3.5. Discussion and conclusions	104
3.6. Plates to Chapter 3	106
CHAPTER 4. LIFE AND DEATH IN THE CHICXULUB IMPACT CRATER: A RECORD OF THE PALEOCENE-EOCENE THERMAL MAXIMUM	136
4.1. Introduction and geologic setting.....	136
4.2. Methods.....	136
4.3. Results.....	138
4.4. Discussion	140
4.5. Conclusions.....	142
CHAPTER 5. PALYNOLOGY AT GROUND ZERO OF THE CHICXULUB IMPACT, SOUTHERN GULF OF MEXICO.....	143
5.1. Introduction and geologic setting.....	143
5.2. Materials and methods	145
5.3. Results.....	147
5.4. Discussion	153
5.5. Conclusions.....	158
CHAPTER 6. CONCLUSIONS	159

APPENDIX A. PERMISSION TO INCLUDE PUBLISHED MANUSCRIPTS	161
APPENDIX B. SUPPLEMENTARY MATERIAL	167
REFERENCES:	169
VITA.....	193

LIST OF PLATES

2.1. Trilete spores.....	30
2.2. Trilete spores.....	32
2.3. Trilete and monolete spores	34
2.4. Gymnosperm pollen.....	36
3.1. Inaperturate, monocolpate, and trichotomocolpate pollen.....	106
3.2. Monocolpate and trichotomocolpate pollen.....	108
3.3. Tricolpate pollen	110
3.4. Tricolpate pollen	112
3.5. Tricolpate pollen	114
3.6. Tricolpate and tricolporate pollen.....	116
3.7. Tricolporate pollen.....	118
3.8. Tricolporate pollen.....	120
3.9. Tricolporate and stephanocolporate pollen.....	122
3.10. Stephanocolporate, monoporate, and triporate pollen	124
3.11. Triporate pollen.....	126
3.12. Triporate and stephanoporate pollen.....	128
3.13. Stephanoporate and pantoporate pollen	130
3.14. Scanning electron microscopy images of spores and pollen	132
3.15. Scanning electron microscopy images of spores and pollen	134

ABSTRACT

At the end of the Cretaceous Period, a large bolide impacted the Earth and formed the Chicxulub impact crater in the Yucatán Peninsula, Mexico. In 2016, International Ocean Discovery Program (IODP) Expedition 364 Site M0077 drilled into the buried peak ring of the crater, recovering a marine Paleocene to early Eocene post-impact section deposited on top of the impact breccia. Palynological analysis of 195 samples from the post-impact section has yielded the first pre-Holocene vegetational record from inside the Chicxulub impact crater and the first palynological record of the recovery of life following the end-Cretaceous mass extinction from inside the Chicxulub impact crater. The pollen and plant spore assemblage has been fully described, including one new genus (*Scabrastephanoporites*) and five new species (*Brosipollis reticulatus*, *Echimonocolpites chicxulubensis*, *Psilastephanocolporites hammenii*, *Scabrastephanoporites variabilis*, and *Striatopollis grahamii*) of angiosperm pollen. Dinoflagellate cysts from the K/Pg (Cretaceous/Paleogene) transitional unit, likely deposited within six years of the impact event, include several probably reworked Maastrichtian specimens, as well as possible *in situ* early Paleocene dinoflagellate cysts. The oldest terrestrial palynomorphs, two specimens of *Deltoidospora*, were not observed until at least 200,000 years after the impact. The PETM has been identified in the Site M0077 core based on biostratigraphy and a negative carbon isotope excursion. Geochemical and microfossil evidence indicates sea surface temperatures of ~38 °C, increased terrestrial input, salinity stratification, and bottom water anoxia. Palynomorph concentrations increase in the PETM, with an acme of the dinoflagellate genus *Apectodinium* in the lower PETM section, and a diverse pollen assemblage derived from a lowland tropical shrubby forest, likely from exposed portions of the Yucatán Peninsula to the south. A second spike in palynomorph concentrations occurs upsection of the PETM in a laminated dark shale, possibly representing the early Eocene hyperthermal event ETM3. Pollen and plant spore concentrations generally increase in sediments deposited during and shortly after the Early Eocene Climatic Optimum (EECO), consistent with infilling and shallowing of the crater basin during the early Paleogene. The EECO pollen and plant spore assemblages indicate a continuously present shrubby lowland tropical forest, with *Malvacipollis*, *Bombacacidites*, *Brosipollis*, and *Crudia* type pollen.

CHAPTER 1. INTRODUCTION

This dissertation focuses on the palynology of International Ocean Discovery Program (IODP) Expedition 364 Site M0077, with additional data from Expedition 364 scientists and other researchers. IODP Expedition 364 was designed to investigate the nature and formation of peak rings in impact craters, deformational impact processes, post-impact hydrothermal circulation, the deep biosphere of the peak ring, the recovery of life following the impact, early Eocene hyperthermal events in the post-impact section, the stratigraphy of the basin infill, and other research questions (Morgan et al. 2017). Numerous papers have been published on various topics related to Site M0077, including peak ring formation (Morgan et al. 2016), physical characteristics of the peak ring rocks (Christeson et al. 2018), impact-related deformation processes (Riller et al. 2018; Rae et al. 2019), the immediate physical and environmental consequences of the impact (Gulick et al. 2019), export productivity and paleoceanography in the early Paleocene (Lowery et al. 2019), and patterns of biotic recovery following the impact (Lowery et al. 2018; Jones et al. 2019; Lowery and Fraass 2019).

The research goals for this dissertation included a full description of the pollen and plant spore taxonomy, investigation of the recovery of life following the impact, interpretation of paleoenvironmental conditions during early Eocene hyperthermal events like the Paleocene-Eocene Thermal Maximum (PETM), biostratigraphic analysis, and paleoecological interpretation of the post-impact palynological assemblages.

The first research goal, a full taxonomic description of the pollen and plant spore assemblages, was particularly necessary due to the limited published information on the taxonomy of early Paleogene pollen and plant spores from Mexico, Central America, and the northern Caribbean. Originally, the taxonomy was going to be handled in a single chapter, but the important diversity in pollen and spores recovered made it necessary to split the evaluation of the taxonomy into two papers, i.e., chapters. Chapter 2 describes the plant spore and gymnosperm pollen assemblage and has been previously published (Smith et al. 2019). Chapter 3 describes the angiosperm pollen assemblage and has also been previously published (Smith, Warny, Jarzen, et al. 2020). Permission to include these publications is provided in Appendix A. In the original publications, only an abbreviated version of the systematic paleontology was published in the main manuscript, with the full text of the systematic paleontology provided as supplementary material. In this dissertation, the full systematic paleontology is included. Plates with images of all plant spore and gymnosperm pollen taxa are provided at the end of Chapter 2, and plates with images of all angiosperm taxa are provided at the end of Chapter 3.

Chapter 4, under peer review at the time of writing (Smith, Warny, Grice, et al. 2020), investigates the PETM section of the Site M0077 core using a variety of paleontological, geochemical, and mineralogical proxies.

Chapter 5 synthesizes the terrestrial and marine palynology through the whole post-impact section, building on the taxonomy developed in Chapters 2 and 3, as well as the paleoclimatic multiproxy interpretations of the PETM made in Chapter 4. The early recovery of life following the K/Pg impact is described in detail in Chapter 5, using high-resolution sampling of the early Paleocene interval. Detailed descriptions of the post-impact dinoflagellate assemblages, as well as statistical analyses of the pollen and plant spore assemblages, are also provided.

Supplementary material related to this research includes quantitative counts of palynomorphs from 195 sample depths in the core, a table containing a list of all pollen and plant

spore taxa with their botanical affinities and paleoecologies, various statistical results, proxy data related to the PETM section, and supplementary methods for Chapter 4. All supplementary material has been stored in a publicly available online file repository for ease of access, with a permanent Digital Object Identifier (DOI) (Smith 2020). The supplemental data relating to the terrestrial palynology, with the exception of statistical analyses presented in Chapter 5, has already been published as online supplements to Smith et al. (2019) and Smith, Warny, Jarzen, et al. (2020). A more detailed description of the supplementary data is provided in Appendix B.

CHAPTER 2. PALEOCENE-EOCENE MIOSPORES FROM THE CHICXULUB IMPACT CRATER, MEXICO. PART 1: SPORES AND GYMNOSPERM POLLEN

2.1. Introduction

At the end of the Cretaceous Period, a massive asteroid collided with Earth and formed an impact crater approximately 200 km in diameter in the shallow carbonate Yucatán Platform, Mexico. This event is generally considered to be the main cause of the Cretaceous–Paleogene (K–Pg) mass extinction event (Schulte et al. 2010). Despite the catastrophic nature of the impact, the presence of trace fossils in the transitional unit between the impact breccia and the overlying Palaeocene limestone indicates that benthic life had returned to the impact crater, possibly within six years after the impact, and by 30 kyr after the impact seafloor conditions had essentially returned to normal (Lowery et al. 2018). The impact crater became a depositional basin which slowly filled in with sediment, and is no longer observable as a surface topographical feature. International Ocean Discovery Program (IODP) borehole 364 targeted the peak ring of the Chicxulub impact crater, an elevated ring inside the crater rim, with the goal of investigating the impact structure as well as the post-impact sedimentary succession (Gulick et al. 2016). Further information about the post-impact sedimentary rocks of IODP 364, including the biostratigraphical age model derived from foraminifera and calcareous nannofossils, can be found in Gulick et al. (2017). A gravity anomaly map of the Chicxulub impact crater is provided in Figure 2.1.

The post-impact rocks are a mix of carbonates and fine-grained clastic rocks such as claystones and black shales. The Palaeocene and Eocene benthic foraminiferal assemblages indicate paleowater depths between approximately 300 and 700 m (Gulick et al. 2017). This means that the pollen and spores recovered from the core have been transported from a terrestrial environment to the submerged peak ring of the impact crater. The Yucatán Platform appears to have been mostly submerged until the Oligocene; however, there is some evidence in the form of collapsed impact breccias and evaporites for subaerial exposure in areas of the platform during the Paleocene (Lefticariu et al. 2006). A possible source area for the pollen and spores in the IODP 364 core is the crater rim, which presumably formed a topographical high around the impact basin. The terrestrial palynomorphs could also be sourced from nearby areas of mainland Mexico to the south and southwest of the Yucatán Platform, from modern Guatemala or the Mexican states of Veracruz or Oaxaca. Alternatively, some of the terrestrial palynomorphs may be sourced from Cuba to the east. The pollen and spore assemblages may be a mix of pollen from one or all of these sources, although the high abundance and excellent preservation in some of the younger Ypresian samples suggests a more proximal source on the Yucatán Platform.

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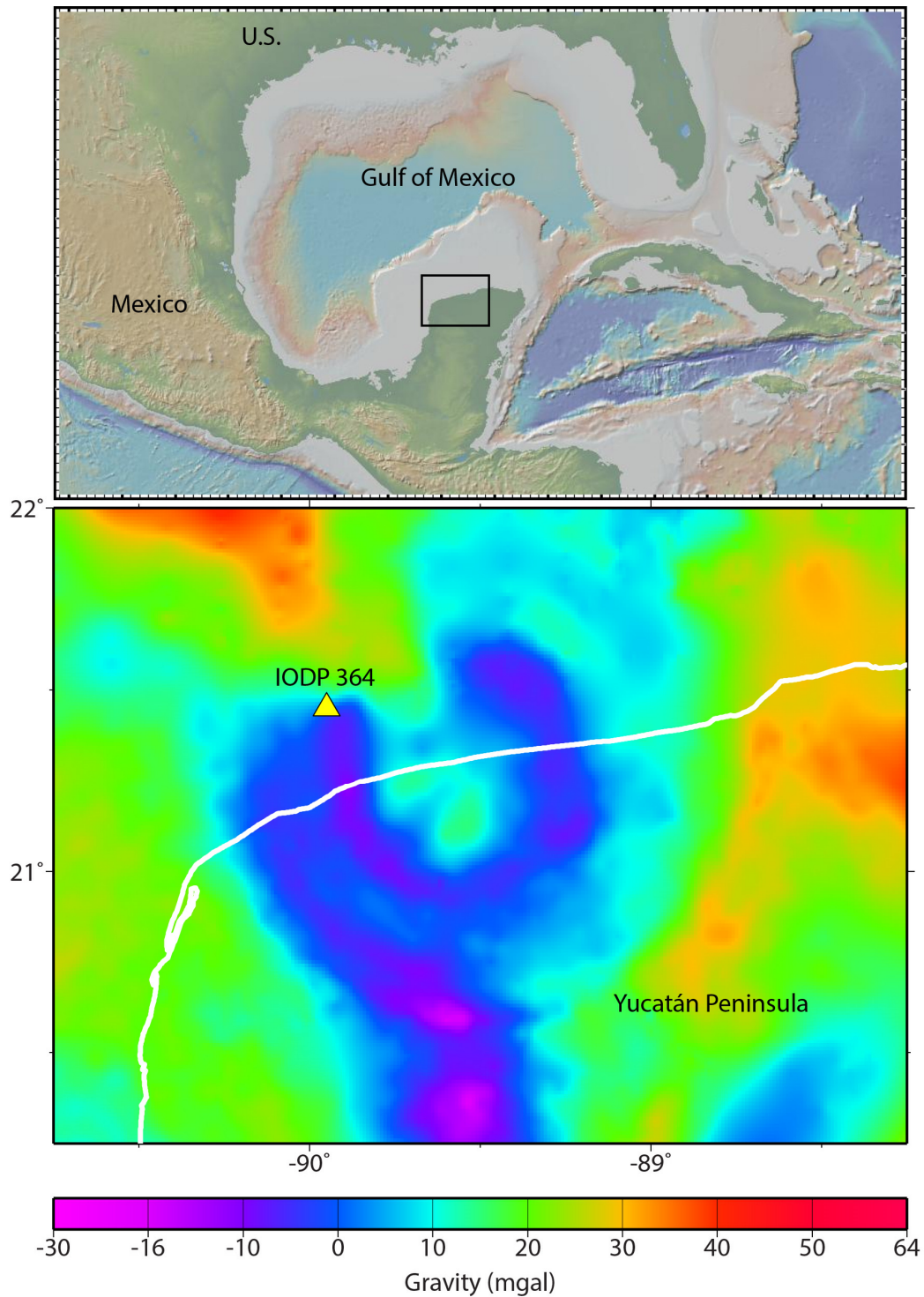


Figure 2.1. Location of the International Ocean Discovery Program (IODP) 364 (site MOO77A) drilling location in the Yucatán Peninsula, Mexico. The upper map shows the geographical extent of the gravity anomaly map on bottom. The position of site MOO77 is marked by a yellow triangle on the gravity anomaly map. Gravity data courtesy of G. Christeson, A. Hildebrand, and M. Pilkington.

2.2. Materials and methods

Approximately 15–40 g of sediment was taken at 149 sample depths from the post-impact section of the IODP 364 core and processed by Global Geolab Ltd using modifications of standard palynological techniques described by Traverse (2007). When possible, two slides were made at each depth and the residue retained for future use. Slides were scanned until 300 identifiable pollen and spore grains were counted, or until the slides at that sample depth were fully scanned. Microscopic examination was conducted using an Olympus BX41 microscope for brightfield microscopy and phase-contrast microscopy. Pollen grains were generally photographed at 1000x magnification. Size measurements for species were made on all specimens of the species if fewer than 10 specimens were observed, and then expressed as a range. If more than 10 specimens were observed, the size ranges were based on measurements of 10 specimens and the mean size is given in parentheses. Occurrence information is given in terms of the total number of specimens of the taxon observed in all samples; for comparison, the total number of identified angiosperm pollen, gymnosperm pollen and spores in this study is 16,247. A review of species occurrences in the literature was greatly aided by the database of Palynodata Inc. and White (2008). A list of the spore and gymnosperm pollen taxa, with their botanical affinities and interpreted paleoecology, is given in the supplementary materials. Quantitative counts for all spore and gymnosperm pollen taxa in the 149 samples are also given in the supplementary materials. None of the gymnosperm pollen or spores described here have any clear biostratigraphical value for the age range covered in the IODP 364 core. Although the first observed occurrence of many species is in the Ypresian, this is probably because the Palaeocene section is nearly barren. Multiple species described in this paper have a wide geographical distribution and were present in the Mesozoic.

2.3. Morphology, nomenclature, and botanical affinities

Morphological terminology generally follows Punt et al. (2007). The term ‘diameter’ is used loosely in this study to refer to shapes which are not strictly spherical, for example in describing the equatorial diameter of trilete spores. Botanical affinities are also provided for each species. Whenever possible, the affinity of a described species is given with reference to the scientific literature. In other cases, the stated botanical affinity may be based on comparison with modern spores or pollen from the Center for Excellence in Palynology (CENEX) research collection at Louisiana State University, Baton Rouge, Louisiana, USA. For some monolete and trilete spores for which the lower botanical affinity is unknown, the botanical affinity is listed as ‘Bryophyta/Pteridophyta sensu lato’, which includes the Polypodiophyta, Lycopodiophyta, Anthocerotophyta, Bryophyta, Marchantiophyta and any other lower plant groups which produce monolete or trilete spores. Whenever possible an appropriate fossil or modern genus and species have been provided; when an appropriate species designation is lacking for a morphotype, the morphotype has been identified by adding ‘sp. A’, ‘sp. B’, etc. Some genera have not been identified to the species level, and in those cases the genus name is followed by ‘spp.’ The angiosperm pollen will be described in a forthcoming paper.

2.4. Systematic paleontology

2.4.1. Trilete spores

Genus *Ceratosporites* Cookson & Dettmann 1958

Discussion. *Ceratosporites* includes trilete spores with a distal surface ornamented by blunt or sharply pointed spines, with a psilate proximal face. Bharadwaj & Kumar (1970) and Backhouse (1988) both consider *Ceratosporites* to be a junior synonym of *Neoraistrickia* Potonié 1956. However, this study considers that *Neoraistrickia* is distinguished from *Ceratosporites* by having an ornamented proximal face, following Dettmann (1963) and Playford & Melo (2009).

Ceratosporites sp. A

Plate 2.2, figures 9-10; Plate 2.3, figure 1

Description. Trilete spores, tuberculate, echinate, and verrucate, equatorial diameter 28–57 μm . Exine variable in thickness, thickened under protrusions, 1–4 μm thick. Amb subtriangular. Laesurae extending full across the proximal face. Laesurae present as a simple slit or with labra. Proximal face essentially smooth, distal face ornamented with long spines generally ranging in size from 4–9 μm , expanded at their base into a bulbous protrusion. Verrucae generally <1 μm in diameter are also present on the distal face. Spines sometimes bifurcate and could be considered tuberculate.

Discussion. In the type species of the genus, *Ceratosporites equalis* Cookson & Dettmann 1958, the protuberances are generally more baculate in shape and are more closely spaced. This species is generally similar to some modern species of *Selaginella* from Panama (Roubik & Moreno 1991). Jaramillo et al. (2014, p.194) describe an echinate trilete spore with affinity to *Selaginella* with bifurcate tips, which they gave the informal name “*Echitriletes* ‘*selaginelloides*’ type ‘bifurcatus.’” This type differs in having a circular amb, a thicker wall, and smaller spines relative to the size of the spore. Some specimens of *Neoraistrickia* sp. A have reduced ornamentation on the proximal face and may represent gradational morphologies with *Ceratosporites* sp. A.

Occurrence. Ypresian; 4 specimens observed.

Botanical affinity. Probably Selaginellaceae (Jansonius & Hills 1976).

Paleoecology. Probably lowland tropical forest. The modern genus *Selaginella* of the Selaginellaceae is often associated with humid, shaded, tropical environments (Graham 1988). Akkiraz et al. (2008) considered that fossil species of Selaginellaceae assigned to *Echinatisporites* were indicative of freshwater swamp environments; however, the Selaginellaceae are also found in the modern deserts of Mexico (Rzedowski 2006).

Genus *Cyathidites* Couper 1953

Discussion. *Cyathidites* includes triangular psilate trilete spores in which the sides of the grain between apices are concave in polar view. Couper (1953) further specified in the original description that the laesurae are over two-thirds the radius of the spore and that both proximal and distal surfaces are convex. The generic name is in reference to the modern genus *Cyathea* (Cyatheaceae), although similar morphologies may be found in several other modern fern

families including the Dicksoniaceae, Gleicheniaceae, and Matoniaceae (Shuklina & Polevova 2007). *Cardioangulina* Maljavkina 1949 ex Potonié 1960 is similar but is distinguished by having laesurae which extend less than half the distance to the equator (Jansonius & Hills 1976). In *Alsophylidites* Cookson 1947 ex Potonié 1956 the laesurae reach the equator.

Cyathidites minor Couper 1953

Plate 2.1, figures 4-5

Description. Trilete spores, psilate, equatorial diameter 24–25 μm . Exine 1 μm thick. Amb subtriangular, sides distinctly concave. Laesurae extend 4/5 the radius of the spore. Laesurae sinuous, with elevated labrum 1 μm wide. Sculpture psilate.

Discussion. *Cyathidites minor* was originally described by Couper (1953) as being 31–45 μm in equatorial diameter, although Shuklina & Polevova (2007) described specimens they identified as *C. minor* which were 23–29 μm in diameter.

Occurrence. Ypresian; 2 specimens observed.

Botanical affinity. Polypodiopsida, probably Cyatheaceae, Dicksoniaceae, Gleicheniaceae, or Matoniaceae (Shuklina & Polevova 2007).

Paleoecology. Wakefield & Monteil (2002) listed the paleoenvironmental preference for *Cyathidites minor* specimens from the Cretaceous and Paleogene of Pakistan as back mangrove or brackish swamp, but this generalized spore morphology is found in a variety of groups with different habitat preferences.

Genus *Deltoidospora* Miner 1935

Leiotriletes Naumova 1939 ex Ishchenko 1952

Lygodiumsporites Potonié, Thomson, & Thiergart 1950 ex Potonié 1956

Psilatrilletes van der Hammen 1954 ex Potonié 1956

Discussion. *Deltoidospora* is here considered to include psilate, scabrate, or faintly infrapunctate trilete spores, with a straight-sided or convex amb. The laesurae are relatively straight, not distinctly sinuous or undulating as in *Undulatisporites* Pflug in Thomson & Pflug 1953 emend. No cingulum, zona, or torus is present. *Cyathidites* and *Leiotriletes* Naumova 1939 ex Ishchenko 1952 are two similar form genera for psilate or lightly sculptured (scabrate) trilete miospores. Much of the confusion surrounding these three genera stems from the incomplete original description given by Miner (1935, p. 618) for *Deltoidospora*: “Small unassigned deltoid or sub-deltoid spores of the type that is commonly found associated with many Mesozoic ferns; such as *Gleichenites*, *Gleicheniopsis*, *Laccopteris*, and others.” Danzé-Corsin & Laveine (1963) attempted to emend *Deltoidospora*, but this emendation is not often cited, and Frederiksen et al. (1983) argued that the emendation does not apply because the authors illegitimately changed the name of the genus to *Deltoidisporites*. The morphological circumscription of *Deltoidospora* is therefore a matter of convention in the literature. *Cyathidites* is generally distinguished from *Deltoidospora* on the basis of having concave or significantly concave sides of the amb (e.g., Dettmann 1963; Jardine 2011).

Leiotriletes Naumova 1939 ex Ishchenko 1952 as originally described included all smooth azonotrillete spores. This description apparently includes both psilate and infrapunctate sculpture types, because the type species *Leiotriletes sphaerotriangulus* (Loose 1932) Potonié &

Kremp 1954 has a faintly infrapunctate exine. The emendation of *Leiotriletes* by Potonié & Kremp (1954) translated by Jansonius & Hills (1976) is somewhat ambiguous, stating that a distinctly triangular amb is diagnostic but also that the sides of the amb can be convex or concave. The emendation includes psilate as well as infrapunctate and infrareticulate sculpture types. Dettmann (1963) considered that *Cyathidites* has a concave triangular amb, *Deltoidospora* has a straight-sided triangular amb and *Leiotriletes* has a convex triangular amb. Jardine (2011), on the other hand, considered that *Leiotriletes* is distinguished from *Deltoidospora* by being distinctly punctate, but this is doubtful, because the sculpture of *Deltoidospora* was not described by Miner (1935), and the proposed emendation of *Deltoidospora* by Danzé-Corsin & Laveine (1963) included infrapunctate forms. This study will follow Frederiksen et al. (1983) and consider *Leiotriletes* a junior synonym of *Deltoidospora*. *Psilatrilites* van der Hammen 1954 ex Potonié 1956 is here considered a junior synonym of *Deltoidospora*, with a similar circumscription but restricted to forms with the laesurae extending at least 3/4 the distance to the equator. The loose interpretation of the systematic nomenclature system of van der Hammen (1954b, 1956) by Potonié (1956) can be ameliorated by the incorporation of *Psilatrilites* into an expanded circumscription of *Deltoidospora*. *Lygodiumsporites* Potonié, Thomson, & Thiergart 1950 ex Potonié 1956 is here considered a junior synonym of *Leiotriletes* and therefore of *Deltoidospora*, following Krutzsch (1959), who transferred the type species of *Lygodiumsporites* to *Leiotriletes*.

Deltoidospora spp.
Plate 2.1, figures 1-3

Description. Trilete spores, psilate, faintly scabrate, or faintly infrapunctate, equatorial diameter 30–(58)–96 µm. Unbordered simple laesurae extend approximately 2/3 to 4/5 the radius. Exine 0.5–2.0 µm thick. Amb subcircular to triangular.

Discussion. This study will follow Jardine (2011) and not speciate this genus. There is no obvious stratigraphic or paleoecological advantage in doing so. If speciated, many specimens could be included in *Deltoidospora microadriennis* (Krutzsch 1959) Frederiksen et al. 1983, which has a size range of 35–65 µm.

Occurrence. Ypresian; 78 specimens observed. The genus *Deltoidospora* is common and globally distributed in the Mesozoic and Cenozoic (Palynodata Inc. & White 2008).

Botanical affinity. Polypodiidae, possibly *Acrostichum* (Pteridaceae) or *Antrophyum* (Pteridaceae). The botanical affinity is somewhat difficult to determine, as psilate, trilete spores are produced by a variety of ferns. The specimens illustrated here are similar to spores produced by the modern genera *Acrostichum* and *Antrophyum*; Graham (1989) noted that, although *Acrostichum* spores tend to have a more scabrate exine than *Antrophyum* spores, the distinction between the two genera is difficult with fossil spores. It is also difficult to distinguish *Acrostichum* spores from *Lygodium* spores (Jarzen & Dilcher 2006). Ramírez-Arriaga et al. (2005) gave similar spores assigned to *Deltoidospora* the botanical affinity of the Cyatheaceae. Jardine (2011) provided a probable affinity with the Cyatheaceae, Lygodiaceae, or Schizaeaceae for thick-walled, unspciated specimens of *Deltoidospora*. Of the psilate trilete spores described from modern Panama by Roubik and Moreno (1991), these specimens most closely resemble *Acrostichum danaifolium* Langsd. & Fisch.

Paleoecology. A botanical affinity with *Acrostichum* or *Antrophyum* both indicate moist conditions, with *Acrostichum* suggesting a more lowland coastal environment, and *Antrophyum* suggesting a more upland moist forest (Graham 1989, 1995; Jarzen & Dilcher 2006).

Genus *Echinatisporis* Krutzsch 1959

Discussion. *Echinatisporis* includes azonate echinate, trilete microspores. Krutzsch (1959) described the spore walls as simple. *Echinatisporis* is differentiated from the otherwise similar *Ceratosporites* by having spines on both the proximal and distal faces. *Acanthotriletes* is distinguished by having a more triangular amb and a different shape of the echinae according to Srivastava (1972b), although the type species, *Acanthosporites primigenus* Naumova 1949, is described as rounded in outline. The form of the spines appear to be a better distinguishing characteristic, with *Acanthotriletes* having smaller, more densely arranged spines. *Verrucatisporites* Nagy 1969 is a similar form species for azonotrilete microspores with spines and verrucae, but is distinguished by having a more triangular amb; also, the verrucae and spines are described as isolated. *Echitriletes* Potonié 1956 is similar but reserved for megaspores. Some authors (e.g., Jaramillo & Dilcher 2001; Hoorn et al. 2014) use *Echitriletes* for echinate, trilete microspores; if this usage is followed *Echitriletes* is a senior synonym of *Echinatisporis*. However, Potonié (1956) clearly restricted *Echitriletes* to megaspores. *Raistrickia* and *Neoraistrickia* are distinguished by having more blunt tipped or baculate spines.

Echinatisporis sp. A
Plate 2.2, figures 7-8

Description. Trilete spores, echinate and verrucate, equatorial diameter 22–(29)–36 μm . Exine generally 1–2 μm thick except in the vicinity of the echinae and verrucae, where it is thicker. Amb subcircular to rounded subtriangular. Laesurae sometimes conspicuous but occasionally obscured by the ornamentation. Laesurae long, sometimes extending to equator, sometimes with thin labra, sometimes ornamented with small spines. Spines and verrucae cover the proximal and distal faces approximately equally, although the spines are usually concentrated at the equator. The spines are generally 1–7 μm long, with wide bases that rapidly taper near the base. Spines are never tuberculate, instead tapering to a single point. Verrucae generally between 0.5–5.0 μm in diameter.

Discussion. This species is morphologically similar to *Ceratosporites* sp. A, from which it differs by having an ornamented proximal face and non-tuberculate spines. *Neoraistrickia* sp. A and *Raistrickia* sp. A both have tuberculate, blunt tipped spines. *Echinatisporis longechinus* Krutzsch 1959 is larger (35–70 μm) than most specimens of *Echinatisporis* sp. A. Jaramillo et al. (2014) described a similar type from the Neogene of Panama which they informally named “*Echitriletes* ‘*selaginelloides*’ type ‘*muelleri*,’” differing mainly in having a triangular amb.

Occurrence. Ypresian; 27 specimens observed.

Botanical affinity. Selaginellaceae; these specimens are morphologically similar to spores identified as *Selaginella* from the Oligocene-Miocene of Mexico (Graham 1999).

Paleoecology. Probably lowland tropical forest (see paleoecology section for *Ceratosporites* sp. A).

Genus *Foveotrilletes* van der Hammen 1954 ex Potonié 1956 emend.

Emended description. Foveolate, trilete spores. Foveolae are here defined as more or less rounded depressions more than one micron in diameter, generally separated from adjacent foveolae by a distance greater than their diameter (Punt et al. 2007).

Discussion. The name *Foveotrilletes* was first proposed as a subgenus of *Triletes* van der Hammen 1954. The intended meaning of *Foveotrilletes* included all foveolate, trilete spores. Potonié (1956) elevated *Foveotrilletes* to generic rank, but significantly limited the original circumscription of *Foveotrilletes* to foveolate, trilete spores with rounded triangular amb and small foveolae that form a dense reticulum, as well as other characteristics which resembled those of the type species *Foveotrilletes scrobiculatus* (Ross 1949 ex Weyland & Krieger 1953) Potonié 1956. Although Potonié (1956) did not specify the size of the “foveolae,” Anderson (1960) later described specimens of *F. scrobiculatus* as having lumina approximately 0.5 microns in diameter, which are technically punctae and not foveolae according to the terminology of Punt et al. (2007). Pierce (1961), apparently unaware of Potonié’s elevation of *Foveotrilletes* to generic rank, later described *Foveotrilletes* as a new genus including all foveolate trilete spores, and assigned *Foveotrilletes triplanus* Pierce 1961 as type species.

Microfoveolatisporis Krutzsch 1962 is supposedly distinguished from *Foveotrilletes* by having a subcircular amb, although the description by Krutzsch (1962) translated by Jansonius and Hills (1976) of the sculpture as finely or minutely foveolate is unclear and may be roughly synonymous with punctate sculpture as defined by Punt et al. (2007). If *Microfoveolatisporis* is punctate, it is a junior synonym of *Punctatrilletes* Pierce 1961, which includes all punctate, trilete spores. If *Microfoveolatisporis* is foveolate, it is a junior synonym of *Foveotrilletes* emend. The genus *Foveotrilletes* is emended here to restore the original meaning of the taxon as proposed by van der Hammen (1954b), on the basis that form genera using the systematic nomenclature system of van der Hammen (1954b, 1956) should follow the original meaning of the system.

Foveotrilletes crater Stover & Partridge 1973

Plate 2.1, figures 11-12

Description. Trilete spores, punctate-foveolate, equatorial diameter 22–30 μm . Exine 0.5–1.0 μm thick. Laesurae extending nearly to edge of grain, laesurae straight to sinuous, labrum absent to well developed. Amb subtriangular. Spore surface irregularly covered with circular to elliptical depressions, ranging in size from punctae <0.5 μm in diameter to foveolae up to 5 μm .

Discussion. As Stover and Partridge (1973) noted, this species is quite similar to *Kuylisporites waterbolkii*, except in lacking the equatorial scutula.

Occurrence. Ypresian; 7 specimens observed. *Foveotrilletes crater* has previously been identified exclusively from the Cenozoic of Australia and New Zealand (Palynodata Inc. & White 2008), although it is possible morphologically similar spores have been identified elsewhere under other species names.

Botanical Affinity. Probably *Cnemidaria* Presl (Cyatheaceae), possibly Lycopodiaceae. The resemblance to *Kuylisporites waterbolkii* suggests affinity with *Cnemidaria*, also known as *Hemitelia* Brown (Pocknall & Mildenhall 1984; Cieraad & Lee 2006); however, Hill (2017) gave the botanical affinity as *Lycopodium* (Lycopodiaceae).

Paleoecology. The probable botanical affinity of this species with *Cnemidaria* suggests a similar paleoecology to *Kuylisporites waterbolkii*, namely montane forest.

Genus *Gemmatriletes* Pierce 1961

Discussion. This genus includes all gemmate, trilete spores. *Bullasporis* Krutzsch 1959 is a somewhat similar form genus possessing one or several bullae. Krutzsch (1959) described bullae as shaped like buttons or belt-buckles. Jardine (2011) described bullae as large bubble-like outgrowths attached to the spore wall. The term is arguably synonymous with gemmae, although perhaps bullae are distinguished by being longer than they are wide and more constricted at the base. Confusingly, the generic description for *Bullasporis* describes it as having a torus, but the description for the type species *Bullasporis bullis* Krutzsch 1959 states that only some specimens have tori. *Bullasporis* is perhaps best reserved for trilete spores with gemmae/bullae and a torus; these are possibly aberrant spores with affinity to the Gleicheniaceae (Skarby 1964). *Bullaspora* Venkatachala 1963 also includes trilete spores with bullae, but this genus is used for Paleozoic spores, and is distinguished by having a conspicuous equatorial thickening.

Gemmatriletes aff. *G. clavatus* Brenner 1968
Plate 2.2, figure 3

Description. Trilete spore, gemmate, equatorial diameter 37 μm . Nexine 0.5 μm thick, featureless, sexine composed of densely and uniformly arranged gemmae. Amb roughly subcircular, deviating slightly towards a triangular shape. Laesurae extend one-half to two-thirds the distance from the center of the grain to the edge, with slightly raised labra 0.5 μm wide in polar view. Sculptural elements generally gemmate, with constricted bases, length and width approximately equal, ranging from 0.5–3.0 μm but usually approximately 1.5 μm . Some sculptural elements more elongate, mushroom-shaped, clavate.

Discussion. Although the description for the type species of the genus, *Gemmatriletes morulus* Pierce 1961, is quite broad, the gemmae in that species can be much larger (up to 6 μm in diameter) than in this specimen. The holotype illustration by Pierce (1961) is more coarsely and irregularly gemmate. *Gemmatriletes clavatus* is somewhat similar to this specimen, but in *G. clavatus* the clavae are not as well developed and the exine is thicker.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato.

Gemmatriletes sp. A
Plate 2.2, figure 2

Description. Trilete spore, gemmate, equatorial diameter 19 μm . Laesurae extending to spore margin, with prominent margos or labra. Amb triangular. Surface ornamented with prominent gemmae, straight-sided or slightly constricted at their bases, 1.0–3.5 μm long, usually slightly longer than they are wide. Gemmae are concentrated along the laesurae and the edges of the spore.

Discussion. Spores somewhat similar to this species have been assigned to *Bullasporis*, for example unspiciated *Bullasporis* specimens described and illustrated by Frederiksen (1980b) and Jardine (2011), which differ from this species most obviously in having bullae which are evenly distributed over the spore surface and in having indistinct laesurae without labra. The type species, *Gemmatriletes morulus* Pierce 1961, differs most obviously from this species in having indistinct laesurae and a more circular amb. *Gemmatriletes multiglobus* Mildenhall & Pocknall

1989 is similar to this species in having prominent labra, but has a more circular amb and has smaller gemmae in proportion to the spore. *Gemmatriletes clavatus* is distinguished from this species by having smaller, more evenly distributed gemmae which have a narrow base, approaching a clavate shape. Also, no prominent labra are present, the laesurae are not prominent, and the amb is more circular. This specimen is similar to spores of the modern *Actinopteris radiata*, which possesses a triangular amb, prominent labra, and verrucate-gemmate sculpture (van Campo 1974).

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato. Mildenhall et al. (2014) give the botanical affinity for the somewhat similar species *Gemmatriletes multiglobus* as Grammitidaceae. Alternatively, *Gemmatriletes* sp. A is also morphologically similar to papillate species of *Selaginella*, for example *Selaginella labordei* (Zhou et al. 2015, Fig. 12 D-F).

Genus *Gleichenioides* Ross 1949 emend. Skarby 1964

Discussion. *Gleichenioides* is used for trilete spores morphologically similar to modern spores produced by *Gleichenia* Smith (Gleicheniaceae). The spore wall along or near the equator is developed into a distinct thickening which is discontinuous at the corners of the spore. The surface is smooth or faintly sculptured and the amb is triangular. *Camarazonosporites* (Pant 1954 ex Potonié 1956) Klaus 1960 differs in having a well-rounded amb and distal rugulate sculpture; *Toroisporites* Krutzsch 1959 has thickenings bordering the laesurae rather than bordering the spore wall along the equator.

Gleichenioides senonicus Ross 1949

Plate 2.1, figure 9

Description. Trilete spores, psilate, equatorial diameter 25–29 µm. Inter-radial thickenings or crassitudes near the equator are present and somewhat irregularly folded over the spore. Amb triangular. Laesurae extend to edge of spore, with 1.5–2.0 µm thick labra. Spore psilate in one specimen and scabrate in a second specimen, possibly due to poor preservation.

Discussion. The two specimens in this study fall within the limits of variation given in the original description for *G. senonicus*. Pocknall & Nichols (1996) did not speciate *Gleichenioides* on the basis of its rarity and apparent lack of biostratigraphic value.

Occurrence. Danian-Ypresian; 2 specimens observed. *Gleichenioides senonicus* is a very common and globally distributed form genus in the Mesozoic and Cenozoic (Palynodata Inc. & White 2008). According to Frederiksen (1980b), *G. senonicus* ranges from the Cretaceous to the Early Oligocene in the Gulf Coastal Plain. *Gleichenioides senonicus* has been identified from Eocene strata in DSDP Site 94 along the Campeche Escarpment (Barron 2015; Barron et al. 2017).

Botanical affinity. Gleicheniaceae (Jardine 2011).

Paleoecology. Possibly montane forest. Graham (1999) noted that *Gleichenia* (Gleicheniaceae) is a common plant of the modern evergreen cloud scrub in Mexico. Alternatively, Wakefield & Monteil (2002) gave the paleoecology for Cretaceous and Paleogene specimens of *G. senonicus* from Pakistan as freshwater marsh.

Genus *Hamulatisporis* Krutzsch 1959 emend. Srivastava 1972

Discussion. *Hamulatisporis* includes microspores with hamulate or rugulate sculpture which lack inter-radial crassitudes. *Camerozonosporites* Pant 1954 ex Potonié 1956 emend. Klaus 1960 is distinguished from *Hamulatisporites* by possessing inter-radial crassitudes. Although the sculpture of *Hamulatisporis* was originally defined as hamulate by Krutzsch (1959), Srivastava (1972b), in his emended description, referred to the sculpture as rugulose (i.e., rugulate). Punt et al. (2007) considered that hamulate sculpture is a type of rugulate sculpture. *Rugutriteles* Pierce 1961, a form genus including all rugulate, trilete spores, is therefore, in part, synonymous with *Hamulatisporis* and, in part, synonymous with *Camerozonosporites*. *Hamulatisporites* Nakoman 1966 is an obligate junior synonym of *Hamulatisporis*, having the same type species.

Hamulatisporis hamulatis Krutzsch 1959

Plate 2.2, figure 1

Description. Trilete spore, hamulate, equatorial diameter. Exine about 1.5 µm thick at equator, possibly cingulate. Amb rounded subtriangular. Laesurae long, without labra, commissure ragged. Sculpture hamulate, composed of winding muri generally 0.5–1.0 µm wide. The hamulate sculpture is more pronounced on the distal face of the spore.

Discussion. *Hamulatisporis hamulatis* was originally described as having more pronounced hamulate sculpture on the distal side of the spore. The laesurae are delicate, the rays extend approximately 3/4 the radius of the spore, the amb is triangular, and the exine has more than one layer. Nichols (2002) described *H. hamulatis* as having a cingulum, which is possibly what Krutzsch (1959) referred to when he described the exine as being multi-layered. Despite the ambiguity about the exine structure and presence or absence of a cingulum, this specimen is clearly conspecific with *H. hamulatis* on the basis of close morphological similarity to described and illustrated specimens of that species. *Hamulatisporis amplius* Stanley 1965 is distinguished from *H. hamulatis* by being >50 µm in equatorial diameter. Although the size range for *H. hamulatis* was not explicitly stated by Krutzsch (1959), Stanley (1965) and Nichols (2002) both describe the species as being approximately 30 µm in equatorial diameter.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Lycopodiaceae (Nichols 2002); Srivastava (1972b) noted that modern spores of *Lycopodium adpressum* Lloyd & Underw. (syn. *Lycopodium appressa*) compare well with the form genus *Hamulatisporis*.

Paleoecology. Possibly lowland tropical forest or swamp. The modern *Lycopodium adpressum* is commonly found on moist banks and the borders of swamps, mainly near the coast (Britton & Brown 1913). Graham (1976, 1988, 1999) described the paleoecology of *Lycopodium* spores from Central America variously as lowland moist tropical forest, lower montane moist forest, deciduous forest, evergreen to semi-evergreen selva, and evergreen cloud scrub.

Genus *Kuylisporites* Potonié 1956

Discussion. *Kuylisporites* includes trilete spores which are morphologically similar to modern *Cnemidaria* spores, particularly in possessing three conspicuous, crescent-shaped elevations or scutula which enclose circular to elliptical, shallow lumina (Potonié 1956; Dettmann 1963). The

scutula are equatorial and interrarial. Small blisters, punctae, and/or foveolae may also be present.

Kuylisporites waterbolkii Potonié 1956

Plate 2.1, figure 13

Description. Trilete spore, punctate-foveolate, equatorial diameter 23 μm . Exine 1 μm thick. Laesurae with thin, slightly sinuous labrum, extending nearly to edge of grain. Amb subtriangular. Spore surface ornamented with sparsely and irregularly distributed circular to slightly elliptical punctae or foveolae 0.5–1.5 μm in diameter. The most prominent features of the spore are three interrarial scutula 5–7 μm in diameter, which enclose elliptical lumina. The scutula are 1.0–1.7 microns high.

Discussion. This specimen closely resembles the holotype illustration of *Kuylisporites waterbolkii* by Potonié (1956, Plate 4, Fig. 39), differing mainly in being much smaller than the holotype of *K. waterbolkii* (45 μm). Despite the size difference, the specimen can be included within *K. waterbolkii* because no size limits were given in the original description. *Kuylisporites mirabilis* (Bolkhovitina 1953) Potonié 1958 is distinguished by having distal as well as equatorial scutula (Dettmann 1963).

Occurrence. Ypresian; 1 specimen observed. The extant genus *Cnemidaria* produces morphologically similar spores and currently inhabits Central America, the Caribbean, and northern South America (Mohr & Lazarus 1994). In the early Paleogene, *K. waterbolkii* was mainly restricted to the Australasian floral province (Mohr & Lazarus 1994; Palynodata Inc. & White 2008), with the first regular South American occurrences in the early Oligocene (C. Jaramillo, personal communication, 2019). Before the identification of this Ypresian specimen, the oldest published Central American or Caribbean occurrence of this spore type was from the Oligocene of Puerto Rico (Graham & Jarzen 1969).

Botanical affinity. *Cnemidaria* C. Presl (Cyatheaceae) or *Cyathea* Smith; Romero Valero (2014) gave the taxonomic affinity as *Hemitelia* Brown, but this study will follow the taxonomy of Graham & Jarzen (1969) and Mohr & Lazarus (1994). Lehnert (2012) relegated *Cnemidaria* to an unranked clade in the genus *Cyathea*, and noted that *Cnemidaria*-type spores are also found outside of this clade in the *Cyathea decurrens* (Hooker) Copeland group.

Paleoecology. Probably montane forest (Trujillo & Roche 2009; Romero Valero 2014); extant *Cnemidaria* predominantly inhabits elevations between 500–2,000 m (Mohr & Lazarus 1994).

Genus *Neoraistrickia* Potonié 1956

Discussion. *Neoraistrickia* includes trilete spores with bacula or spines, as well as tuberculate protuberances; the genus is distinguished from the similar *Raistrickia* Schopf, Wilson & Bentall 1944 by having a subtriangular rather than subcircular amb (Playford & Melo 2009).

Ceratosporites has been argued to be a junior synonym of *Neoraistrickia*, but in this study *Neoraistrickia* will be restricted to forms with ornamentation on both the proximal and distal faces, even if the proximal ornamentation is reduced (see discussion for *Ceratosporites*). The botanical affinity is with the Selaginellaceae (Dettmann 1963). As with *Raistrickia*, *Neoraistrickia* has been identified exclusively from Paleozoic and Mesozoic strata (Palynodata Inc. & White 2008), but similar morphologies are found in modern Selaginellaceae (e.g., Zhou et

al. 2015). The absence of any Cenozoic records of *Neoraistrickia* may be the result of taxonomic practices rather than stratigraphic reality.

Neoraistrickia sp. A
Plate 2.3, figures 2-4

Description. Trilete spores, echinate, tuberculate, and verrucate, equatorial diameter 20–35 μm . Exine 1–2 μm thick, except in the vicinity of the protuberances, where the exine is somewhat thickened. Amb subtriangular. Laesurae extend to the equator, labrate, the laesurae sometimes ornamented with spines. The sculpture is quite variable, ranging from low verrucae to narrow spines or broad tuberculate protuberances. The spines and tuberculate protuberances range in height from 1–7 μm . The ornamentation is concentrated along the equator, and present but more sparsely distributed on the distal face. The ornamentation is more or less reduced on the proximal face relative to the distal face, but never entirely absent.

Discussion. This species has similar ornamentation to *Ceratosporites* sp. A, which is distinguished by lacking ornamentation on the proximal face, and *Raistrickia* sp. A, which is distinguished by having a more circular amb. These morphologies appear to be transitional to one another to some extent, and all have probable botanical affinity with the Selaginellaceae. No attempt was made to place this morphotype in a previously existing species because of the disjunct stratigraphic distribution between these specimens and existing Paleozoic and Mesozoic species of *Neoraistrickia*.

Occurrence. Ypresian; 6 specimens observed.

Botanical affinity. Probably Selaginellaceae, because of the similarity of this type with extant species of *Selaginella* (Zhou et al. 2015).

Paleoecology. Probably lowland tropical forest (see paleoecology section for *Ceratosporites* sp. A).

Genus *Punctatriletes* Pierce 1961

Discussion. *Punctatriletes* includes all trilete, punctate spores. *Punctatisporites* Ibrahim 1933 is a similar form genus with a complicated taxonomic history (Jansonius & Hills 1976, Doweld 2017). The original genus description for *Punctatisporites* is rather vague, and includes trilete spores having an exine with a fine sandy texture. Multiple authors have provided conflicting emendations of *Punctatisporites*, variously including trilete spores with psilate, punctate, rugulate, and reticulate sculpture (Jansonius & Hills 1976). *Punctatisporites* is here considered a nomen ambiguum. *Foveotriletes* emend. is distinguished by being foveolate (lumina >1 μm in diameter). To the extent that *Microfoveolatisporis* includes punctate, trilete spores, it is a junior synonym of *Punctatriletes* (see discussion for *Foveotriletes*).

Punctatriletes sp. A
Plate 2.1, figure 10

Description. Trilete spore, punctate, equatorial diameter 23 μm . Exine 1.0–1.5 μm thick. Laesurae prominent, slightly sinuous, long. The labrum is faintly present as a poorly defined raised area around the laesurae. Amb rounded subtriangular. The spore surface is irregularly, fairly densely covered with roughly circular punctae averaging 0.5 μm in diameter, ranging from

<0.5 to 1 μm in diameter. A few lumina slightly exceed 1 μm in diameter and are technically foveolae rather than punctae. In some areas the punctae are quite densely arranged and technically could be described as reticulate, but in other areas the punctae are more widely spaced and clearly punctate. The irregular arrangement of the punctae, the predominantly wide spacing of the punctae, and the lack of clearly definable muri argue against describing the ornamentation as reticulate.

Discussion. Although a few of the lumina in this specimen slightly exceed 1 μm in diameter and are technically foveolae, the majority of the lumina are punctae, so the specimen has been assigned to *Punctatriletes* rather than *Foveotriletes*. This specimen resembles *Punctatriletes parvimundus* Pierce 1961 in its size, the thickness of its exine, and its triangular amb. This specimen differs from *P. parvimundus* in that the laesurae do not appear to extend to the equator and the commissures are slightly sinuous rather than straight as in *P. parvimundus*. Graham (1988) described somewhat similar punctate-foveolate spores and assigned them to *Lycopodium*; his specimens differed mainly in having a psilate proximal face.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato, possibly Lycopodiaceae (see discussion).

Genus *Raistrickia* Schopf, Wilson & Bentall 1944

Discussion. *Raistrickia* includes verrucate to spinose trilete spores. Characteristically, the spines or bacula are blunt tipped and branched or dissected into two or more terminal papillae, a sculpture type also known as tuberculate. The amb is subcircular or only slightly triangular, the equatorial diameter is generally 40-90 μm , and the laesurae are generally not prominent. *Neoraistrickia* Potonié 1956 is similar to *Raistrickia* in ornamentation but is generally distinguished by having a more strongly triangular amb. *Raistrickia* has seemingly only been identified from the Paleozoic and Mesozoic (Palynodata Inc. & White 2008). However, the tuberculate spore morphology found in *Raistrickia* is also present in some extant species of the Selaginellaceae (Zhou et al. 2015). Knox (1950) stated that the morphology of *Raistrickia* corresponds with species groups represented by *Selaginella biformis* Braun ex Kuhn and *Selaginella latifrons* Warburg, and tentatively suggested a botanical relationship between *Selaginella* (Selaginellaceae) and *Raistrickia*. The absence of any Cenozoic records of *Raistrickia* may therefore be more a matter of taxonomic convention than a true disappearance of the spore morphology from the stratigraphic record.

Raistrickia sp. A Plate 2.3, figures 5-6

Description. Trilete spores, tuberculate, echinate, and verrucate, equatorial diameter 27–33 μm . Exine 1–2 μm thick except in the vicinity of the sculptural projections, where it may gradually or abruptly thicken at the base of the projections. Amb subcircular or slightly subtriangular. Laesurae not clearly observable in two specimens, laesurae extending nearly to equator in two other specimens with labra 1 μm wide. Labra ornamented with small verrucae and tuberculate projections. Spore surface covered in blunt tipped tuberculate projections, generally slightly taller than they are wide, often with two or several small papillae or spines extending from the end of the projections. Tuberculate projections generally slowly tapering through their length, sometimes straight-sided or expanded at the base and tips. Tuberculate projections generally 1.0–

4.5 μm tall, 1–4 μm wide. Echinate projections with broad bases are also present but are less common. Low rounded verrucae 0.5–3.5 μm in diameter are scattered across the spore surface. The tuberculate and echinate projections are concentrated along the equator but also scattered across both the proximal and distal faces.

Discussion. The Chicxulub occurrence of the genus *Raistrickia* is the first Cenozoic record of the genus. It is unlikely that these spores are reworked from older deposits because no other exclusively Mesozoic palynomorphs have been observed in the assemblage; also, the morphology of this species resembles some modern species of *Selaginella*. No attempt was made to place this morphotype in a previously existing species because of the disjunct stratigraphic distribution between these specimens and existing Paleozoic and Mesozoic species of *Raistrickia*. *Raistrickia* sp. A is similar to a photograph of an undescribed spore identified as *Selaginella* from the Lower Miocene of Panama (Graham 1988), specifically in having blunt tipped projections, although it is unclear from the photograph whether the projections are tuberculate.

Occurrence. Ypresian; 6 specimens observed.

Botanical affinity. Probably Selaginellaceae (Knox 1950).

Paleoecology. Probably lowland tropical forest (see paleoecology section for *Ceratosporites* sp. A).

Genus *Retitriletes* Pierce 1961

Discussion. This genus includes all reticulate, trilete spores. The proposed emendation of *Retitriletes* by Döring et al. in Krutzsch (1963) is rejected because *Retitriletes* was established using the artificial nomenclature of van der Hammen (1954b, 1956) and should include all reticulate, trilete spores. Other form genera for reticulate, trilete spores exist, with overlapping synonymies. *Lycopodiumsporites* Thiergart 1938 ex Delcourt & Sprumont 1955 includes trilete spores with a rounded triangular amb, a straight or convex outline, and a reticulum with lumina 6 μm or less in diameter. Krutzsch (1963) considered *Lycopodiumsporites* a nomen ambiguum, probably synonymous with *Ischyosporites* Balme 1957. Srivastava (1975) described these taxonomic issues in more detail. *Microreticulatisporites* Knox 1950 as originally defined was restricted to monolete spores, although the genus was later emended by Potonié & Kremp (1954) and Bharadwaj (1955) to include only certain types of reticulate, trilete spores. *Zlivisporis* Pacltová 1961 includes trilete spores with a psilate or slightly rugulate proximal surface, a reticulate distal surface, and thin and delicate muri. *Rouseisporites* Pocock 1962 is arguably a junior synonym of *Zlivisporis* (Jansonius & Hills 1976). Ziemińska-Tworzydło et al. (1994) proposed a new genus for spores with affinity to the Selaginellaceae, *Lycopodiaceasporis* Ważyńska 1994, and relegated *Retitriletes* to a subgenus within that genus. This taxonomic action conflicts with the purely morphological definition of *Retitriletes* and will not be followed here. The botanical affinity for *Retitriletes* is generally with the Lycopodiaceae (Srivastava 1975).

Retitriletes sp. A Plate 2.1, figure 14

Description. Trilete spores, reticulate, equatorial diameter 26–33 μm . Exine excluding muri height 0.5–1.0 μm thick. Amb subtriangular. Laesurae inconspicuous and unbordered, extending

nearly to equator. Sculpture reticulate, more prominent on the distal face, lumina rounded polygonal in shape, muri 0.5–1.0 μm wide and 0.5–1.0 μm high, the muri forming a crenulate pattern on the edge of the spore in distal and proximal view.

Discussion. These specimens are morphologically similar to trilete, reticulate forms of *Lycopodium* (Lycopodiaceae) spores. The reticulum is quite delicate, and more clearly observable in phase contrast microscopy. Fossil spores with affinity to *Lycopodium* in the fossil record of Central America (Graham 1976, 1988, 1989) are commonly punctate-foveolate rather than reticulate, although Graham & Jarzen (1969) briefly described some reticulate *Lycopodium* spores from the Oligocene of Puerto Rico. Their specimens, however, appear more thick-walled and have more conspicuous laesurae. Ramírez-Arriaga et al. (2005) described an unnamed species of *Retitriletes*, but their species was much larger (59–84 μm) than *Retitriletes* sp. A.

Occurrence. Ypresian; 2 specimens observed.

Botanical affinity. Probably Lycopodiaceae (see discussion).

Paleoecology. Possibly lowland tropical forest or swamp (see paleoecology section for *Hamulatisporis hamulatis*).

Retitriletes sp. B
Plate 2.1, figure 15

Description. Trilete spore, reticulate, equatorial diameter 20 μm . Exine 1 μm thick. Amb strongly triangular, straight-sided. Laesurae extend nearly to equator, prominent, with high labra 3 microns wide from labra edge to labra edge. Irregular reticulum composed of elliptical to rounded polygonal lumina generally 1.5–2.5 microns in diameter. Muri generally 1.0–1.5 μm wide.

Discussion. The single observed specimen of this type is distinguished from *Retitriletes* sp. A most obviously by its prominent labra. An alternative generic assignment is to *Ischyosporites* Balme 1957, as the reticulum is somewhat irregular, but the distal side of the spore is not clearly arched and thickened in the single observed specimen.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato, possibly Lycopodiaceae; the unusual morphology of the specimen precludes a confident assignment of botanical affinity.

Genus *Rugutriletes* Pierce 1961

Discussion. *Rugutriletes* includes all rugulate, trilete spores. *Camarozonosporites* Pant 1954 ex Potonié 1956 emend. Klaus 1960, *Hamulatisporis* Krutzsch 1959 emend. Srivastava 1972, and *Inundatisporis* (Krutzsch 1963) Srivastava 1972 are all genera of rugulate, trilete spores. *Camarozonosporites* has a rugulate distal face and a psilate proximal face with inter-radial crassitudes, *Hamulatisporis* is strongly hamulate on one or both faces and inter-radial crassitudes are not present, and *Inundatisporis* has rugulate proximal and distal faces and inter-radial crassitudes. *Rugutriletes* is used here for rugulate, trilete spores that cannot be included within these three genera.

Rugutritetes sp. A
Plate 2.1, figure 16

Description. Trilete spore, proximal face verrucate-rugulate near laesurae, otherwise psilate, distal face psilate, equatorial diameter 45 µm. Exine 1 µm thick. Amb subtriangular. Laesurae extend nearly to edge of grain, widely gaping (possibly a preservational artifact), with labra 2–3 µm wide near the center of the grain, thinning at edges of grain. Cingulum present but not entire, possibly due to poor preservation. The proximal face has distinct ornamentation limited to the vicinity of the laesurae, with low raised verrucae and rugulae which are partially fused into ridges paralleling the laesurae.

Discussion. This species is somewhat similar to spores of the modern *Pteris grandifolia* L. (Polypodiaceae), particularly in having a cingulum and a proximal face with verrucae and rugulae partially fused into ridges paralleling the laesurae (Palacios-Rios et al. 2017). However, the distal face of the spore in *P. grandifolia* is verrucate to rugulate, and in *Rugutritetes* sp. A the distal face is psilate. This species cannot be placed in *Hamulatisporis* because that genus is described as strongly rugulate or hamulate. An alternative generic assignment for this species is *Verrucosisporites*, but the dominant sculptural elements in *Rugutritetes* sp. A are rugulae rather than verrucae.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato, possibly *Pteris* L. (Polypodiaceae) (see discussion).

Paleoecology. Possibly lowland tropical forest. Modern *Pteris* in Central America currently inhabits riparian or shaded lowland tropical forest (Palacios-Rios et al. 2017).

Genus *Undulatisporites* Pflug in Thomson & Pflug 1953 emend.

Haradisporites Singh & Kumar 1972

Emended description. Trilete miospores <200 µm in diameter or longest dimension. Laesurae with raised, sinuous or undulating labra, which may or may not extend to the equator. No torus or zona is present. The surface sculpture is psilate, scabrate, or granulate, lacking prominent sculptural elements. Amb rounded convexly triangular.

Discussion. *Undulatisporites* as originally defined was reserved for trilete miospores with a rounded convexly triangular amb, laesurae which extend approximately 3/5–4/5 the distance to the equator, psilate or subdued sculpture, and most importantly, raised more or less sinuous or undulating laesurae, hence the name. A broader sense of the genus has been used previously in the literature to include types in which the laesurae extend to the equator or nearly so, for example *Undulatisporites fossulatus* Singh 1971 and *Undulatisporites elsikii* Frederiksen 1973. This emendation simply formalizes this expanded circumscription. The term miospore in the original description is understood here to mean spores smaller than approximately 200 µm (Punt et al. 2007). *Undulatisporites* Klein 1959 is a similar form genus distinguished by possessing a zona. *Haradisporites* Singh & Kumar 1972 is here considered a junior synonym of *Undulatisporites*; both include psilate or lightly sculptured trilete spores with a rounded triangular amb, elevated labra, and sinuous or undulating laesurae. *Haradisporites*, however, has apparently only been identified from the Mesozoic of India (Palynodata Inc. & White 2008). Tripathi & Vijaya (2006) seem to indicate that the two genera are differentiated on the basis of

laesurae length, with *Undulatisporites* having laesurae reaching up to 3/4 the spore radius, and *Haradisporites* having laesurae reaching more than 3/4 the spore radius. This is problematic, because *Undulatisporites* was originally described as having laesurae extending approximately 3/5-4/5 the spore radius, and also because the distinction between the two genera becomes rather arbitrary. *Haradisporites* was originally described as being 20-48 µm in equatorial diameter and having an exine less than 1.5 µm thick, but this is not helpful for distinguishing the genus from *Undulatisporites*, which is not restricted on the basis of size or exine thickness.

Undulatisporites elsikii Frederiksen 1973 sensu lato
Plate 2.1, figure 8

Description. Trilete spore, psilate, equatorial diameter 24 µm. Exine 1.5 µm thick. Amb convexly triangular with pointed edges formed by the protruding labra. Sinuous laesurae extend to the equator, with labra 2.5 µm wide measured from the edges of the labra perpendicular to the commissure. Grain surface psilate.

Discussion. *Undulatisporites elsikii* was briefly described but not named by Elsik (1968a). Although in the description for *U. elsikii* by Frederiksen (1973) the labra are described as not quite reaching the equator, in Elsik's (1968a) specimens the labra do reach the equator. Elsik (1968a) did not describe the dimensions of his species, but a photograph of one of his specimens shows labra approximately 2 µm wide. Frederiksen (1973) described his specimens as having labra approximately 0.5–1.0 µm wide. However, Frederiksen (1973) measured the labrum width from the edge of the labrum to the commissure, so his specimens have a labrum width of 1–2 µm measured from the edges of the labra. The Chicxulub specimen has a slightly broader labrum than *U. elsikii* sensu stricto.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Probably Polypodiaceae (Frederiksen 1980b), although Galván-Escobedo et al. (2015) assigned unspeciated specimens of *Undulatisporites* to the Ophioglossaceae.

Undulatisporites mineri (Singh & Kumar 1972) n. comb.
Plate 2.1, figures 6-7

Basionym. *Haradisporites mineri* Singh & Kumar 1972, holotype specimen photographed on Plate 1, figures 1-2.

Description. Trilete spores, psilate, equatorial diameter 25–26 µm. Exine 0.5 µm thick. Amb convexly rounded triangular. Sinuous laesurae extend nearly to the equator, becoming indistinct at the margins of the grain. Raised labra present, approximately 0.8 µm wide measured from the edges of the labra perpendicular to the commissure.

Discussion. Because *Haradisporites* is here considered a junior synonym of *Undulatisporites*, *H. mineri* is transferred to *Undulatisporites*. Singh & Kumar (1972) originally described *U. mineri* as a psilate trilete spore with a thin exine, a rounded triangular amb, and sinuous laesurae with raised labra which extend at least 3/4 the distance to the edge of the spore. *Undulatisporites mineri* has a thinner exine than *Undulatisporites elsikii* (1.0-1.5 µm thick), *Undulatisporites microcutis* Pflug in Thomson & Pflug 1953 (>3 µm thick), and *Undulatisporites undulapolus* Brenner 1963 (1.5-2.0 µm thick). The labra are also narrower in *U. mineri* than in *U. elsikii*. *Undulatisporites sinuosis* Groot & Groot 1962 is somewhat similar, but the laesurae reach the equator and the exine is faintly scabrate rather than psilate.

Occurrence. Ypresian; 2 specimens observed. This is the first published occurrence of *U. mineri* outside the Mesozoic of India (Palynodata Inc. & White 2008); the presence of this species in the Ypresian of Central America may be the result of morphological convergence. Similar unnamed psilate trilete spores with undulating laesurae have been described from the Eocene of Panama (Graham 1985, figs. 9-10).

Botanical affinity. Probably Polypodiaceae, also possibly Ophioglossaceae, assuming a similar botanical affinity to *Undulatisporites elsikii*.

Genus *Verrucosisporites* Ibrahim 1933 emend. Smith 1971

Discussion. Multiple form genera with similar names have been proposed to include trilete, verrucate spores. *Verrucosisporites* is the oldest proposed genus, and as originally formulated includes all verrucate, trilete spores. This genus was emended multiple times, as described in detail by Jansonius & Hills (1976). As emended by Smith (1971), *Verrucosisporites* includes verrucate, trilete miospores with a small proportion of other ornamentation such as rugulae, coni, and bacula, and excludes strongly triangular forms. *Verrucatotriletes* van Hoeken-Klinkenburg 1964 is distinguished by having larger and more irregularly shaped verrucae. *Converrucosisporites* Potonié and Kremp 1954 is distinguished by having a strongly triangular amb. *Verrutriletes* Pierce 1961 is a junior homonym of *Verrutriletes* van der Hammen 1956 ex Potonié 1956, which is used for trilete verrucate megaspores. *Verrucatisporites* Nagy 1969 is not often used (Palynodata Inc. & White 2008), and is probably best distinguished from *Verrucosisporites* by having more isolated verrucae, as both genera may have coni or spines (Jansonius & Hills 1976). *Echinatisporis* and *Ceratosporites* may have verrucae but the dominant sculptural elements are coni/spines. *Verrucosisporites* is commonly used for Paleozoic spores, but has been identified from Cenozoic assemblages as well (Palynodata Inc. & White 2008).

Verrucosisporites sp. A
Plate 2.2, figures 4-6

Description. Trilete spores, verrucate and usually sparsely echinate, equatorial diameter 20– (25) –33 μm . Exine generally 1–2.5 μm thick, quite variable in thickness due to verrucae. Amb broadly rounded subtriangular, rarely approaching subcircular. Laesurae extending nearly to edges of grain with prominent 1–2 μm wide raised labra, in places overgrown with verrucae. Ornamentation present on both proximal and distal faces. Verrucae densely arranged, occasionally overlapping, variable in size but generally 1–3 μm in diameter, low and rounded. Most specimens of this type have been observed with sparsely distributed straight-sided spines 0.5–3.0 μm in length.

Discussion. *Verrucosisporites* sp. A is similar to *Echinatisporis* sp. A, but the spines are sparsely distributed or rarely absent. It is possible that *Echinatisporis* sp. A and *Verrucosisporites* sp. A are spores produced by a single species or a species complex in the Selaginellaceae.

Occurrence. Thanetian; 14 specimens observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato, possibly Selaginellaceae.

2.4.2. Monolete spores

Genus *Laevigatosporites* Ibrahim 1933 emend. Schopf et al. 1944

Discussion. This genus as emended includes all psilate, reniform to oval, monolete spores. Jaramillo and Dilcher (2001) included some granulate, monolete spores in this genus.

Laevigatosporites haardtii (Potonié & Venitz 1934) Thomson & Pflug 1953
Plate 2.3, figures 7-8

Laevigatosporites gracilis Wilson & Webster 1946

Laevigatosporites ovatus Wilson & Webster 1946

Description. Monolete, psilate to scabrate, length 25– (33) –40 μm , width 17– (25) –34 μm . Exine generally 0.5–1.0 μm thick. Shape broadly oval to slightly reniform. Monolete mark a simple slit extending 2/3-4/5 the length of the grain.

Discussion. *Laevigatosporites haardtii* is here considered synonymous with *Laevigatosporites ovatus* Wilson & Webster 1946 and *Laevigatosporites gracilis* Wilson & Webster 1946, following Srivastava (1972b) and Jardine (2011). *Laevigatosporites major* Cookson 1947 is distinguished by being over 50 μm long according to Nichols (1970).

Occurrence. Ypresian; 11 specimens observed. *Laevigatosporites haardtii* is a common and globally distributed species in the Cenozoic (e.g., Lenoir & Hart 1988; Vajda & Raine 2003, Palynodata Inc. & White 2008; Smith et al. 2018), with some Mesozoic occurrences (e.g., Palynodata Inc. & White 2008; Garzon et al. 2012; Akyuz et al. 2016). This nondescript morphology is similar to modern Gleicheniaceae and Polypodiaceae spores from Panama (Roubik & Moreno 1991).

Botanical affinity. Probably Polypodiales (Jardine 2011), also possibly Isoetaceae (Knox 1950).

Paleoecology. Akkiraz et al. (2008) considered that *L. haardtii* indicated lowland freshwater swamp environments. Graham et al. (2000) noted with some reservation that similar monolete, psilate spores assigned to *Laevigatosporites* may indicate the development of marsh or swamp habitats. Ferns producing *Laevigatosporites* spores were the first pioneers to recover following the Chicxulub impact, and these spores often dominate within the K-Pg fern-spike (e.g., Nichols et al. 1986; Nichols & Johnson 2008; Vajda et al. 2001; Vajda & Raine 2003). However, *Laevigatosporites haardtii* was not observed in the Paleocene section, possibly due to poor preservation.

Genus *Microfoveolatosporis* Krutzsch 1959

Discussion. This genus includes reniform monolete spores with foveolate sculpture. Potonié's (1966) emendation is rejected here, because he describes *Microfoveolatosporis* as sometimes having foveolate-reticulate ornamentation, and this is contradictory using the terminology of Punt et al. (2007).

Microfoveolatosporis cf. *M. fromensis* (Cookson 1957) Harris 1965
Plate 2.3, figure 9

Description. Monolete, foveolate to punctate, length 50 µm microns, width 29 µm. Exine 1.5–2.0 µm thick. Reniform shape. Monolete mark not clearly observable, presumably present at spore margin. Circular foveolae and punctae 0.5–2.0 µm in diameter are scattered fairly densely across the whole surface of the spore, generally separated from each other by muri which are wider than the diameter of the foveolae.

Discussion. This specimen differs from the type species, *Microfoveolatosporis pseudodentatus* Krutzsch 1959, in lacking a two-layered wall structure. This specimen is quite similar to a specimen of *Microfoveolatosporis fromensis* photographed by Scholtz (1985), who stated that *M. fromensis* is indistinguishable from spores of the modern *Actinostachys pennula* (Sw.) Hook. (Schizaeaceae). The original species description and holotype photograph for *M. fromensis* by Cookson (1957) is quite similar to the specimen in this study, although the holotype specimen of *M. fromensis* is larger than this specimen (70 x 50 µm). Also, the monolete laesura is described as rather prominent, but due to the orientation of the specimen in this study the monolete mark is not clearly observable. Spores of *A. pennula* imaged in light microscopy and SEM microscopy by Giacosa and Barakat (2018) are quite similar to this specimen, although this specimen lacks the spheroids seen in *A. pennula*. *Microfoveolatosporis mahadekensis* Kar & Singh 1986 and *Microfoveolatosporis skottsbergii* (Selling 1946) Srivastava 1971 are both larger than this specimen.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Schizaeaceae (see discussion).

Genus *Polypodiisporonites* Potonié 1931

Discussion. *Polypodiisporonites* includes reniform, verrucate, monolete spores (Jardine 2011). This study will follow Potonié (1966) and Frederiksen (1980b) and consider *Polypodiidites* Ross 1949, *Verrucatosporites* Thomson & Pflug 1953, and *Polypodiisporites* Potonié 1956 junior synonyms of *Polypodiisporonites*. *Verrumoneletes* van der Hammen 1956, which includes all verrucate, monolete spores, is also essentially a junior synonym of *Polypodiisporonites* as broadly defined.

Polypodiisporonites sp. A
Plate 2.3, figure 12

Description. Monolete, verrucate, length 32 µm, width 20 µm. Exine 2 µm thick. Reniform shape. Monolete mark narrow, slightly thickened. Spore surface densely covered in low, rounded, circular to elliptical verrucae 0.5–2.5 µm in diameter. Some verrucae are partially fused or coalescent with adjacent verrucae. Verrucae height generally <0.5 µm, although a few verrucae are up to 0.8 µm in height.

Discussion. The type species, *Polypodiisporonites favus* Potonié 1931, differs in possessing a negative reticulum. *Polypodiisporonites alienus* (Potonié 1931) Frederiksen 1980 and *Polypodiisporonites afovus* (Krutzsch 1959) Frederiksen 1980 are larger (>40 µm long). *Polypodiisporites usmensis* (van der Hammen 1956) Khan & Martin 1972 has higher verrucae (approx. 1 µm) than this specimen. *Polypodiisporites minimus* (Couper 1960) Khan & Martin

1971 emend. Pocknall & Mildenhall 1984 is similar in size to *Polypodiisporonites* sp. A, but again the verrucae are higher (approx. 1 µm).

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Probably Polypodiaceae; Jardine (2011) gave the probable botanical affinity as Polypodiaceae for a visually similar but unspciated and undescribed specimen of *Polypodiosporonites*. Verrucate monolete spores are found in modern Polypodiaceae and Schizaeaceae from Panama (Roubik & Moreno 1991).

Paleoecology. Possibly lowland tropical forest or swamp; Wakefield & Monteil (2002) give a suggested paleoecology of tropical fern swamp for the similar species *P. afavus* from the Cretaceous-Tertiary of Pakistan.

Genus *Reticuloidosporites* Pflug in Thomson & Pflug 1953

Discussion. *Reticuloidosporites* includes all reniform, reticulate, monolete spores.

Microfoveolatosporis Krutzsch 1959 is foveolate rather than reticulate. *Reticulosporis* Krutzsch 1959 includes azonomonolete microspores with a positive reticulum and is arguably a junior synonym of *Reticuloidosporites*, although Srivastava (1971) and Potonié (1966) considered *Reticulosporis* a junior synonym of *Microfoveolatosporis*. *Retimonoletes* Pierce 1961 includes all reticulate monolete spores and is a junior synonym of *Reticuloidosporites*.

Reticuloidosporites pseudomurii Elsik 1968

Plate 2.3, Figures 10-11

Description. Monolete, punctate and foveolate, ambiguously pseudo-reticulate, length 25–38 µm, width 21–29 µm. Exine about 1 µm thick. Shape broadly reniform, outline slightly undulose due to foveolate depressions. Monolete mark prominent, not extending full length of spore, 12–18 µm long. Surface sculpture in the form of low, rounded depressions or punctae/foveolae generally 0.7–1.5 µm in diameter, densely arranged in an irregular pattern with some clustering of the foveolae, forming a weakly developed pseudo-reticulum. Rugulae, if present, are only visible as poorly developed interstitial ridges between foveolae.

Discussion. Elsik (1968a) described the surface sculpture in *Reticuloidosporites pseudomurii* as foveolate, but Frederiksen (1980a) considered that the species was reticulate on the basis that the lumina are much wider than the muri. The sculpture may technically be reticulate, but the sculpture pattern does not resemble a mesh or network; although not stated by Elsik (1968a), the “pseudo-muri” present in this species is presumably the basis for the species name. Depending on how the reticulum is defined, *R. pseudomurii* could be reassigned to *Microfoveolatosporis*. However, the use of *Reticuloidosporites* for this species is well established and will not be contested here. Leffingwell (1970) and Pocknall & Nichols (1996) have described this species as being verrucate and rugulate as well as foveolate; the specimens observed in this study are foveolate but not clearly verrucate or rugulate.

Occurrence. Ypresian; 4 specimens observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato.

2.4.3. Gymnosperm pollen

Genus *Cycadopites* Wodehouse 1933 ex Wilson & Webster 1946

Discussion. This form genus was created for monocolpate pollen grains resembling modern *Cycas*, and with a presumed botanical affinity to the Cycadophyta. Wodehouse (1933) originally described *Cycadopites* as including ellipsoidal monocolpate pollen grains with a colpus extending nearly to the edges of the grain and gaping open at the ends. The colpus is often constricted in the middle, or the sides of the colpus are overlapping. The exine is described as thin but firm, and generally psilate, although other sculptural types have been described in this genus; for example *Cycadopites scabratus* Stanley 1965 is scabrate, *Cycadopites fusus* (Nakoman 1965) Kedves 1974 is granulate, and *Cycadopites balinkaense* Kedves 1974 is punctate. According to Jardine (2011), *Monocolpopollenites* is differentiated by being smaller and having a shorter colpus that is not closed in the middle. Wodehouse (1933) gave no restrictions on the size range for *Cycadopites*, other than that his specimens ranged from 25–45 μm long. Also, Wodehouse (1933) did not clearly restrict the genus to forms with a colpus closed in the middle, and one of his illustrations of *Cycadopites follicularis* (Fig. 2, p. 485) appears to show a non-overlapping colpus. Nichols et al. (1973) considered that the primary characteristic distinguishing *Cycadopites* from *Arecipites*, *Liliacidites*, and *Monocolpopollenites* is that the colpus is gaping open at the ends in *Cycadopites*.

Cycadopites follicularis Wilson & Webster 1946

Plate 2.4, figure 9

Description. Monocolpate, psilate, length 35 μm , width 14 μm . Exine 1 μm thick, featureless, hyaline. Ellipsoidal, ends of grains flattened. Colpus extends full length of grain, open and gaping at the ends, nearly closed in the center of the grain.

Discussion. The single specimen of this type has a slightly thinner exine and is slightly smaller than *C. follicularis* as originally described, but otherwise is a close morphological match.

Occurrence. Ypresian; 1 specimen observed. *Cycadopites follicularis* is common and globally distributed in the Mesozoic and Cenozoic (Palynodata Inc. & White 2008).

Botanical affinity. Cycadaceae (Wodehouse 1933).

Paleoecology. Probably lowland tropical forest. Akkiraz et al. (2008) considered that *Cycadopites* spp. indicated lowland-riparian paleoenvironments. Wakefield & Monteil (2002) considered that *Cycadopites* spp. indicated freshwater lowland marsh.

Genus *Ephedripites* Bolkovitina 1953 ex Potonié 1958 emend. Krutzsch 1961

Discussion. The nomenclature for fossil pollen grains referable to the Ephedraceae will generally follow Han et al. (2016). The pollen of modern *Ephedra* has multiple ridges or plicae separated by furrows or pseudosulci which may be branched or unbranched, and fuse at the ends of the grain. It should be noted that, although it may appear that the polar axis is parallel to the plicae, developmental studies have shown that it is the equatorial axis that is parallel to the plicae (Bolinder et al. 2016), and most if not all ephedroid pollen grains are oblate. The fossil form genus *Ephedripites* is split into three subgenera. *Ephedripites* subgenus *Distachyapites* has

generally between 3-8 plicae with straight to slightly sinuous branched pseudosulci. *Ephedripites* subgenus *Ephedripites* has generally between 8–20 plicae with straight to slightly sinuous unbranched pseudosulci. *Ephedripites* subgenus *Spiralipites* has numerous plicae and unbranched pseudosulci, and is distinguished by having the plicae rotated around the equatorial axis. *Gnetaceaepollenites* Thiergart 1938 emend. Jansonius 1962 is distinguished from *Ephedripites* by having plicae which are not fused at the ends of the grain.

Ephedripites (Distachyapites) eocenipites (Wodehouse 1933) Krutzsch 1961 sensu lato
Plate 2.4, figure 1

Description. Polyplicate, psilate to faintly scabrate, polar axis length 21–24 μm , equatorial width 48–58 μm , P/E ratio 0.37–0.46. Exine about 1 μm thick. Grains oblate, ellipsoidal, ends of grain moderately rounded. Approximately 5–7 plicae, pseudosulci with first-order branching. Plicae more or less distinct, fused at their ends, essentially parallel to the equatorial axis.

Discussion. This species is distinguished from other ephedroid pollen grains in the assemblage by having fused plicae with branched pseudosulci. A broad species concept for *Ephedripites eocenipites* is used here, which includes specimens smaller than the original size range given by Wodehouse (1933) of 57–74 μm in length. This is justifiable on the basis that Wodehouse (1933) likely did not intend for his measurements to provide strict limits on the circumscription of a species; several of his descriptions do not include a size range, only the measurements of the holotype specimen. Multiple similar species have been described, often with overlapping size ranges, and the taxonomy of this pollen type is probably in need of revision.

Occurrence. Ypresian; 5 specimens observed. *Ephedripites eocenipites* is common and globally distributed in the Mesozoic and Cenozoic (Palynodata Inc. and White 2008).

Botanical affinity. Ephedraceae, probably *Ephedra*.

Paleoecology. Dry and warm tropical scrub. Modern *Ephedra* is a xerophytic plant, but the palynological record indicates a greater ecological range for this group in the geological past. Frederiksen (1985) has an extensive discussion on the paleoecology of fossil pollen referable to the Ephedraceae. A great variety of *Ephedripites* was recovered from a Turonian section from Tanzania, during an interval of time that was clearly warm and relatively dry, as indicated notably by the rarity of humidity-dependent bryophytes and pteridophytes (Warny et al. 2018). Akkiraz et al. (2008) considered that Eocene *Ephedra* and *Ephedripites* were indicative of back-mangrove estuarine environments; this study will follow Ramírez-Arriaga, Prámparo, et al. (2014) and Warny et al. (2018) and consider that *Ephedripites* spp. indicates dry and warm scrub.

Ephedripites (Ephedripites) spp.
Plate 2.4, figures 2-4

Description. Polyplicate, psilate to faintly scabrate, polar axis length 15–(23)–29 μm , equatorial width 26–(45)–58 μm , P/E ratio 0.33–(0.52)–0.69. Exine 0.5–1.0 μm thick. Grain ellipsoidal, ends of grain broadly rounded to sharply tapered. Approximately 8–14 unbranched longitudinal plicae. Plicae distinct, fused at their ends, straight or curved, roughly parallel to the equatorial axis, generally 2–5 μm wide.

Discussion. The taxonomy of *Ephedripites* subgenus *Ephedripites* is complex, many species have overlapping definitions, and arguably the group is oversplit. Similar forms are probably

described under different names depending on the geographic location; extensive taxonomic discussions of the group can be found in Kedves (1995), Shaw (1998), and Han et al. (2016), among others. Many of these specimens could be included within *Ephedripites notensis* (Cookson 1957) Doubinger & Chotin 1976, which was originally described as being 25–47 µm long, 14–28 µm broad, with 10–15 psilate, unbranched longitudinal plicae. Some larger specimens could probably be included within *Ephedripites lanceolatus* Zhu & Wu 1985 as described by Han et al. (2016). This subgenus was not speciated due to its taxonomic complexity and the lack of any clear biostratigraphic or paleoecological rationale for splitting the subgenus.

Occurrence. Ypresian; 29 specimens observed. *Ephedripites* subgenus *Ephedripites* is common and globally distributed in the Mesozoic and Cenozoic (Palynodata Inc. & White 2008).

Botanical affinity. Ephedraceae, probably *Ephedra*.

Paleoecology. Likely indicative of dry and warm climate. See the paleoecology section for *Ephedripites eocenipites*.

Genus *Gnetaceaepollenites* Thiergart 1938 emend. Jansonius 1962

Discussion. Although originally, *Gnetaceaepollenites* included all ephedroid pollen grains, this study will follow Han et al. (2016) and restrict the use of the genus to polyaplicate forms in which the plicae are not fused at the ends of the grain. Frederiksen et al. (1983) note that there has been some disagreement in the literature over whether these forms may actually be schizaeaceous spores rather than pollen produced by ephedroid plants. Han et al. (2016) concluded that this type is not a spore and is in fact pollen related to modern *Ephedra*. In the literature these forms have previously been placed in *Ephedra* (e.g., Frederiksen et al., 1983) or *Ephedripites* subgenus *Spiralipites* (e.g., Jardine 2011). Because these grains are considered to have an affinity with the Ephedraceae, the equatorial axis is considered the long axis parallel to the plicae.

Gnetaceaepollenites sp. A

Plate 2.4, figures 5–8

Description. Polyaplicate, psilate, polar axis length 16–(19)–24 µm, equatorial width 31–(37)–44 µm, P/E ratio 0.41–(0.52)–0.61. Exine 0.5–1.5 µm thick. Grains ellipsoidal, oblate, ends of grain broadly rounded to moderately tapered. Approximately three to six plicae spiral around the long equatorial axis of the grain, not fusing at the tips, rather looping around to the other side of the grain. The number and pattern of the plicae is often difficult to determine due to folding or orientation of specimens.

Discussion. This species is synonymous with grains identified as “*Ephedripites* subgenus *Spiralipites* spp.” by Jardine (2011, p. 226), although this study follows Han et al. (2016) and assigns these grains to the genus *Gnetaceaepollenites*. Many of these specimens are probably also conspecific with *Ephedra voluta* Stanley 1965, which has been regularly identified from the Paleogene of the Gulf Coastal Plain (Palynodata Inc. & White 2008). *Gnetaceaepollenites* sp. B is distinguished by having plicae with a sinusoidal pattern.

Occurrence. Ypresian; 90 specimens observed.

Botanical affinity. Ephedraceae, possibly *Ephedra* (Jardine 2011).

Paleoecology. Probably an arid tropical scrub environment. See the paleoecology section for *Ephedripites eocenipites*.

Gnetaceaepollenites sp. B
Plate 2.4, figure 8

Description. Polyplicate, psilate, polar axis length 22 μm , equatorial width 34 μm , P/E ratio 0.65. Exine 0.8 μm thick. Grain ellipsoidal, oblate, ends of grain moderately tapered. Approximately eight plicae are roughly parallel to the equatorial axis, not fused at the tips. Several plicae have a sinusoidal pattern near the center of the grain.

Discussion. This species is similar to *Ephedripites* (*Distachyapites*) *zigzagus* Sun & He 1980 and a grain identified as “*Ephedra* sp. 1” by Frederiksen et al. (1983) in possessing plicae which undulate in a sinusoidal pattern. This specimen differs from those two species most notably in having plicae which are not fused at the tips of the grain. A new species has not been erected because only one specimen was observed.

Occurrence. Ypresian; 1 specimen observed.

Botanical affinity. Ephedraceae.

Paleoecology. Probably arid tropical scrub. See the paleoecology section for *Ephedripites eocenipites*.

Class Pinopsida
Plate 2.4, figures 10-11

Description. Bisaccate pollen, sacci scabrate to reticulate, corpus scabrate to reticulate. Grain length of specimens 43–(56)–67 μm . Specimens in polar view with expanded sacci; specimens in equatorial view with sacci oriented towards the distal pole, constricted at the junction with the colpus.

Discussion. The general morphology of most of these specimens is similar to modern *Pinus* pollen, particularly in the grain size and the shape of the sacci. This study will follow Pocknall & Nichols (1996), Nichols (2002), and Jardine (2011) in not speciating bisaccate pollen grains referable to the Class Pinopsida. Generic differentiation is often difficult or not possible in specimens not observed in equatorial view. If split, the majority of these specimens would probably be best placed in *Pinuspollenites* Raatz 1938, which is distinguished from *Abiespollenites* Thiergart 1938 ex Raatz 1938 and *Piceaepollenites* Potonié 1931 by having proportionally larger sacci which are more than hemispherical (i.e., constricted at the junction with the colpus). Also, the proximal attachment line is closer to the proximal pole than in *Abiespollenites* and *Piceaepollenites* (Jansonius & Hills 1976, card 2012).

Occurrence. Danian-Ypresian; 37 specimens observed.

Botanical affinity. Pinopsida, probably Pinaceae, possibly *Pinus*.

Paleoecology. Probably montane forest. More specifically, upland evergreen forest (*Pinus* forest) according to Ramírez-Arriaga, Prámparo, et al. (2014); however, Frederiksen (1985) cautioned that some modern species of *Pinus* live in lowland swamps and may have lived in similar environments in the Paleogene.

2.5. Conclusions

Palynological analysis of Danian–Ypresian post-impact rocks from the IODP 364 core yielded a diverse assemblage of 23 plant spore taxa and six gymnosperm pollen taxa. The spore and gymnosperm pollen assemblage exhibits a low relative abundance in comparison to the

angiosperm pollen assemblage, representing only about 2% of the total pollen and spore counts. The low relative abundance of spores is suggestive of generally arid or seasonally dry environmental conditions, similar to modern conditions in the northern Yucatán Peninsula, Mexico. None of the gymnosperm pollen or spores had any clear biostratigraphical value in the core interval. Most species were not observed in the Paleocene section of the core due to low abundance, with the exception of *Gleicheniidites senonicus* and bisaccate Pinopsida pollen, which were both observed in the Danian. Palaeoecologies suggested by the spore and gymnosperm pollen assemblage include lowland tropical forest, estuarine or mangrove environment, warm and dry tropical scrub, and montane forest.

The bolide impact at the end of the Cretaceous Period caused a mass extinction in plants, with approximately 18–30% of plant genera and families and 57% of species disappearing at the K–Pg boundary in North American localities (McElwain and Punyasena 2007). In North Dakota, at least 30% of the Cretaceous palynoflora became extinct at the K–Pg boundary (Nichols and Johnson 2002). A distinctive post-impact recovery assemblage dominated by fern spores has been observed in North America (e.g. Tschudy et al. 1984; Wolfe and Upchurch 1986; Nichols et al. 1992), Japan (Saito et al. 1986), New Zealand (e.g. Vajda et al. 2001, 2004; Vajda and Raine 2003; Ferrow et al. 2011), and Gorgonilla Island, Colombia (Bermúdez et al. 2018; Renne et al. 2018).

In the IODP 364 core, the oldest sample with observed terrestrial palynomorphs, specifically two specimens of *Deltoidospora*, is at 615.50 mbsf. Foraminiferal biostratigraphy constrains the age of this sample depth to between 65.25 and 65.72 Ma (Gulick et al. 2017). The initial terrestrial floral recovery following the bolide impact has therefore not been observed in the IODP 364 core, and the spore and gymnosperm pollen record in the Paleocene is too scarce to draw any definite conclusions about the overall Paleocene assemblage. The low abundance in the Paleocene section may be related to poor preservational conditions for palynomorphs or low terrestrial input to the crater basin, or a combination of these two factors. This is likely to be the case elsewhere in the crater basin as well. Palynological analysis of more inland sections to the south along the buried Chicxulub crater rim or outside the impact crater in the Yucatán Peninsula may provide better conditions for observation of the initial post-impact floral recovery in the future.

2.6. Plates to Chapter 2

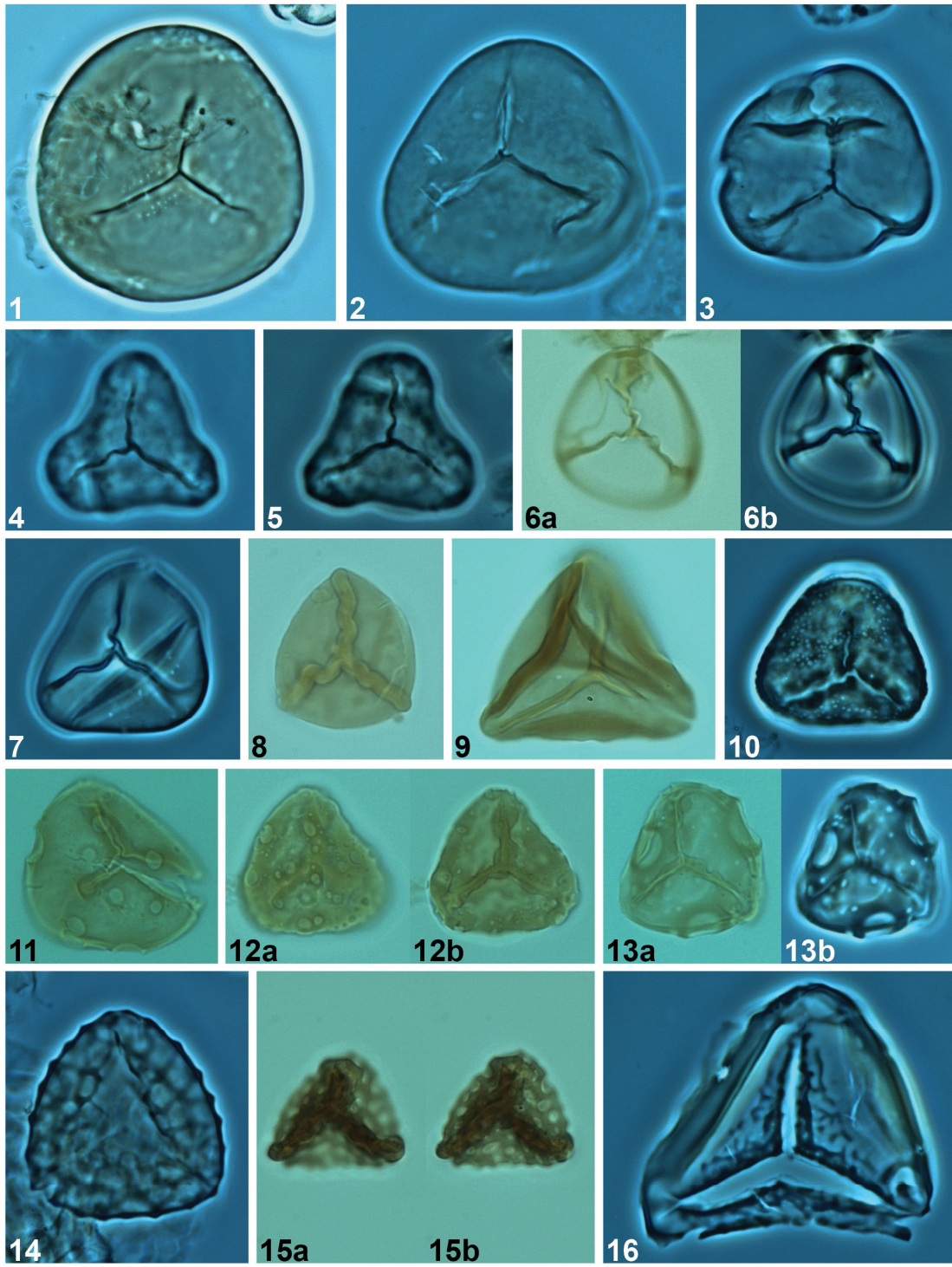


Plate 2.1

Plate 2.1. Trilete spores from International Ocean Discovery Program (IODP) 364.

1. *Deltoidospora* sp. 505.88 mbsf (meters below seafloor), slide 2, EFS (England Finder Slide) R22/0.
2. *Deltoidospora* sp. 548.96 mbsf, slide 1, EFS P40/0.
3. *Deltoidospora* sp. 514.14 mbsf, slide 1, EFS T29/2.
4. *Cyathidites minor*. 510.90 mbsf, slide 1, EFS T29/2.
5. *Cyathidites minor*. 510.90 mbsf, slide 1, EFS P33/4.
6. *Undulatisporites mineri*. 544.11 mbsf, slide 1, EFS N26/4.
7. *Undulatisporites mineri*. 572.75 mbsf, slide 2, EFS U44/1.
8. *Undulatisporites elsikii*. 607.22 mbsf, slide 2, EFS G18/3.
9. *Gleicheniidites senonicus*. 607.22 mbsf, slide 2, EFS S38/0.
10. *Punctatriletes* sp. A. 582.78 mbsf, slide 2, EFS Q13/1.
11. *Foveotriletes crater*. 582.78 mbsf, slide 2, EFS P26/2.
12. *Foveotriletes crater*. 582.78 mbsf, slide 2, EFS V18/0.
13. *Kuylisporites waterbolkii*. 533.27 mbsf, slide 1, EFS Q30/2.
14. *Retitriletes* sp. A. 606.60 mbsf, slide 2, EFS H31/3.
15. *Retitriletes* sp. B. 607.04 mbsf, slide 2, EFS X21/2.
16. *Rugutriletes* sp. A. 563.21 mbsf, slide 1, EFS S27/2.

Scale bar=10 μ m.

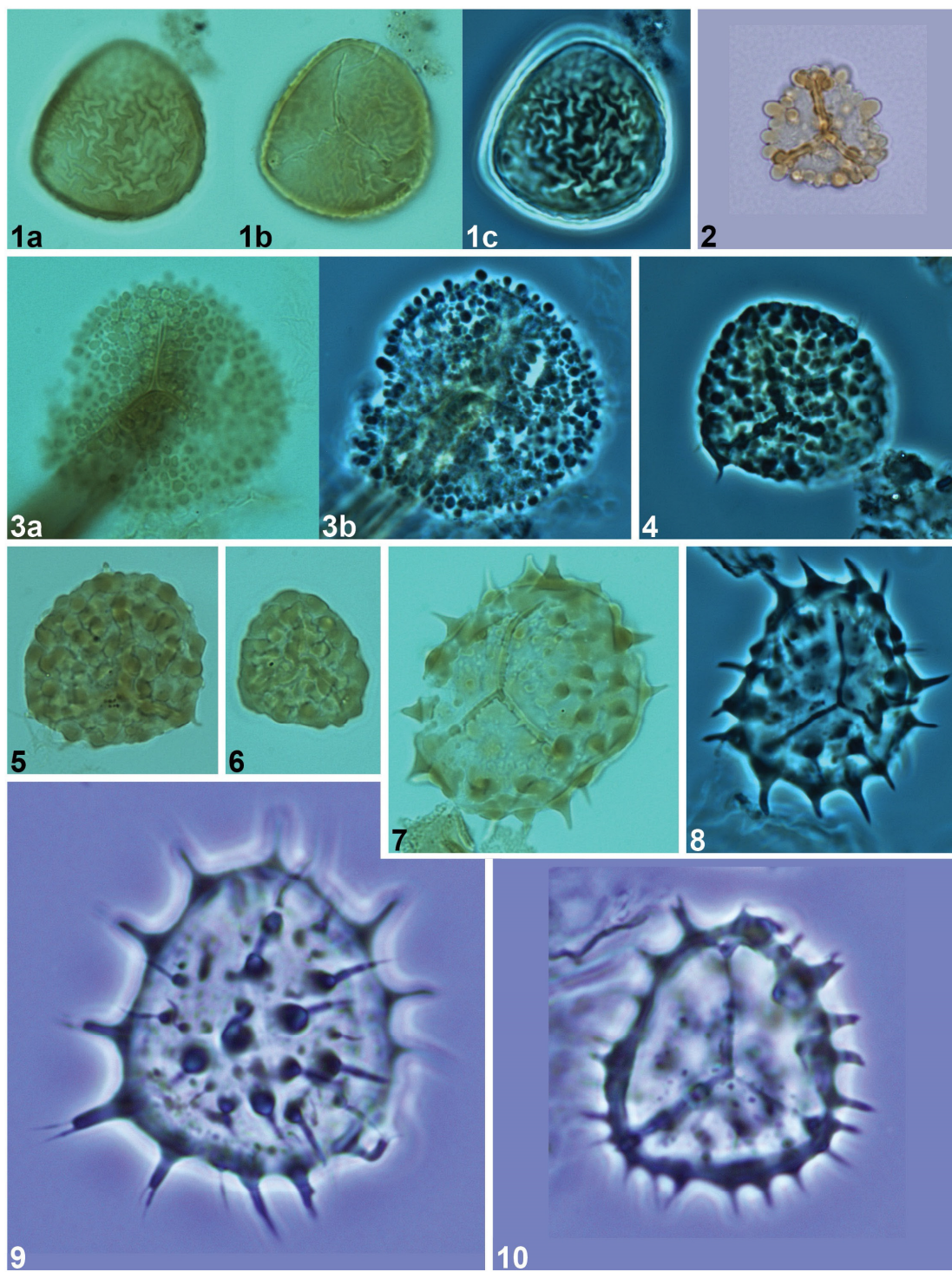


Plate 2.2

Plate 2.2. Trilete spores from IODP 364.

1. *Hamulatisporis hamulatis*. 582.78 mbsf, slide 1, EFS V47/0.
2. *Gemmatriletes* sp. A. 577.73 mbsf, slide 2, EFS P31/0.
3. *Gemmatriletes* aff. *G. clavatus*. 564.86 mbsf, slide 1, EFS U19/2.
4. *Verrucosisporites* sp. A. 607.18 mbsf, slide 1, EFS 041/0.
5. *Verrucosisporites* sp. A. 607.22 mbsf, slide 2, EFS U43/0.
6. *Verrucosisporites* sp. A. 607.22 mbsf, slide 2, EFS J42/0.
7. *Echinatisporis* sp. A. 539.43 mbsf, slide 1, P23/2.
8. *Echinatisporis* sp. A. 556.58 mbsf, slide 1, EFS R37/1.
9. *Ceratosporites* sp. A. 505.88 mbsf, slide 2, EFS N43/0.
10. *Ceratosporites* sp. A. 505.88 mbsf, slide 2, EFS Q25/4.

Scale bar=10 μ m.

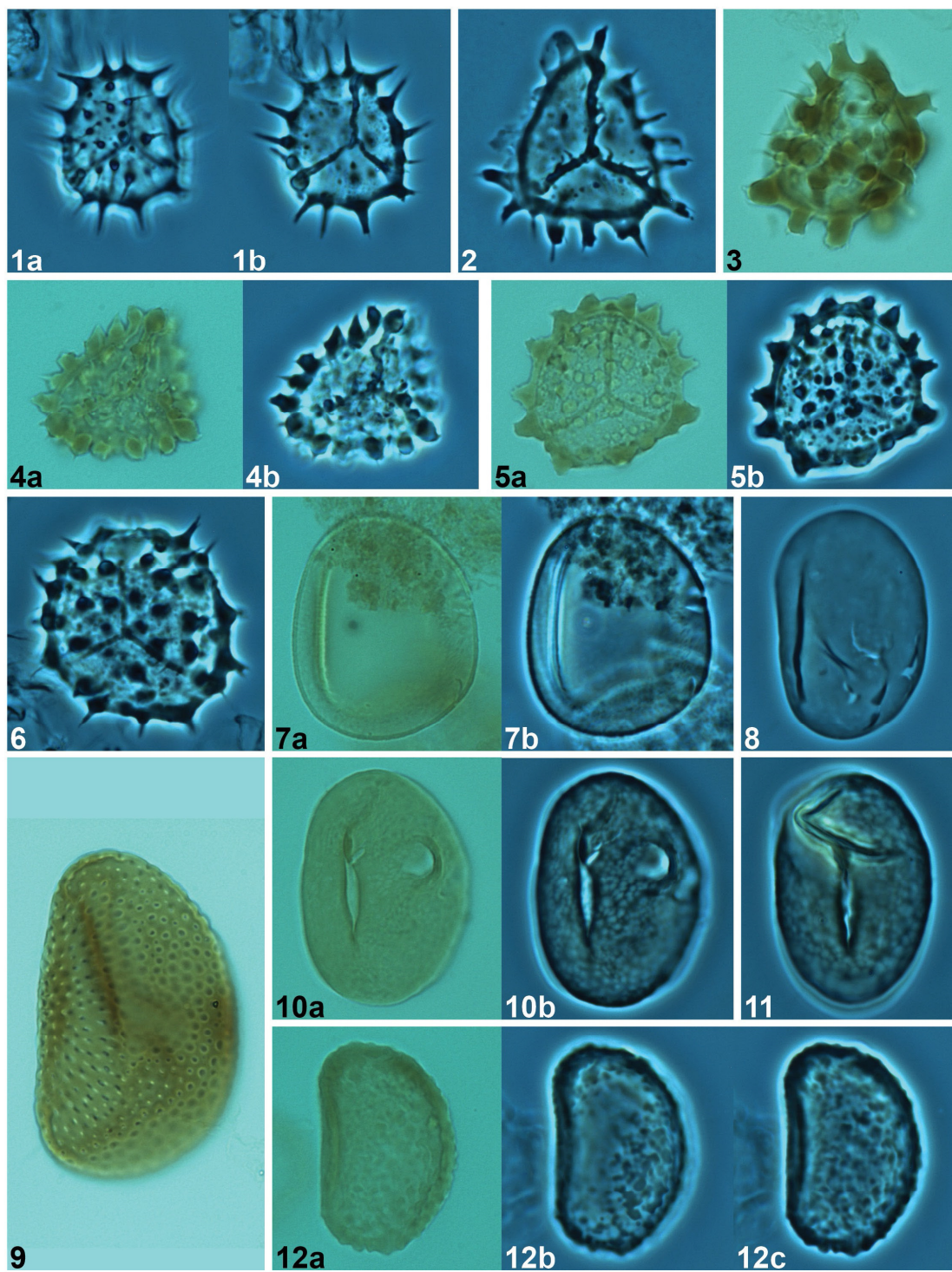


Plate 2.3

Plate 2.3. Trilete and monolete spores from IODP 364.

1. *Ceratosporites* sp. A. 540.89 mbsf, slide 1, EFS T41/0.
2. *Neoraistrickia* sp. A. 516.00 mbsf, slide 1, EFS U24/0.
3. *Neoraistrickia* sp. A. 574.35 mbsf, slide 1, EFS V16/0.
4. *Neoraistrickia* sp. A. 539.43 mbsf, slides 1, EFS T33/2.
5. *Raistrickia* sp. A. 555.07 mbsf, slide 1, EFS 042/1.
6. *Raistrickia* sp. A. 576.04 mbsf, slide 1, EFS S33/1.
7. *Laevigatosporites haardtii*. 564.86 mbsf, slide 1, EFS U34/1.
8. *Laevigatosporites haardtii*. 563.29 mbsf, slide 1, EFS Q35/2.
9. *Microfoveolatosporis* cf. *M. fromensis*. 592.23 mbsf, slide 1, EFS T32/2.
10. *Reticuloidosporites pseudomurii*. 582.78 mbsf, slide 2, EFS V24/0.
11. *Reticuloidosporites pseudomurii*. 582.78 mbsf, slide 2, EFS V16/1.
12. *Polypodiisporonites* sp. A. 556.58 mbsf, slide 1, EFS Q46/0.

Scale bar=10 μ m.

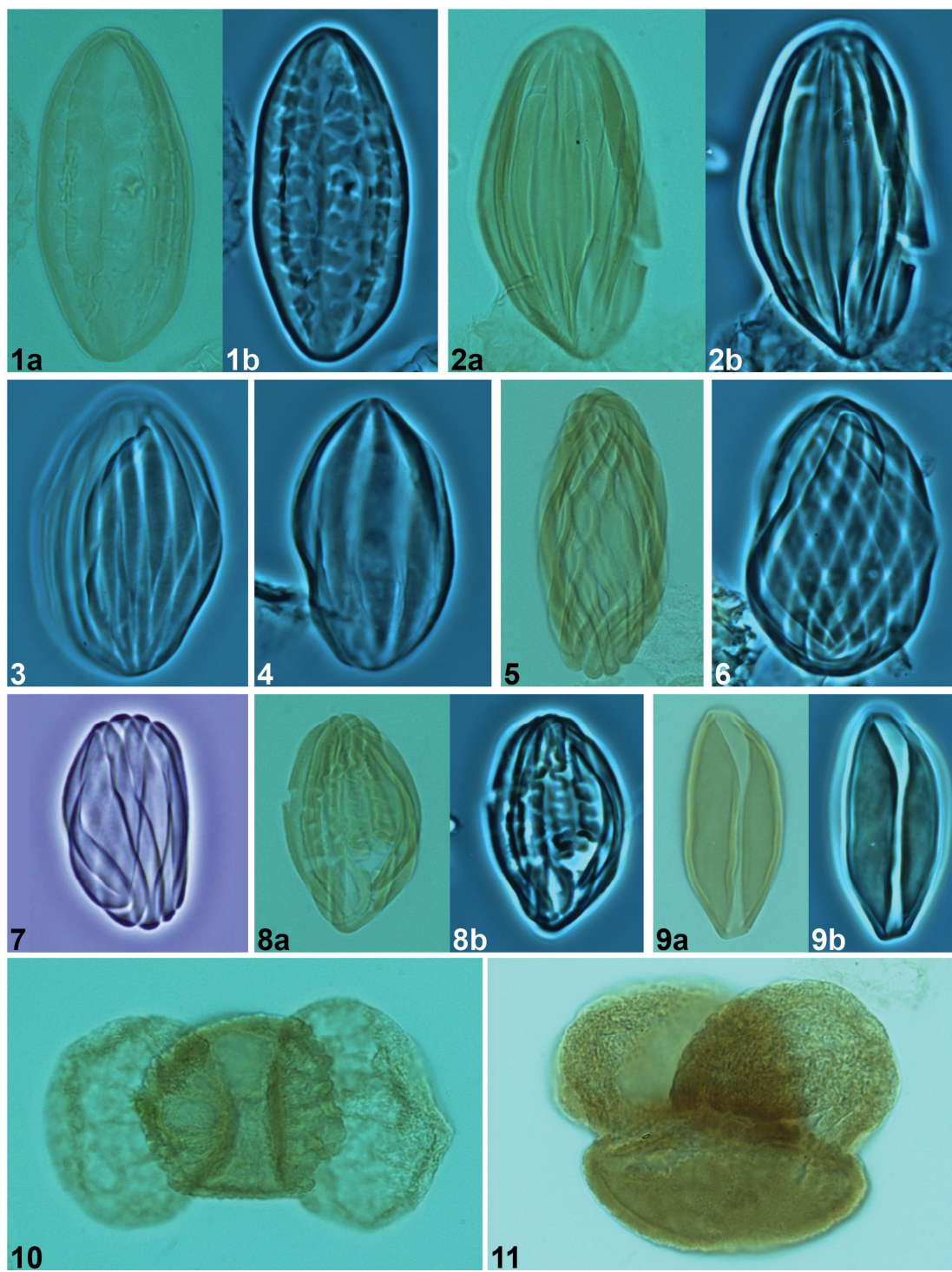


Plate 2.4

Plate 2.4. Gymnosperm pollen from IODP 364.

1. *Ephedripites eocenipites*. 545.67 mbsf, slide 1, EFS V33/1.
2. *Ephedripites (Ephedripites)* sp. 533.27 mbsf, slide 1, EFS W44/0.
3. *Ephedripites (Ephedripites)* sp. 555.07 mbsf, slide 1, EFS Q46/0.
4. *Ephedripites (Ephedripites)* sp. 509.17 mbsf, slide 1, EFS P32/1.
5. *Gnetaceaepollenites* sp. A. 569.50 mbsf, slide 1, EFS Q39/1.
6. *Gnetaceaepollenites* sp. A. 519.31 mbsf, slide 2, EFS S29/2.
7. *Gnetaceaepollenites* sp. A. 525.48 mbsf, slide 1, EFS L36/0.
8. *Gnetaceaepollenites* sp. B. 547.42 mbsf, slide 2, EFS Q14/1.
9. *Cycadopites follicularis*. 563.29 mbsf, slide 1, EFS R24/2.
10. Class Pinopsida. 569.50 mbsf, slide 1, EFS R36/1.
11. Class Pinopsida. 592.23 mbsf, slide 2, EFS J41/1.

Scale bar=10 μ m.

CHAPTER 3. PALEOCENE-EOCENE PALYNOMORPHS FROM THE CHICXULUB IMPACT CRATER, MEXICO. PART 2: ANGIOSPERM POLLEN

3.1. Introduction

The geologic background for the International Ocean Discovery Program (IODP) 364 core has been described in Smith et al. (2019). Further information about IODP 364 and the Chicxulub impact event can be found in Schulte et al. (2010), Morgan et al. (2016, 2017), Gulick et al. (2017, 2019), and Lowery et al. (2018). The systematic paleontology of the angiosperm pollen presented here provides an essential basis for the interpretation of the terrestrial palynology within the Chicxulub impact crater, and the development of the vegetation in the vicinity of the crater through the Paleocene to early Eocene. The Paleogene palynology of the Yucatán Peninsula is nearly unknown. Apart from Holocene palynological studies (e.g. Correa-Metrio et al. 2011; Aragón-Moreno et al. 2012), the only publications on the palynology of the Yucatán Peninsula are based on Deep Sea Drilling Project (DSDP) Site 94 on the Campeche escarpment, where a late Eocene to early Miocene pollen assemblage was recovered (Barron 2015; Barron et al. 2017). During the Cretaceous, the Yucatán Peninsula was part of the *Aquilapollenites* province (Herngreen et al. 1996; Vajda and Bercovici 2014), characterized by abundant representatives of the morphologically distinctive *Aquilapollenites* pollen group. The K–Pg mass extinction affected most representatives of this group, and the post-extinction palynological assemblages are thus clearly different compared with the Maastrichtian ones, within both the *Aquilapollenites* province and the Palmae province located in the paleo-tropical belt. Geographically proximal Paleogene palynological assemblages have been described from the Eocene and Oligocene of Cuba (Arecas-Mallea 1987, 1988, 1990; Graham et al. 2000), the Oligocene of Puerto Rico (Graham and Jarzen 1969), the Eocene of Jamaica (Graham 1993), the Eocene of Panama (Graham 1985), and various Paleocene–Oligocene sections in mainland Mexico (e.g. Biaggi 1978; Martínez-Hernández et al. 1980; Tomasini-Ortiz and Martínez-Hernández 1984; Graham 1999; Martínez-Hernández and Ramírez-Arriaga 1999; Altamira-Areyán 2002; Ramírez-Arriaga et al. 2006; Carrasco-Velázquez et al. 2009; Ramírez-Arriaga, Prámparo, et al. 2014; Ramírez-Arriaga and Reyes-Salas 2014; Ramírez-Arriaga et al. 2017).

3.2. Methods

The palynological sample processing methods used here are identical to those described in Smith et al. (2019), and essentially follow methods described by Traverse (2007). Slides were scanned until 300 identifiable pollen and spore grains were counted, or until the slides at a sample depth were fully scanned. For each species, size ranges are given, with a mean size given in parentheses for species with more than 10 measured specimens. Abundance data for all samples are provided in the supplementary materials. Absolute age estimates for biostratigraphic events are constrained by foraminiferal and nannofossil biostratigraphy. The age model is provided as supplementary material, modified from Gulick et al. (2017) (Chris Lowery, personal

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communication, 2019), following the Gradstein et al. (2012) time scale. The bottom and top of the Paleocene–Eocene Thermal Maximum (PETM) are given age estimates of 55.93 Ma and 55.71 Ma, respectively (Westerhold et al. 2017; Hollis et al. 2019). Potentially useful biostratigraphic events are given an age range based on age estimates of the nearest biostratigraphic events, with an estimated age in parentheses based on linear interpolation, assuming a constant sedimentation rate. Age estimates are also provided for each sample depth along with the quantitative counts, using the age model and linear interpolation (linear extrapolation for the top sample depth). Observed ranges of common and biostratigraphically useful taxa are illustrated in Figure 3.1.

3.3. Morphology, systematic nomenclature, and paleoecological interpretation

As in Smith et al. (2019), morphological terminology generally follows Punt et al. (2007); however, in this study, the term ‘striae’ will refer to the elevated sculptural elements in striate sculpture, following Hesse et al. (2009). Botanical affinities are based on reviews of the scientific literature or by comparison with modern pollen from the Center for Excellence in Palynology (CENEX) research collection at Louisiana State University (LSU). Paleoecological interpretations are generally based on the modern ecologies of plants which produce pollen similar to the observed fossil pollen, or based on previous paleoecological interpretations in the literature, particularly those of Ramírez-Arriaga, Prámparo et al. (2014). The paleoecologies of Paleocene and lower Eocene ancestors of modern plants may be different than those of their modern descendants (e.g. Frederiksen 1985), so the paleoecological interpretations provided here are considered tentative.

A list of all pollen and plant spore taxa, with their interpreted botanical affinities, paleoecologies, and paleogeographic ranges, is given in the supplementary material. Paleoecologies are only listed for taxa where an interpretation has been made. More questionable or tentative interpretations of the paleoecology are given with a question mark. The paleoecology for taxa given in the supplementary materials is simplified from the more detailed discussion given in the taxonomic descriptions, and is divided into lowland tropical forest, montane forest, estuarine, and arid tropical scrub. This division is similar to the paleoecological types listed in Ramírez-Arriaga, Prámparo, et al. (2014), although chaparral is not included, *Pinus* and cloud forest are combined into montane forest, and an estuarine paleoecology has been added. These paleoecological types are a simplification of modern vegetation types described by Rzedowski (2006) and Correa-Metrio et al. (2011) for Mexico and the Yucatán Peninsula. For example, no attempt was made to subdivide deciduous and non-deciduous lowland tropical forest. Two additional columns in the spreadsheet state whether a taxon has previously published occurrences in the Paleogene of North America (including Mexico) and South America. This information is only given for taxa with reasonably well-established paleogeographic ranges in the literature. Paleogeographic distribution was determined using the database of Palynodata Inc. and White (2008), Graham (2010), and a review of the literature.

Pollen are generally identified using form genera, in many cases using informal species names (sp. A, sp. B, etc.). Several genera named in this study were first proposed (originally as subgenera) by van der Hammen (1954b, 1956) in an attempt to create a standardized system of classification based on pollen morphology. Because he chose modern pollen as his type species for these form genera, technically his form genera are all junior synonyms of whatever natural genus the modern pollen belonged to (Jansonius and Hills 1976; Potonié 1960). This is an

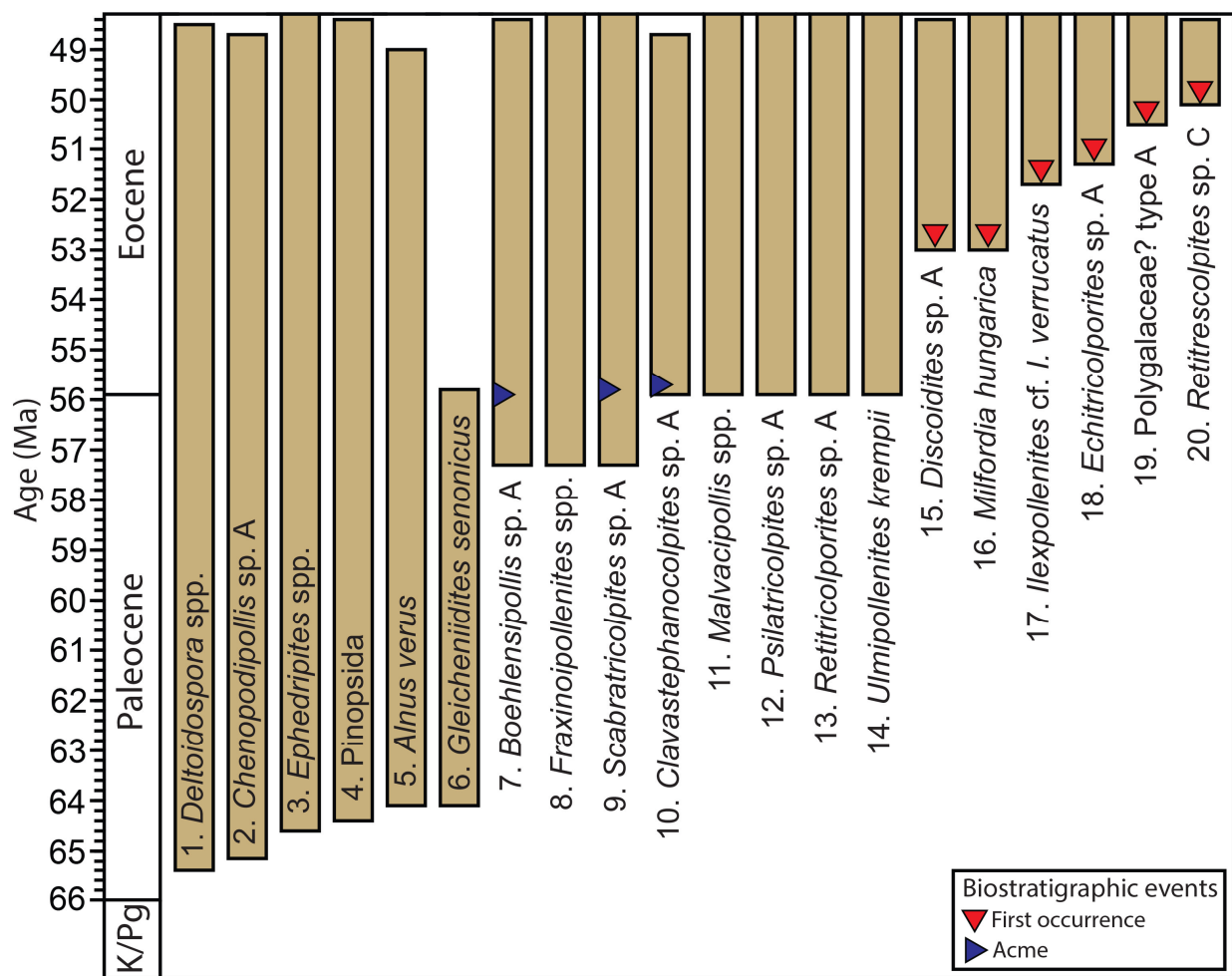


Figure 3.1. Observed stratigraphic ranges and events for selected taxa recovered from the IODP 364 core, organized by first occurrence datum. Ranges are illustrated for biostratigraphically important taxa (ranges 7, 9–10, 15–20), particularly abundant taxa (ranges 8, 11–14), and taxa with observed ranges in the Paleocene (ranges 1–9). One species present in the Paleocene, *Betula?* sp. A, was not included because only a single specimen was observed. The actual ranges of many taxa may extend into the Paleocene, but have not been observed, possibly because of low recovery in the Paleocene section. No biostratigraphically reliable last occurrence datums have been confidently observed. Absolute ages are estimated using linear interpolation of the age model provided in the Supplementary material.

unfortunate technicality, because the reasoning was sound; by choosing modern species as the type species of form genera, access to the ‘type material’ only requires access to pollen or spores of the modern species. Despite the questionable validity of some of van der Hammen’s genera, his form generic names are quite useful for classifying pollen of unknown botanical affinity using morphology. For some of these genera, new type species of fossil pollen were later chosen, validating the generic name (e.g. van der Hammen and Wymstra 1964). Hoorn (1993) has argued that invalidly published form genera can be later validated by designating a new holotype and type species.

Light microscopy (LM) images are provided in Plates 3.1–3.13, organized by aperture class and exine sculpture, and scanning electron microscopy (SEM) images are provided in

Plates 3.14–3.15. Plate 3.14 also includes some SEM images of spore and gymnosperm pollen taxa previously described in Smith et al. (2019), namely *Raistrickia* sp. A (Plate 3.14, figure 1), *Gnetaceaepollenites* sp. A (Plate 3.14, figure 2), and Class Pinopsida (Plate 3.14, figure 3). LM images with a dark gray or blue background are phase contrast images. Depending on the specimen, phase contrast images sometimes provided a better visualization of morphological features, particularly more transparent specimens and specimens with finely reticulate sculpture. In other cases, standard bright-field microscopy provided better results. Often, the same specimen is imaged using both methods (e.g. Plate 3.1, figures 3a,b). LM was conducted using an Olympus BX41 microscope at 600x and 1000x magnification. Electron microscopy was conducted using an FEI Quanta 3 D DualBeam FEG FIB-SEM microscope located in the Shared Instrumentation Facility at LSU. A list of all described angiosperm pollen taxa, along with their aperture class, botanical affinity, and paleoecology, is provided in the supplementary material. Occurrence information is given both in terms of total specimens observed and in terms of relative abundance compared to the total identified pollen and plant spores in all samples from the IODP 364 core (16,246 specimens).

3.4. Systematic Paleontology

3.4.1. Inaperturate Pollen (Plate 1)

Genus *Retipollenites* González Guzmán 1967

Discussion: *Retipollenites* includes reticulate, inaperturate pollen grains. The reticulum does not appear to be inserted on a basal layer (González Guzmán 1967).

Retipollenites? sp. A

Plate 3.1, figure 1; Plate 3.14, figure 4

Description: Inaperturate, coarsely reticulate, diameter 28-(50)-60 μm . Exine 1-3 μm thick. Shape approximately spherical. No pores or colpi are visible. A single specimen observed in SEM (Plate 3.14, Fig. 4) possesses small columellae which appear to be inserted on a basal layer, as well as free-standing baculae, under the reticulum. Lumina wider than muri, irregularly rounded polygonal in shape, 1-8 μm in diameter.

Discussion: Graham et al. (2000, figs. 76-77) describe pollen with a similar morphology from the Middle Eocene of Cuba, which they identified as “*Retipollenites* cf. *confusus*.” However, SEM microscopy indicates that the reticulum in this taxon is inserted on a basal layer, so the generic assignment is somewhat questionable.

Occurrence: Ypresian; 18 specimens observed (0.1%).

Botanical affinity: Probably eudicots, lower affinity unknown.

3.4.2. Monocolpate and Trichotomocolpate Pollen (Plate 1, Plate 2)

Genus *Arecipites* Wodehouse 1933 emend. Anderson 1960

Discussion: *Arecipites* as emended by Anderson (1960) includes monocolpate pollen with a tapered colpus and punctate to micro-reticulate sculpture. Anderson (1960) distinguished

Arecipites from *Liliacidites* Couper 1953 by having lumina with a diameter less than 0.5 μm . Nichols et al. (1973) also emended *Arecipites*, explicitly rejecting the emendation by Anderson (1960), and excluding micro-reticulate pollen. The emendation by Nichols et al. (1973) is not used here because the *Arecipites* specimens in this study show a continuous morphological gradation from punctate to micro-reticulate sculpture. Generally, the lumina are near the resolving limit of light microscopy, and it is not entirely clear whether the sculpture is punctate or reticulate using the terminology of Punt et al. (2007).

Arecipites tenuixinous Leffingwell 1970 sensu lato
Plate 3.1, figures 4-5

Description: Monocolpate, punctate or micro-reticulate, polar axis length 26-(34)-41 μm , equatorial diameter 17-(20)-25 μm , P/E ratio 1.20-(1.72)-2.35. Exine ca. 0.5-1.0 μm thick, rarely up to 1.5 μm thick, tectate with visible columellae, although the columellae are not clearly visible in some thin-walled specimens. Grains elongate parallel to colpus, ellipsoidal. Colpus in the form of a thin slit, extending full length of grain, generally tapered but rarely with one or both ends of the colpus gaping as in *Cycadopites* Wodehouse 1933 ex Wilson and Webster 1946, probably as preservational artifacts. The sculpture is punctate or micro-reticulate, with lumina 0.5 μm or less in diameter.

Discussion: *Arecipites punctatus* Wodehouse 1933, the type species of *Arecipites*, was described as minutely pitted by Wodehouse (1933). Nichols (2010) redescribed but did not formally emend *A. punctatus*; he described the sculpture as psilate to scabrate. The sculpture of *Arecipites tenuixinous* was originally described as micro-reticulate, but Nichols and Brown (1992) noted that some specimens of *A. tenuixinous* have smaller, more widely separated lumina, forming a sculpture better described as punctate. A broad species concept is used here, which includes specimens outside the original size range given by Anderson (1960) of 25-30 μm in length.

Occurrence: Ypresian; 214 specimens observed (1.3%). *Arecipites tenuixinous* has mainly been identified from the Cretaceous and Paleogene of North America, with other occurrences in South America, China, Africa, and Antarctica (Palynodata Inc. and White 2008). Specimens from the Late Eocene to Early Oligocene of Mexico identified as *Arecipites* sp. by Ramírez-Arriaga, Prámparo, et al. (2014, fig. 3.1) are conspecific with *A. tenuixinous* as defined here. *Arecipites* specimens identified by Jarzen and Klug (2010, plate 1, figs. 2-3) from the lower to middle Eocene of Florida are also similar to the IODP 364 specimens, except in having a slightly thicker exine (ca. 1.5-2.0 μm).

Botanical affinity: Arecaceae (Nichols and Brown 1992).

Paleoecology: Possibly arid tropical scrub, based on the suggested paleoecology given by Ramírez-Arriaga, Prámparo, et al. (2014) for similar *Arecipites* specimens. Alternatively, Akkiraz et al. (2008) gave the paleoecology of *Arecipites* spp. as back-mangrove.

Genus *Clavamonocolpites* González Guzmán 1967 emend. Muller et al. 1987

Discussion: *Clavamonocolpites* includes all clavate, monocolpate pollen.

Clavamonocolpites sp. A Muller et al. 1987
Plate 3.1, figure 10

Description: Monocolpate, conspicuously clavate, polar axis length 32 μm , equatorial diameter 23 μm . Nexine ca. 0.7 μm thick, featureless in light microscopy, sexine composed of isolated clavae ca. 1 μm long, which are densely and evenly spread across the surface of the grain. Grain ellipsoidal. Colpus tapered and extending nearly the full length of the grain.

Discussion: *Clavamonocolpites* sp. A is similar to *Clavamonocolpites lorentei* Muller et al. 1987, but larger. Although no size range was given in the original description for *C. lorentei*, the holotype specimen was 23 μm in length. *Clavamonocolpites terrificus* González Guzmán 1967 has longer (ca. 3.2 μm) clavae.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Echimonocolpites* van der Hammen & Garcia 1966

Discussion: *Echimonocolpites* includes echinate, monocolpate pollen. The echinae do not have visible roots or extensions into the exine. *Mauritiidites* van Hoeken-Klinkenburg 1964 is also echinate and monocolpate, but the echinae or baculae are deep-rooted, with indentations of the exine under the echinae. *Spinizonocolpites* Muller 1968 emend. Muller et al. 1987 is echinate and zonacolpate.

Echimonocolpites chicxulubensis sp. nov.
Plate 2, figures 9-11

Holotype: The specimen in Plate 3.2, fig. 9 (523.92 mbsf, slide 1, EFS M13/1).

Repository: CENEX, LSU, Baton Rouge, Louisiana, USA.

Type locality: IODP 364 Site M0077, Chicxulub impact crater, Mexico.

Derivation of name: The species name is in reference to the Chicxulub impact crater, itself named after the town of Chicxulub Pueblo and Chicxulub Puerto in the Mexican state of Yucatán.

Description: Monocolpate, occasionally longicolpate to ambiguously zonacolpate, echinate to baculate, length 30-(35)-48 μm , width 16-(23)-33 μm . Exine ca. 0.5-1.0 μm thick, not visibly columellate. Shape elliptical to circular in equatorial view. The colpus may extend to the edge of the grain (e.g., Plate 3.2, fig. 9), but in some specimens (e.g., Plate 3.2, figs. 10-11) the colpus appears to partially or entirely encircle the grain, and could be interpreted as longicolpate or even zonacolpate. Commonly, the pollen grain is folded, and the morphology of the colpus is difficult to determine with certainty. Exine covered in scattered spines, otherwise psilate to scabrate, possibly indistinctly punctate. Spines broadly conical to slender, sometimes with expanded bases, occasionally baculate, 0.5-3 μm long. The spines are not deep-rooted, and do not indent the underlying exine as in *Mauritiidites* van Hoeken-Klinkenburg 1964.

Discussion: The colpus in *Echimonocolpites chicxulubensis* sp. nov. is quite variable, and in some specimens the colpus appears to nearly completely encircle the grain (i.e., zonacolpate). These possibly zonacolpate specimens have not been assigned to *Spinizonocolpites*, first because they are otherwise similar to clearly monocolpate specimens of *Echimonocolpites chicxulubensis*

sp. nov., and second because this would incorrectly imply that *Echimonocolpites chicxulubensis* sp. nov. has a botanical affinity with the modern mangrove palm *Nypa* van Wurmb (Arecaceae). **Botanical affinity:** Probably Arecaceae. Echinate, monocolpate pollen is produced by many species in the family. In particular, *Echimonocolpites chicxulubensis* is morphologically similar to pollen of the modern *Socratea hecatonandra* (Dugand) Bernal photographed by Pocknall and Jarzen (2012), who described the colpus as incomplete zonosulcate, although the echinae in *S. hecatonandra* are $\leq 1\ \mu\text{m}$ in length.

Genus *Liliacidites* Couper 1953

Discussion: The genus *Liliacidites* was originally described by Couper (1953) to include reticulate monocolpate, or occasionally trichotomocolpate, pollen grains of presumed liliaceous affinities; however, the botanical affinities of many species in this form genus are probably with other families, such as Amaryllidaceae, Arecaceae, Bromeliaceae, or Iridaceae (Krutzsch 1970; Frederiksen 1983; Graham et al. 2000). Anderson (1960) included some finely reticulate ($<0.5\ \mu\text{m}$ lumina) pollen in *Arecipites*, reserving *Liliacidites* for more coarsely reticulate ($>1\ \mu\text{m}$ lumina) pollen. Krutzsch (1970) emended *Liliacidites* and restricted it to only coarsely reticulate, medium sized to large forms. According to Nichols et al. (1973), *Liliacidites* is generally differentiated from other genera such as *Arecipites*, *Cycadopites*, and *Monocolpopollenites* by the presence of a tapered colpus and a non-tectate, reticulate exine (Nichols et al. 1973). However, some species assigned to *Liliacidites* have colpi that are open or gaping at the ends; for example, *Liliacidites vittatus* Frederiksen 1973 was originally described as sometimes having a gaping or open sulcus. *Retimonocolpites* Pierce 1961 includes all reticulate, monocolpate pollen, and is in part synonymous with *Liliacidites*. Singh (1983) considered that *Liliacidites* has a heterobrochate reticulum, and is distinguished on that basis from *Retimonocolpites*; however, this characteristic was not mentioned in the original description, and Singh (1983) did not formally emend either genus.

Liliacidites sp. A Plate 3.1, figure 9

Description: Monocolpate, coarsely reticulate, polar axis length 35-38 μm , equatorial diameter 21-23 μm . Exine 1-2 μm thick, semitectate. Grain elongated parallel to colpus, elliptical. Colpus without margo, tapered and extending nearly the full length of the grain. Lumina 1-3 μm in diameter, with at least some lumina $>2\ \mu\text{m}$ in diameter. Lumina elliptical to rounded polygonal in shape, muri ca. 0.5-1.0 μm wide, simplicolumellate, with a faintly beaded appearance.

Discussion: *Liliacidites* sp. A is somewhat similar to *Liliacidites vittatus*, although *L. vittatus* was described as duplibaculate (i.e., duplicolumellate) rather than simplicolumellate. *Liliacidites intermedius* Couper 1953 is also similar, having lumina ca. 2-3 μm in diameter near the center of the grain, decreasing to ca. 1 μm at the ends of the grain. However, *L. intermedius* is larger (44-53 μm long), and in *Liliacidites* sp. A the lumina are not significantly finer at the grain ends. *Liliacidites* sp. A is distinguished from *Liliacidites variegatus* Couper 1953 by having some lumina $>2\ \mu\text{m}$ in diameter.

Occurrence: Ypresian; 2 specimens observed ($<0.1\%$).

Botanical affinity: Angiospermae, possibly Amaryllidaceae, Arecaceae, Bromeliaceae, Iridaceae, or Liliaceae (see generic discussion).

Liliacidites sp. B
Plate 3.1, figure 8

Description: Trichotomocolpate, micro-reticulate, polar axis length 36 μm . Exine ca. 0.5 μm thick, columellate. Grain subtriangular. Lumina ≤ 0.5 μm in diameter.

Discussion: The single observed specimen arguably bears a closer morphological resemblance to *Arecipites tenuixinous* than other species of *Liliacidites* in this study, but *Arecipites* is restricted to monocolpate pollen. This specimen falls within the generic circumscription of *Liliacidites* as originally defined by Couper (1953), which includes finely reticulate forms.

Occurrence: Ypresian; 1 specimen observed ($<0.1\%$).

Botanical affinity: Possibly Arecaceae, based on the similarity to *A. tenuixinous*, although the Liliaceae can also produce symmetric trichotomocolpate pollen (Kruttsch 1970).

Liliacidites variegatus Couper 1953 sensu lato
Plate 3.1, figures 6-7

Selected synonymy:

Desmoncus-type Graham 1989, figs. 33-34.

Liliacidites sp. 3 Ramírez-Arriaga, Prámparo, et al. 2014, fig. 3.8.

Description: Monocolpate, micro-reticulate to reticulate, polar axis length 24-(32)-35 μm , equatorial diameter 12-(19)-26 μm . Exine ca. 0.5-1.5 μm thick, semitectate. Grain elongated parallel to colpus, elliptical. Colpus with absent or weakly developed margo, usually tapered and extending the full length of the grain. Occasionally the colpus is open at one or both ends of the grain. Lumina 0.5-2.0 μm in diameter, fining slightly at edges of grain, subcircular to rounded polygonal in shape. The reticulum is heterobrochate, the reticulum usually fining slightly towards the ends of the grain, although there is also substantial variability in lumina size near the center of the grain.

Discussion: *Liliacidites variegatus* was originally described by Couper (1953) as having a size range of 26-36 μm in length and 16-26 μm in width. The lumina were described as usually ca. 1 μm in diameter in the center of the grain, occasionally up to 2 μm in diameter, and <1 μm in diameter at the edges of the grain. A broad species concept is used here, which includes specimens which are more finely reticulate (<1 μm lumina diameter) or have a thinner exine (<1.5 μm thick) than stated in the original description for *L. variegatus*.

Occurrence: Ypresian; 63 specimens observed (0.4%). *Liliacidites variegatus* is a common and globally distributed species in the Cretaceous and Cenozoic (Palynodata Inc. and White 2008). Palm pollen from the Miocene of Panama identified by Graham (1989) as “*Desmoncus*-type” falls within the range of morphological variation for *L. variegatus* as defined here. Ramírez-Arriaga, Prámparo, et al. (2014) described a “*Liliacidites* sp. 3” from the Late Eocene to Early Oligocene of Mexico, which is similar to *L. variegatus* as broadly defined.

Botanical affinity: Angiospermae, possibly Amaryllidaceae, Arecaceae, Bromeliaceae, Iridaceae, or Liliaceae (see generic discussion).

Genus *Monocolpopollenites* Pflug and Thomson in Thomson and Pflug 1953 emend. Nichols et al. 1973

Discussion: *Monocolpopollenites* has a somewhat tortuous history in the taxonomic literature, due in part to the broad circumscription of the genus as originally defined. Nichols et al. (1973) revised *Monocolpopollenites*, restricting it to monocolpate pollen with a flared or rounded colpus that does not extend to the ends of the grain. They specifically included psilate, scabrate, and reticulate grains, and specifically excluded granulate or verrucate grains. Because Nichols et al. (1973) only specifically excluded granulate or verrucate grains, it is here interpreted that all other sculptural types are permitted. The emendation of *Monocolpopollenites* by Saxena (2010) is rejected, because the revision did not include the flared or rounded colpus as a diagnostic character.

Monocolpopollenites cf. *M. tranquilloides* Nichols et al. 1973
Plate 3.1, figures 2-3

Description: Monocolpate, psilate or faintly scabrate, polar axis length 16-(20)-27 μm , equatorial diameter 13-(14)-21 μm . Exine ca. 0.5-1.5 μm thick, thickening near the poles, columellae present but often obscure, shape indeterminate. Shape oval in equatorial view. Colpus extends nearly the full length of the grain, with flared or rounded ends. Colpus with prominent thickened margo, straight to undulating.

Discussion: In the original description for *Monocolpopollenites tranquilloides*, Nichols et al. (1973) gave a size range of 29-37 μm . They distinguished *M. tranquilloides* from *Monocolpopollenites tranquillus* (Potonié 1934) Thomson and Pflug 1953 on the basis of larger size and a tendency to develop margo-like folds bordering the colpus. The thickened margins found in the specimens in this study suggests placement in *M. tranquilloides*, but the size range is more similar to *M. tranquillus*. *Monocolpopollenites tranquillus*, however, was originally described as granulate (Jansonius and Hills 1976).

Occurrence: Ypresian; 27 specimens observed (0.2%).

Botanical affinity: Spermatophyta, possibly Arecaceae or Cycadophyta (Nichols et al. 1973).

Monocolpopollenites tranquillus (Potonié 1934) Jansonius & Hills 1976 sensu lato
Plate 3.1, Figure 3

Description: Monocolpate, faintly scabrate, polar axis length 27 μm , equatorial diameter 21 μm . Exine ca. 0.7 μm thick, not visibly columellate. Shape oval in equatorial view. Colpus extends nearly the full length of the grain, with flared ends. Colpus with moderately thickened margo.

Discussion: A broad species concept is used here. The original description for *M. tranquillus* described the exine as 0.3 μm thick. The exine in the single observed specimen is ca. 0.7 μm thick, but is otherwise similar to *M. tranquillus* as originally described, and specimens figured by Nichols et al. (1973).

Occurrence: Ypresian; 1 specimen observed (<0.1%). *Monocolpopollenites tranquillus* has been commonly described from the Cenozoic of Europe and North America, but Central or South American occurrences are lacking (Palynodata Inc. and White 2008), other than an occurrence from the middle Eocene of Cuba (Arecas-Mallea 1988).

Botanical affinity: Spermatophyta, possibly Arecaceae (Nichols et al. 1973).

Genus *Rugumonocolpites* Pardo-Trujillo and Roche 2009 emend.

Emended description: Monocolpate or trichotomocolpate pollen grains with rugulate sculpture.

Discussion: *Rugumonocolpites* is emended here with a broadended circumscription in order to restore the original meaning of the taxon in the nomenclatural system of van der Hammen (1954b, 1956). The circumscription has also been broadened to include rugulate, trichotomocolpate forms, on the basis that modern plant species can produce both monocolpate and trichotomocolpate pollen (e.g., Harley and Baker 2001).

Rugumonocolpites sp. A

Plate 3.2, figures 1-2

Description: Monocolpate, rugulate, polar axis length 25-26 μm , equatorial diameter 15-16 μm . Shape oval in equatorial view. Colpus extends nearly the full length of the grain, slightly gaping at the ends, with prominent thickened margo. Exine ca. 1.5-2.5 μm thick, thickening towards the poles, sexine thicker than nexine, semitectate. Rugulae ca. 0.5-1.0 μm wide, densely distributed, the depressions between the rugulae ca. 0.5-1.0 μm wide.

Discussion: *Rugumonocolpites* sp. A is more prominently clavate than *Rugumonocolpites* sp. B and *Rugumonocolpites* sp. C.

Occurrence: Ypresian; 2 specimens observed (<0.1%).

Botanical affinity: Spermatophyta, lower classification unknown.

Rugumonocolpites sp. B

Plate 3.2, figures 3-4

Description: Monocolpate, rugulate, polar axis length 26-40 μm , equatorial diameter 16-24 μm . Exine ca. 1 μm thick, finely columellate, the edges of the grain appearing finely corrugated due to the surface sculpture. Outline in equatorial view elliptical, ends of grain broadly rounded. Colpus extending nearly full length of grain. In one specimen (Plate 3.2, fig. 3) the ends of the colpus are flared as in *Monocolpopollenites*, while in a second specimen (Plate 3.2, fig. 4) one end of the colpus is slightly flared and the other end of the colpus is tapered. Surface sculpture rugulate, somewhat resembling mudcracks. Rugulae ca. 0.5-1.0 μm wide, separated by thinner, elongate, interstitial lumina or depressions <0.5 μm wide.

Discussion: *Rugumonocolpites pacificus* Pardo-Trujillo and Roche 2009 is similar, but the rugulae are wider (ca. 2 μm) in *R. pacificus*. Also, the colpus in *R. pacificus* is consistently wider at the ends, while in *Rugumonocolpites* sp. B the colpus may be tapered.

Occurrence: Ypresian; 2 specimens observed (<0.1%).

Botanical affinity: Spermatophyta, lower classification unknown.

Rugumonocolpites sp. C

Plate 3.2, figures 5-8

Description: Monocolpate or trichotomocolpate, rugulate or vermiculate with isolated verrucae. Monocolpate specimens with polar axis length 37-40 μm , equatorial diameter 24-29 μm . Trichotomocolpate specimen with diameter ca. 36 μm . Colpus extends to the ends of the grain or nearly so, gaping at the ends, constricted in the middle. Monocolpate specimens elliptical in

equatorial view, trichotomocolpate specimen triangular. Nontectate, nexine ca. 0.5 μm thick, sexine ca. 0.5-1.0 μm thick. Sexine composed of isolated to anastomosing rugulae ≤ 0.5 μm wide and ca. 0.5-1.0 μm high. In one specimen (Plate 3.2, fig. 6), the rugulae are widely spaced and mainly isolated, while in the three other observed specimens the rugulae are more densely arranged and anastomosing, approaching a pseudo-reticulate pattern, with irregularly shaped lumina 1-3 μm in diameter. Some of the positive sculptural elements are verrucate. Aside from the positive sculptural elements, the exine is quite psilate.

Discussion: The distinctive sculpture, and the occurrence of a trichotomocolpate specimen, suggests that this type may be worth naming as a new species, but not enough specimens have been observed to justify doing so in this study.

Occurrence: Ypresian; 4 specimens observed ($<0.1\%$).

Botanical affinity: Angiospermae, lower affinity unknown, but possibly Arecaceae or Liliaceae. The occurrence of both monocolpate and trichotomocolpate aperture types provides some suggestion of possible botanical affinities for *Rugumonocolpites* sp. C. Symmetric trichotomocolpate pollen forms are found in the families Arecaceae and Liliaceae, often produced by species which also produce monocolpate pollen (Kruttsch 1970), although in some species of the Arecaceae the pollen is exclusively trichotomocolpate (Harley and Backer 2001). Pollen produced by *Phormium* and related genera in the Asphodelaceae is exclusively trichotomocolpate (Moar et al. 2011).

3.4.3. Tricolpate Pollen (Plate 3, Plate 4, Plate 5, Plate 6)

Genus *Clavatricolpites* Pierce 1961

Discussion: *Clavatricolpites* includes all clavate, tricolpate pollen grains. Practically, the use of this genus is restricted to forms in which the clavae are particularly prominent and free-standing. *Gemmatricolpites* Pierce 1961 is a form genus which intergrades with *Clavatricolpites*. According to Punt et al. (2007), clavae are distinguished from gemmae by being taller than they are wide. Hesse et al. (2009) define these terms differently, considering that clavae are club-shaped and gemmae are globular, but note that transitional types between these two end members are the rule rather than the exception. *Ilexpollenites* Thiergart 1937 ex Potonié 1960 is similar in being prominently clavate; although in the description by Potonié (1960), the genus is restricted to tricolporate forms, tricolpate forms have also been described, for example *Ilexpollenites clifdensis* McIntyre 1968.

Clavatricolpites aff. *C. gracilis* González Guzmán 1967

Plate 3.6, figures 3-4

Description: Tricolpate, prominently clavate to gemmate, polar axis length 25-(32)-40 μm , equatorial diameter 18-(23)-29 μm . Exine thickness 1.5-2.5 μm , nexine ca. 1 μm thick, sexine 0.5-1.5 μm thick. Sexine composed of free-standing clavae or gemmae, in shape resembling flat-topped mushrooms or clubs, expanded at their tips, 0.5-1.5 μm long. Prolate, ends of grain moderately tapered. Colpi long, margins weakly to moderately developed.

Discussion: *Clavatricolpites prolatus* Pierce 1961 and *Clavatricolpites firmus* Pierce 1961 are both smaller in overall size (ca. 14-20 μm), with less prominent clavae. *Clavatricolpites gracilis* was originally described as being clavate to gemmate, intectate, and tricolpate. The colpi are

marginate. The shape is prolate to subprolate. The clavae are $<1\ \mu\text{m}$ in diameter and ca. $1\ \mu\text{m}$ in length, and the polar axis length ranges from 25-33 μm . The specimens observed in the IODP 364 core have not been assigned to *C. gracilis* because they tend to have larger and more widely separated clavae. *Clavatricolpites* sp. A is similar, but oblate.

Occurrence: Ypresian; 29 specimens observed (0.2%).

Botanical affinity: Eudicots, lower affinity unknown.

Clavatricolpites sp. A

Plate 3.6, figure 5

Description: Tricolpate, prominently clavate, equatorial diameter 26-44 μm . Exine thickness 2-4 μm , nexine 0.5-1.0 μm thick, sexine composed of free-standing clavae 1-3 μm long, 1-2 μm wide. Oblate, amb subcircular. Colpi extend 1/2 to 2/3 the distance to the poles, widely gaping, with ragged margins.

Discussion: The oblate shape and large clavae distinguish this type from other commonly described species of *Clavatricolpites*.

Occurrence: Ypresian; 6 specimens observed ($<0.1\%$).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Cupuliferoideaepollenites* Potonié et al. 1950 ex Potonié 1960

Discussion: *Cupuliferoideaepollenites* includes psilate, prolate, tricolpate pollen. The poles are well-rounded. *Cupuliferoipollenites* Potonié 1951 ex Potonié 1960 is similar, but tricolporate. *Quercoidites* Potonié 1960 as originally described and as emended by Stanley (1965) has a geniculus. Frederiksen (1980a) also emended *Quercoidites*, restricting the genus to prolate to subprolate, tricolpate, tricolporoidate, or tricolporate pollen with a rough, granulate exine.

Cupuliferoideaepollenites spp.

Plate 3.3, figure 1

Description: Tricolpate, psilate to faintly scabrate, polar axis length 16-(24)-34 μm , equatorial diameter 9-(14)-19 μm . Exine 0.5-1.0 μm thick, tectate, but often with obscure columellae. Prolate, poles moderately tapered to well rounded. Colpi long, equal in length, margins absent to moderately developed. Some prolate, tricolpate specimens observed in SEM have minute sculpturing which would probably not be visible in LM, for example the specimen in Plate 14, fig. 7. These specimens have therefore been identified as *Cupuliferoideaepollenites*. Multiple sculptural morphotypes are present in SEM which are not distinguishable in LM.

Discussion: This study will follow Frederiksen (1980a) and Jardine (2011), grouping all specimens of *Cupuliferoideaepollenites* into one morphotype. The type species of the genus, *Cupuliferoideaepollenites librarensis* (Thomson 1950) Potonié 1960, is smaller ($<20\ \mu\text{m}$) than most specimens observed in this study. Some specimens (e.g., Plate 3.3, fig. 1) have poles which are arguably not well rounded; this aspect of the generic circumscription has been broadly interpreted.

Occurrence: Ypresian; 535 specimens observed (3.3%). *Cupuliferoideaepollenites* is a common and widely distributed form genus in the Cenozoic, although South American occurrences are lacking (Palynodata Inc. and White 2008). This may be due to differing taxonomic practices.

Botanical affinity: Possibly Fabaceae or Fagaceae (Frederiksen 1980b).

Paleoecology: Ramírez-Arriaga, Prámparo, et al. (2014) suggested a tropical deciduous forest paleoecology for unspecialized specimens of *Cupuliferoidapollenites* from the Late Eocene to Early Oligocene of Pueblo, Mexico. Pflug (1952) described Eocene coal beds from Germany, and interpreted pollen of *Cupuliferoidapollenites librarensis* as indicating a lowland forest proximal to the swamp where the coal was deposited (Frederiksen 1985). The uncertainty about the botanical affinity of the IODP 364 specimens suggests caution in assigning a paleoecology.

Genus *Discoidites* Muller 1968

Discussion: *Discoidites* includes brevicolpate grains, with a columellate exine, and a verrucate surface sculpture. Muller (1968) noted that *Discoidites* is similar to pollen produced by the genera *Brownlowia* Roxb. and *Pentace* Hassk. of the Tilioideae. Fossil pollen morphologically similar to modern Tiliaceae pollen has been placed in *Tiliaepollenites* Potonié 1931 or *Intratropipollenites* Pflug and Thomson in Thomson and Pflug 1953. *Discoidites* differs from *Tiliaepollenites* in having short colpi and lacking vestibulate pores (Muller 1968).

Discoidites sp. A Plate 3.5, figures 11-13

Description: Brevicolpate, scabrate, finely punctate, or microreticulate, usually with variously developed larger verrucae, equatorial diameter 23-(26)-31 μm . Exine 1-2 μm thick, visibly columellate, columellae baculate, possibly digitate. Oblate, amb rounded subtriangular to subcircular. Colpi 1.5-4.5 μm wide, incised 2-4 μm in equatorial view, the exine often overhanging the colpi at the grain edge to a variable extent. A semicircular region of darkened exine surrounding the apertures, more obvious in phase contrast, is variously developed. Lumina, if present, <0.5 μm in diameter. Scattered verrucae are also often present, usually concentrated in the polar region, ranging from <0.5 μm in diameter and poorly developed, up to 4 μm diameter and strongly developed. Some specimens have a fine but well developed reticulum.

Discussion: This species differs from the type species of the genus, *Discoidites borneensis* Muller 1968, in being punctate to micro-reticulate rather than psilate to finely verrucate. Verrucae are present in most but not all specimens of *Discoidites* sp. A, in some cases up to 4 μm in diameter. The columellae are also more conspicuous in *Discoidites* sp. A.

Occurrence: Ypresian; 188 specimens observed (0.7%). The similar species *Discoidites borneensis* is mainly known from the Cenozoic of southeastern Asia, with a single African occurrence (Palynodata Inc. and White 2008). FAD: 597.10 mbsf. 50.5-(52.95)-53.7 Ma.

Botanical affinity: Probably Tilioideae of the Malvaceae (see discussion for genus).

Paleoecology: Probably estuarine. Muller (1964) compared specimens of this general type with modern *Brownlowia argentata* Kurz, which inhabits mangrove forests of insular Southeast Asia.

Genus *Echitricolpites* Regali et al. 1974

Discussion: *Echitricolpites* includes all echinate, tricolpate or tetracolpate pollen.

Echitricolpites sp. A
Plate 3.6, figures 6-7

Description: Tricolpate or tetracolpate, echinate, equatorial diameter 32-41 μm . Exine excluding spines ca. 1 μm thick, not visibly columellate. Oblate, amb subcircular. Colpi moderately incised, slightly marginate. Spines broadly conical, ca. 1-2 μm long, sparsely scattered across the grain. Other than the echinae, the sculpture is psilate to faintly scabrate.

Discussion: The similar species *Echitricolpites communis* Regali et al. 1974 includes tricolpate or tetracolpate pollen, with long, pointed colpi, and a fine exine with scattered spines; the size is ca. 23-30 μm (Regali et al. 1974). *Echitricolpites communis*, however, is smaller than these specimens, possesses distinct columellae, and lacks colpi margines.

Occurrence: Ypresian; 2 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Eucommia*? Oliver

Discussion: The circumscription of pollen grains assigned to *Eucommia* is somewhat uncertain because, unlike pollen form genera, there is no authoritative reference on the limits of morphological variation in pollen from modern plant genera. *Eucommia ulmoides* Oliv. is the one living species of the genus *Eucommia* and the family Eucommiaceae, and is endemic to China. The palynological record indicates a much wider distribution in the past (Palynodata Inc. and White 2008). In light microscopy, the pollen of modern *Eucommia* appears tricolpate or weakly tricolporate (tricolporoidate), has a psilate or scabrate exine, is prolate, has colpi with narrow margines, and often has colpi of apparently unequal length (Erdtman 1966; Jardine 2011). A detailed investigation of *E. ulmoides* using scanning electron microscopy and light microscopy by Rowley et al. (1992) found that the pollen is actually tricolporate, but the pores are difficult to observe in light microscopy. The colpi are of equal length, and only appear to be different sizes in light microscopy, possibly due to compression. This study will follow Frederiksen (1983) and Pocknall and Nichols (1996) in assigning Paleogene specimens of this type to “*Eucommia*?” The form genus *Eucommiidites* Erdtman 1948 ex Potonié 1958 emend. Scheuring 1970 was originally presumed to have some affinity with *Eucommia*, but the morphology is quite different (Jansonius and Hills 1976, cards 967-968) and the pollen of *Eucommiidites* is not angiospermous (Traverse 2007). *Eucommioipollis* Ziemiańska-Tworzydło et al. 1994 is a form genus for pollen with affinity to *Eucommia*, but the generic description is quite restricted, for example in restricting the genus to forms with exines ca. 3 μm thick, and is not commonly used (Palynodata Inc. and White 2008). For this study, *Eucommia*? is differentiated from *Cupuliferoideaepollenites* and *Psilatricolpites* Pierce 1961 by possessing apparently unequal colpi.

Eucommia? sp. A
Plate 3.3, figures 2-3; Plate 3.14, figure 6

Description: Tricolpate or tricolporoidate, psilate to faintly scabrate in LM, polar axis length 18-(22)-27 μm , equatorial diameter 13-(17)-20 μm . Exine tectate, columellate, columellae usually obscure but occasionally visible, exine thickness 0.5-1.0 μm . Exine often thicker at poles than equator. Grains prolate, sometimes essentially isopolar but sometimes significantly heteropolar,

with one pole more tapered than the other. Colpi marginate, long, with the exception of one colpus, which appears shorter than the others. Often the margins fuse together at one or both poles, occasionally resembling a monocolpate grain. In light microscopy no pores are visible. In SEM it proved difficult to observe the diagnostic unequal colpi, but a single potential specimen of *Eucommia?* sp. A was observed in SEM (Plate 3.14, fig. 6). An equatorial pore is visible, and the surface is finely verrucate/conate and punctate.

Discussion: If the SEM specimen (Plate 3.14, fig. 6) is in fact *Eucommia?* sp. A, the fine verrucate/conate and punctate exine structure is remarkably similar to *Psilatricolpites* sp. A (Plate 3.14, figure 5). Also, a small pore is visible in the single observed SEM specimen (Plate 3.14, fig. 6b), although this feature is not apparent in light microscopy. *Psilatricolpites* sp. A may be conspecific with *Eucommia?* sp. A, the oblate shape and equal colpi resulting from compression perpendicular to the polar axis, but these two morphologies have been identified separately due to the uncertainty of their relationship. The SEM specimen is similar to SEM specimens of *Eucommia ulmoides* in having fine conate or spinulate ornamentation, but the modern species does not have fine punctae, and verrucae may also be absent (Zavada and Dilcher 1986; Rowley et al. 1992).

Occurrence: Ypresian; 605 specimens observed (3.7%).

Botanical affinity: Possibly Eucommiaceae.

Paleoecology: Ramírez-Arriaga, Prámparo, et al. (2014) suggested a cloud forest paleoecology for unspiciated specimens of *Eucommia* from the Late Eocene to Early Oligocene of Pueblo, Mexico.

Genus *Fraxinoipollenites* Potonié 1951 ex Potonié 1960

Discussion: As originally described, *Fraxinoipollenites* included prolate, tricolpate pollen with no geniculus and a granulate to reticulate exine; however, punctate forms have also been included in *Fraxinoipollenites*, for example *Fraxinoipollenites fragilis* Burger 1993. Although the description by Potonié (1960) places no restrictions on the coarseness of the reticulum in *Fraxinoipollenites*, this study will follow Burden and Hills (1989) and Jardine (2011) in excluding coarsely reticulate ($>1\ \mu\text{m}$ diameter lumina) types from the generic concept. Using the terminology of Punt et al. (2007), *Tricolpites* Cookson 1947 ex Couper 1953 emend. Jarzen and Dettmann 1989 is distinguished from reticulate *Fraxinoipollenites* specimens by being oblate to subprolate (P/E ratio <1.33) rather than prolate (P/E ratio 1.33-2.00). *Tricolpopollenites* Pflug and Thomson in Thomson and Pflug 1953 has an extremely broad circumscription which technically includes all subprolate to prolate tricolpate forms with meridional, symmetrical colpi. According to Jardine (2011), the use of *Tricolpopollenites* should be reserved for tricolpate types which can not be accommodated within a more narrowly defined form genus.

Fraxinoipollenites spp.

Plate 3.3, figures 9-11; Plate 14, figure 8

Description: Tricolpate, micro-reticulate or punctate in LM, polar axis length 23-(29)-37 μm , equatorial diameter 14-(19)-24 μm , P/E ratio 1.35-(1.55)-1.93 (20 specimens measured). Exine 0.5-2 μm thick, tectate, with clearly visible columellae. Fusiform in equatorial view, the poles generally moderately tapered but occasionally broadly rounded. Colpi extending near full length of grain, deeply to moderately incised, margo well developed to nearly absent. Sculpture finely

reticulate or punctate, with roughly circular or irregularly polygonal lumina up to 1 μm in diameter but usually $\leq 0.5 \mu\text{m}$ in diameter. In SEM the surface sculpture is often composed of larger shallow depressions or lumina, with small punctae in the center of the lumina (Plate 3.14, fig. 8); this feature is not observable in LM.

Discussion: This morphotype is quite heterogenous and includes a variety of prolate tricolpate grains with punctate or micro-reticulate sculpture. Attempts to consistently separate this morphotype resulted in a profusion of quite similar and intergrading species. In the end it was decided that subdivision of this morphotype would only confuse the taxonomy. Some *Fraxinoipollenites* specimens are morphologically similar to specimens of *Retitricolporites* sp. A, differing only in the absence of a pore. Subdivision of *Fraxinoipollenites* into species in the literature is often quantitative and depends on the size and P/E ratio of the grain. If speciated, some of the grains assigned to this morphotype could be placed in *Fraxinoipollenites artus* Frederiksen 1983, *Fraxinoipollenites medius* Frederiksen 1973, *Fraxinoipollenites pudicus* (Potonié 1934) Potonié 1951 ex Potonié 1960, *Fraxinoipollenites scoticus* (Simpson 1961) Frederiksen 1980, *Fraxinoipollenites variabilis* Stanley 1965, or *Tricolpopollenites haraldii* Manum 1962. Some of these species have overlapping definitions.

Occurrence: Ypresian; 2,596 specimens observed (16.0%). *Fraxinoipollenites* is a common and widely distributed genus in the Cretaceous and Cenozoic (Palynodata Inc. and White 2008).

Botanical affinity: Eudicots, lower affinity uncertain. *Fraxinoipollenites* is named after the modern genus *Fraxinus* L. (Oleaceae), but the general botanical affinity of fossil grains of *Fraxinoipollenites* with *Fraxinus* is questionable (Stanley 1965). Various *Fraxinoipollenites* species have been tentatively placed in Bignoniaceae or Menispermaceae (Frederiksen 1983), Platanaceae (Wing and Harrington 2001), and Oleaceae (Ramírez-Arriaga et al. 2017).

Genus *Insulapollenites* Leffingwell 1970

Discussion: *Insulapollenites* includes oblate, parasyncolpate pollen, with colpi that bifurcate near the poles and the equator to form equatorial and polar islands. *Insulapollenites* is distinguished from *Duplopollis* Krutzsch 1959 and *Cupaniedites* Cookson and Pike 1954 by being syncolpate rather than syncolporate, and by possessing equatorial islands (Leffingwell 1970). Pocknall and Nichols (1996) noted that it is difficult to determine whether *Insulapollenites* is syncolpate or syncolporate, because the equatorial islands obscure the aperture structure at the equator, and because specimens are essentially always seen in polar view.

Insulapollenites aff. *I. rugulatus* Leffingwell 1970

Plate 3.5, figure 10

Description: Parasyncolpate or parasyncolporoidate, rugulate, equatorial diameter 27 μm . Exine ca. 1.0-1.5 μm thick, not visibly columellate, outline in polar view appearing corrugate due to variations in exine thickness caused by rugulate sculpture. Oblate, amb subtriangular. Colpi bifurcate near the poles and the equator to form equatorial and polar islands. Pores, if present, obscure. Sculpture in the form of rugulae, the rugulae ca. 0.7-2.0 μm wide, separated by narrower valleys. The rugulae are anastomosing, but preferentially aligned parallel to the polar axis, and the sculpture could be described as rugulate-striate.

Discussion: This specimen is similar to *Insulapollenites rugulatus* in most respects, but the specimen in this study exhibits a distinct tendency for the rugulae to align parallel to the polar axis, a feature not described or visible in illustrated specimens of the species by Leffingwell (1970), Nichols and Ott (1978), or Pocknall and Nichols (1996).

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, possibly Sapindaceae or Myrtaceae (Pocknall and Nichols 1996), assuming a similar botanical affinity with *I. rugulatus* sensu stricto.

Genus *Psilatricolpites* Pierce 1961

Discussion: *Psilatricolpites* includes all psilate, tricolpate pollen. Although technically falling within the broad circumscription of *Psilatricolpites*, psilate to faintly scabrate tricolpate grains which are prolate have been placed in *Eucommia*? sp. A or *Cupuliferoidaepollenites* spp.

Psilatricolpites sp. A

Plate 3.3, figures 4-5; Plate 3.14, figure 5

Description: Tricolpate, psilate to faintly scabrate in LM, equatorial diameter 20-(23)-27 μm . Exine 0.5-1.5 μm thick, usually not visibly columellate. Oblate to spheroidal, amb subcircular to rounded subtriangular. Colpi wide, 3-9 μm deep, sometimes with ragged colpi membranes (Plate 3.3, fig. 5; Plate 3.14, fig. 5). Colpi margins absent. A specimen observed in SEM (Plate 3.14, fig. 5) has granulate or micro-verrucate surface sculpture with scattered punctae. The colpi membranes are coarsely and irregularly granulate.

Discussion: *Psilatricolpites* sp. A is common in the assemblage, but its botanical affinity is unknown. The species closely resembles *Eucommia*? sp. A, but is oblate, with colpi of equal length. As discussed earlier, these differences may be compressional artifacts. One argument against an affinity with *Eucommia* is that described fossil grains of *Eucommia* are generally, if not always, prolate (e.g., Frederiksen 1983; Roehler 1987; Pocknall and Nichols 1996; Ramírez-Arriaga, Prámparo, et al. 2014). *Scabratricolpites* sp. A is distinguished by being clearly granulate in light microscopy, although possibly transitional forms rarely occur. *Psilatricolpites brevis* González Guzmán 1967 is similar, but the colpi are more deeply incised in *Psilatricolpites* sp. A.

Occurrence: Ypresian; 1,334 specimens observed (8.2%).

Botanical affinity: Eudicots, lower affinity uncertain.

Genus *Retitrescolpites* Sah 1967

Discussion: *Retitrescolpites* as originally defined included tricolporate or tricolporoidate pollen with a retipilate or reticulate sculpture. The shape is spheroidal, sub-spheroidal, or rounded triangular. Although the coarseness of reticulum is not specified in the original description, *Retitrescolpites* is generally restricted to coarsely reticulate (lumina diameter >1 μm) forms in order to distinguish it from *Tricolpites* Cookson 1947 ex Couper 1953 emend. Jarzen and Dettmann 1989 (e.g., Frederiksen 1979; Demchuk 1990; Nichols and Brown 1992). This study will follow Jardine (2011) and consider that *Retitrescolpites* is restricted to oblate and spheroidal forms. Frederiksen (1979) considered *Albertipollenites* Srivastava 1969 a junior synonym of *Retitrescolpites*.

Retitrescolpites anguloluminosus (Anderson 1960) Frederiksen 1979 sensu lato
Plate 3.3, figures 15-16

Description: Tricolpate, coarsely reticulate, equatorial diameter 20-32 μm . Nexine $<0.5 \mu\text{m}$ thick, sexine composed of high-walled muri, 1.0-2.5 μm thick. Oblate, amb subcircular. Colpi extend approximately 1/4 to 1/3 the distance to the poles, widely gaping, the colpi sometimes with a faint margo formed by the muri. Reticulum with high-walled muri $\leq 0.5 \mu\text{m}$ wide, lumina rounded polygonal in shape, lumina diameter generally ca. 2-3 μm but with some elongate lumina up to 4 μm across.

Discussion: *Retitrescolpites anguloluminosus* is distinguished from other oblate, reticulate, tricolpate pollen by its coarse reticulation and narrow, delicate muri. As originally described by Anderson (1960), *R. anguloluminosus* has lumina approximately 2 μm in diameter.

Retitrescolpites bathyreticulatus (Stanley 1965) Demchuk 1990 is a similar species, with lumina up to 3 μm in diameter. This study will follow Nichols and Brown (1992) and consider these species synonymous. A broad species concept is used here to include specimens with shorter colpi and larger lumina than *R. anguloluminosus* as originally described, as well as specimens that fall within the circumscription of *R. bathyreticulatus* but not *R. anguloluminosus* sensu stricto, for example specimens lacking a margo.

Occurrence: Ypresian; 8 specimens observed ($<0.1\%$). *Retitrescolpites anguloluminosus* and *R. bathyreticulatus* have been commonly identified from the Cretaceous and Paleogene of North America, with scattered occurrences elsewhere, mainly in the Cretaceous and Paleogene; South American and Central American occurrences are lacking (Palynodata Inc. and White 2008).

Botanical affinity: Eudicots, lower affinity unknown, but possibly Hamamelidaceae or Oleaceae. Stanley (1965) noted the similarity of *R. bathyreticulatus* to modern pollen of *Exbucklandia* (Hamamelidaceae) and *Fraxinus excelsior* (Oleaceae).

Retitrescolpites sp. A
Plate 3.3, figure 17; Plate 3.4, figures 1-2

Description: Tricolpate, coarsely reticulate, equatorial diameter 27-39 μm . Exine 1-2 μm thick. Oblate, amb subcircular. Colpi extend 1/3 to 2/3 the distance to the poles, widely gaping, sometimes with margins and/or colpi membranes. Colpi margins smooth. Muri 0.5-1.0 μm wide, generally curvilinear, lumina 1-3 μm in diameter. In some specimens (ex., Plate 3.4, fig. 2) the capita of the columella are conspicuous, giving the muri a beaded appearance. Although morphologically quite variable, this morphotype was not subdivided due to the low number of observed specimens.

Discussion: *Retitrescolpites anguloluminosus* is similar but has more delicate muri.

Retitrescolpites sp. B has ragged, clavate colpi margins.

Occurrence: Ypresian; 8 specimens observed ($<0.1\%$).

Botanical affinity: Eudicots, lower affinity unknown.

Retitrescolpites sp. B
Plate 3.4, figure 3

Description: Tricolpate to tricolporoidate, coarsely reticulate, equatorial diameter 30-(33)-37 μm . Nexine ca. 0.5 μm thick, sexine ca. 1 μm thick. Oblate, amb subcircular to rounded

subtriangular. Colpi extend ca. $\frac{3}{5}$ the distance to the poles, widely gaping, the margins quite ragged, lined with isolated clavae. Reticulum with irregularly polygonal to elliptical lumina 1-2 μm in diameter. Muri 0.5-1.0 μm wide. Usually the capita of the columellae are conspicuous, giving the muri a beaded appearance.

Discussion: *Retitrescolpites* sp. B is distinguished from other species of *Retitrescolpites* in the assemblage by its distinctive ragged, clavate colpi margins. Some specimens may be tricolporate, the pores somewhat ambiguous due to the ragged margins.

Occurrence: Ypresian; 36 specimens observed (0.2%).

Botanical affinity: Eudicots, lower affinity unknown.

Retitrescolpites sp. C

Plate 3.4, figures 4-5, 8; Plate 3.14, figure 11

Description: Tricolpate, coarsely reticulate, equatorial diameter 34-(47)-55 μm . Exine 1-3 μm thick. Reticulum is not inserted on a basal layer. Oblate, amb subtriangular. Colpi short, often obscure. Sculpture coarsely reticulate, muri 1-3 μm wide, lumina 1-6 μm in diameter, but occasionally larger, with some elongated lumina >11 μm in longest dimension. Some specimens are more finely reticulate, with numerous lumina <1 μm in diameter. Lumina subcircular, elliptical, rounded polygonal, or sinuous. The exterior surface of the muri is nearly psilate in SEM, although small verrucae or conate protrusions, possibly isolated columellae, are visible on the interior of the muri (Plate 14, fig. 11).

Discussion: There is a great degree of variability in the coarseness of the reticulum, but it was not considered useful to subdivide *Retitrescolpites* sp. C. Possible transitional forms between *Retitrescolpites* sp. C and *Boehlensipollis*? sp. A have been observed (e.g., Plate 4, fig. 4), with a relatively fine reticulum and longer colpi than most specimens of *Retitrescolpites* sp. C.

Occurrence: Ypresian; 69 specimens observed (0.4%). FAD: 561.48 mbsf. 49.11-(50.13)-50.2 Ma.

Botanical affinity: Eudicots, lower affinity unknown, although the presence of apparently transitional forms with *Boehlensipollis* sp. A suggests a similar botanical affinity, possibly Elaeagnaceae or Sapindaceae.

Genus *Retitricolpites* van der Hammen 1956 ex van der Hammen & Wymstra 1964

Discussion: *Retitricolpites* includes all reticulate, tricolpate pollen, but in this study the circumscription of *Retitricolpites* is restricted to prolate, reticulate, tricolpate pollen with lumina diameter >1 μm . Burden & Hills (1989) defined *Retitricolpites* in a similar fashion.

Retitricolpites is arguably invalid, because, like the other subgenera named by van der Hammen (1956), the type specimen was pollen from a recent genus. Van der Hammen & Wymstra (1964) attempted to legitimize *Retitricolpites* by raising it to generic rank and providing *Retitricolpites ovalis* van der Hammen & Wymstra 1964 as lectogenotype. According to Jansonius and Hills (1976) and Jaramillo and Dilcher (2001), this was not sufficient to validate *Retitricolpites*.

Regardless of its technical validity, *Retitricolpites* is useful as a form genus for reticulate, tricolpate pollen which can not be placed in a more specific form genus. Oblate to spheroidal, reticulate, tricolpate pollen can generally be placed into either *Tricolpites* if the pollen is finely reticulate and homobrochate (<1 μm diameter lumina), or *Retitrescolpites* if the pollen is coarsely reticulate (>1 μm diameter lumina). This study will follow Burden and Hills (1989) and

Jardine (2011) in restricting *Fraxinoipollenites* to finely reticulate (<1 µm diameter lumina) pollen.

Retitricolpites sp. A
Plate 3.5, figures 1-2

Description: Tricolpate, reticulate, polar axis length 25-(36)-44 µm, equatorial diameter 18-(21)-30 µm, P/E ratio 1.32-(1.76)-2.15. Exine 1-2 µm thick, tectate. Prolate, ends of grain moderately rounded. Colpi long, straight to slightly sinuous, with absent to moderately developed costae colpi. Maximum diameter of lumina 1-2 µm. Lumina elliptical to rounded polygonal.

Discussion: Coarsely reticulate, tricolpate, prolate pollen is common in the IODP 364 assemblage, and has been subdivided on the basis of the maximum lumina diameter.

Retitricolpites sp. A has a maximum lumina diameter of 1-2 µm, *Retitricolpites* sp. B has a maximum lumina diameter of 2-4 µm, and *Retitricolpites* sp. C has a maximum lumina diameter >4 µm. Attempts to subdivide these morphotypes on the basis of pollen size, colpus morphology, exine morphology, or lumina shape were considered unproductive.

Occurrence: Ypresian; 310 specimens observed (1.9%).

Botanical affinity: Eudicots, lower affinity unknown.

Retitricolpites sp. B
Plate 3.5, figures 3-4

Description: Tricolpate, coarsely reticulate, polar axis length 26-(34)-41 µm, equatorial diameter 17-(23)-29 µm, P/E ratio 1.28-(1.51)-1.71. Exine 1-2 µm thick, tectate. Prolate, ends of grain moderately rounded. Colpi long, costae colpi absent to moderately developed. Maximum diameter of lumina 2-4 µm. Lumina elliptical to rounded polygonal.

Discussion: This morphotype includes prolate, reticulate, tricolpate pollen with maximum lumina diameter of 2-4 µm.

Occurrence: Ypresian; 220 specimens observed (1.4%).

Botanical affinity: Eudicots, lower affinity unknown.

Retitricolpites sp. C
Plate 3.5, figure 5

Description: Tricolpate, coarsely reticulate, polar axis length 29-(40)-47 µm, equatorial diameter 22-(29)-39 µm, P/E ratio 1.13-(1.38)-1.95. Exine 2-4 µm thick. Prolate, ends of grain broadly rounded. Colpi long, costae colpi weakly to moderately developed. Maximum diameter of lumina >4 µm. Lumina elliptical to rounded polygonal.

Discussion: This type is more coarsely reticulate (maximum lumina diameter >4 µm) than other species of *Retitricolpites* in this assemblage.

Occurrence: Ypresian; 24 specimens observed (0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Rousea* Srivastava 1969

Discussion: *Rousea* is distinguished from other reticulate, tricolpate genera by its heterobrochate reticulum, which is coarser in the mesocolpium and finer toward the colpi margins and apocolpium.

Rousea sp. A
Plate 3.5, figure 6

Description: Tricolpate, reticulate, equatorial diameter 34 μm . Exine ca. 1.5 μm thick, tectate. Oblate, amb subcircular. Colpi extend ca. 4/5 the length of the grain, widely gaping, spanned by a faint colpus membrane, colpi margins with equatorial thickening. Reticulum heterobrochate, lumina 1.5-2.5 μm in diameter at mesocolpia, ≤ 0.5 μm in diameter at colpi margins and apocolpia.

Discussion: *Rousea subtilis* Srivastava 1969, the type species of *Rousea*, is larger (42-50 μm), has a thicker exine (ca. 4 μm thick), and is more coarsely reticulate (lumina diameter 4-5 μm in mesocolpia). Graham and Jarzen (1969) identified heterobrochate, tricolpate pollen from the Oligocene of Puerto Rico as *Salix*, but their specimens were observed in equatorial view and clearly prolate.

Occurrence: Ypresian; 1 specimen observed ($<0.1\%$).

Botanical affinity: Eudicots, probably Salicaceae. *Rousea* sp. A is similar to the modern species *Salix laevigata* Bebb. (Salicaceae), particularly in being tricolpate, marginate, and heterobrochate, with the reticulum coarsest at the mesocolpia; *S. laevigata* is spheroidal to subprolate (Kapp et al. 2000).

Paleoecology: If the botanical affinity with the Salicaceae is correct, *Rousea* sp. A may indicate a moist paleoenvironment; Graham and Jarzen (1969) noted that *Salix* L. is most common in moist environments, but occupies a wide range of habitats.

Genus *Scabratricolpites* (van der Hammen 1956) González Guzmán 1967

Discussion: *Scabratricolpites* includes all scabrate, tricolpate pollen. Using the terminology of Punt et al. (2007), all sculpture types with sculptural elements less than one micron in size are considered scabrate. In this study, *Scabratricolpites* is restricted to tricolpate pollen grains which are granulate or have an indistinctly roughened surface.

Scabratricolpites sp. A
Plate 3.3, figures 7-8

Description: Tricolpate, granulate, equatorial diameter 17-(23)-30 μm . Exine 1-2 μm thick, tectate, columellae obscure to conspicuous. Oblate, amb subcircular. Colpi extend 2/3-3/4 of the way to the poles. Colpi marginate, colpi edges sometimes ragged. Costae colpi absent. Sculpture in the form of minute granulae <0.5 μm in diameter.

Discussion: *Scabratricolpites* sp. A resembles some species of *Quercoidites* in being tricolpate and granulate, but can't be placed in *Quercoidites* as emended by Stanley (1965) because it lacks a geniculus and can't be placed in *Quercoidites* as emended by Frederiksen (1980a) because it is

oblate. *Psilatricolpites* sp. A is similar, but is psilate or indistinctly scabrate in light microscopy, not granulate.

Occurrence: Ypresian; 526 specimens observed (3.2%).

Botanical affinity: Eudicots, lower affinity unknown.

Scabratricolpites sp. B

Plate 3.3, figure 6

Description: Tricolpate, scabrate, equatorial diameter 28 μm . Exine quite variable in thickness, usually thinner at the intercolpia, 1-3 μm thick, visibly columellate, sexine thicker than nexine. Oblate, amb subtriangular, planaperturate, with the edges of the triangle flattened or slightly concave. Colpi long, moderately incised, slightly ragged, margo absent. Surface sculpture indistinctly scabrate.

Discussion: The planaperturate morphology of this specimen serves to distinguish it from *Scabratricolpites* sp. A.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical Affinity: Eudicots, lower affinity unknown.

Genus *Spirosyncolpites* González Guzmán 1967 emend. Legoux 1978

Discussion: *Spirosyncolpites* was originally described as tricolpate, subspheroidal to spheroidal, with furrows forming rings and helices, and a reticulum which is usually not tightly affixed to a basal layer. Legoux (1978) emended *Spirosyncolpites*, adding that the colpi are sometimes strongly reduced, and not always arranged in a syncolpate or spiral fashion; the sculpture is coarsely reticulate and attached to the nexine by sparse and widely separated columellae (Jansonius and Hills 1976). Jaramillo and Dilcher (2001) noted that the colpi in the type species *Spirosyncolpites spiralis* González Guzmán 1967 are rarely distinct, and not visibly syncolpate. Additionally, the holotype specimen is damaged and not observable.

Spirosyncolpites spiralis González Guzmán 1967 sensu lato

Plate 3.4, figures 6-7, 9; Plate 3.14, figure 12

Selected synonymy:

Retitricolpites amapaensis Regali et al. 1974, plate 16, figs. 1-1c

Description: Tricolpate or rarely tricolporate, coarsely reticulate, equatorial diameter 33-(41)-53 μm . Grains approximately spherical to slightly prolate. Exine 2-6 μm thick, sexine composed of high-walled muri. Colpi often obscure, shallowly incised, brevitriloculate, occasionally with an observable margo. A single observed specimen is visibly tricolporate (Plate 3.4, fig. 9). The individual supporting columellae are clearly visible in more coarsely reticulate specimens (Plate 3.4, fig. 7). The coarseness of the reticulum is quite variable. Muri generally 1-2 μm wide, rarely up to 3 μm wide, lumina rounded polygonal to sinuous in shape, 1-10 μm in diameter or longest dimension. In SEM, the sculpture underneath the reticulum, which appears infragranulate in LM, is composed of free-standing cylindrical, conate, or pilate protuberances longer than they are wide (Plate 3.14, fig. 12b).

Discussion: The IODP 364 specimens are similar to *Spirosyncolpites spiralis* as originally described by González Guzmán (1967) and as imaged by Hoorn (1994, Plate 4, fig. 1). Jaramillo

and Dilcher (2001) provide additional descriptions of this species. The ring or helical shape of the colpi as described for *S. spiralis* has not been clearly observed in these specimens, although it is often difficult to observe the colpi at all. Specimens assigned to “*Reticulataepollis* cf. *intergranulata*” by Graham et al. (2000, figs. 35-36) are also morphologically similar to the IODP 364 specimens, although smaller and less coarsely reticulate. A single tricolporate specimen, otherwise similar to *Spirosyncolpites spiralis*, has not been speciated separately. The observation of additional tricolporate specimens in future work may justify the creation of a new taxon.

Occurrence: Ypresian; 88 specimens observed (0.5%). *Spirosyncolpites spiralis* has mainly been described from the Miocene to Eocene of Africa and South America (Palynodata Inc. and White 2008). Jaramillo et al. (2005) placed the FAD of *Spirosyncolpites spiralis* in the Cuervos Formation of Colombia near the base of the Eocene.

Botanical affinity: Fabaceae (Carlos Jaramillo, personal communication, October 31, 2019).

Genus *Striatopollis* Krutzsch 1959

Discussion: *Striatopollis* is used here in a broad sense which includes all prolate, striate, tricolporate pollen, following Jardine (2011). Jaramillo and Dilcher (2001) gave a similar circumscription for *Striatopollis*, including all striate tricolporate pollen grains which are tectate and subprolate to prolate. *Striatricolpites* (van der Hammen 1956) González Guzmán 1967 includes all striate, tricolporate pollen, but is arguably illegitimate (Jansonius and Hills 1976). Kedves (1978) considered *Striatricolpites* and *Striopollenites* Rouse 1962 junior synonyms of *Striatopollis*, implying that the circumscription of *Striatopollis* should include all striate, tricolporate pollen. *Rutiheperipites* Srivastava 1977 was considered a junior synonym of *Striatopollis* by Ward (1986) and Farabee and Canright (1986). Pedersen et al. (2007), however, proposed maintaining *Rutiheperipites* for striate, tricolporate pollen with anastomosing muri bearing transverse suprategal ornamentation.

Striatopollis grahamii sp. nov.

Plate 3.5, figures 7-9; Plate 3.15, figure 3

Holotype: The specimen in Plate 3.5, fig. 8 (520.79 mbsf, slide 1, EFS S39/1).

Repository: CENEX, LSU, Baton Rouge, Louisiana, USA.

Type locality: IODP 364 Site M0077, Chicxulub impact crater, Mexico.

Derivation of name: The species name is in honor of Dr. Alan Graham, whose contributions to the palynological literature of Mexico and Central America have been invaluable (e.g., Graham 2010).

Description: Tricolporate, striate, polar axis length 23-(32)-36 μm , equatorial diameter 15-(19)-23 μm , P/E ratio 1.28-(1.75)-2.20. Exine ca. 1 μm thick, not visibly columellate. Prolate, ends of grain moderately tapered, fusiform in shape. Colpi in the form of thin slits extending nearly the full length of the grain, often obscured by striae and difficult to observe. Striae roughly parallel to polar axis, sinuous, rarely bifurcating, usually $\leq 0.5 \mu\text{m}$ wide, rarely up to 1 μm wide. The individual striae are essentially psilate even under SEM (Plate 15, fig. 3b).

Discussion: *Striatopollis grahamii* sp. nov. is somewhat similar to *Striatopollis catatumbus* (González Guzmán 1967) Takahashi & Jux 1989, but *S. catatumbus* is larger (49-56 μm in length) and has a thicker exine (ca. 3 μm) than *S. grahamii* sp. nov. The circumscription of *S.*

catatumbus was interpreted loosely by Graham et al. (2000), who described a specimen of *S. catatumbus* 40 µm in length with a wall thickness of ca. 1 µm. *Striatopollis grahamii* sp. nov. is similar to Cenozoic Central American fossil pollen grains identified as the modern genus *Crudia* Schreb. (Fabaceae) by Graham (1988, 1989, 1991, 1999), although the specimens in this study are generally more prolate and smaller, with a thinner exine and finer, more anastomosing striae. Pollen grains with an observable pore, but otherwise similar to *Striatopollis grahamii* sp. nov., have been placed in *Striatricolporites conspicuus* Muller 1968. *Striatopollis minor* (Wijmstra 1971) Jaramillo & Dilcher 2001 is distinguished from *Striatopollis grahamii* sp. nov. by its smaller size, *Striatricolpites semistriatus* González Guzmán 1967 is distinguished by having furrows that bifurcate at the poles, and *Striatricolpites saramacensis* Wijmstra 1971 has a thicker exine (2-3 µm thick) and distinct columellae.

Occurrence: Ypresian; 305 specimens observed (1.9%).

Botanical affinity: Eudicots, probably Fabaceae, possibly *Crudia*.

Paleoecology: The similarity to modern *Crudia* pollen, a genus today found primarily in tropical lowlands and riverine environments of the Amazon (Graham 1991, 2003), suggests that *Striatricolpites grahamii* sp. nov. was sourced from a tropical lowland paleoenvironment.

Genus *Tricolpites* Cookson 1947 ex Couper 1953 emend. Jarzen & Dettmann 1989

Discussion: As originally described, *Tricolpites* included virtually all tricolpate pollen. Potonié (1960) later restricted the circumscription of *Tricolpites* to spheroidal or oblate, trilobate, finely reticulate, tricolpate pollen. Jarzen and Dettmann (1989) emended *Tricolpites* and specified that the reticulum is homobrochate, with lumina <1 µm in diameter. Oblate to subprolate forms are included. The amb is either circular or trilobate; however, Jardine (2011) placed some straight-sided specimens in *Tricolpites hians* Stanley 1965. *Retitrescolpites* Sah 1967 is distinguished from *Tricolpites* by being more coarsely reticulate (lumina >1 µm in diameter). *Fraxinoipollenites* and *Retitricolpites* are here distinguished from *Tricolpites* by being prolate.

Tricolpites hians Stanley 1965 sensu lato
Plate 3.3, figures 12-13

Description: Tricolpate, micro-reticulate, equatorial diameter 21-(28)-32 µm. Exine ca. 1 µm thick. Oblate, amb circular to rounded subtriangular, mesocolpia convex. Colpi extend ca. 2/3 the distance to the poles, margins smooth or slightly ragged. Costae colpi absent or weakly developed. Exine slightly thickened at equatorial region on colpi margins in some specimens. Lumina ≤0.5 µm in diameter, subcircular.

Discussion: As originally described by Stanley (1965), *Tricolpites hians* is restricted to oblate, reticulate tricolpate pollen, with a ca. 1 µm thick exine and lumina ca. 0.2-0.3 µm in diameter. The amb is circular, and the equatorial diameter is 18-20 µm. Pocknall and Nichols (1996) synonymized *T. hians*, *Tricolpites parvus* Stanley 1965, and *Tricolpites varius* Norton in Norton & Hall 1969, with *T. hians* chosen as the senior synonym. Although they did not formally emend *T. hians*, Pocknall and Nichols (1996) significantly expanded the circumscription of the species, providing a size range of 18-25 µm and including specimens with lumina diameter <0.5 µm. Jardine (2011) included specimens with equatorial diameter up to 34 µm in *T. hians*. *Tricolpites asper* Frederiksen 1978 is distinguished from *T. hians* by having shallower colpi with rougher edges. *Tricolpites reticulatus* Cookson 1947 ex Couper 1953 emend. Jarzen & Dettmann 1989 is

similar to *T. hians*, but is more strongly trilobate. Jardine (2011) also noted that in *T. reticulatus* the colpi have slightly concave sides in polar view.

Occurrence: Ypresian; 178 specimens observed (1.1%). *Tricolpites hians* is commonly identified from the Cretaceous and Cenozoic of North America, with some European and Asian

occurrences; Central and South American occurrences are lacking (Palynodata Inc. and White 2008).

Botanical affinity: Eudicots, possibly Platanaceae (Pocknall and Nichols 1996).

Tricolpites sp. A
Plate 3.3, figure 14

Description: Tricolpate, micro-reticulate, equatorial diameter 18-(24)-28 μm . Exine 0.5-1.5 μm thick, columellae clavate. Oblate, amb circular to rounded subtriangular. Colpi moderately to deeply incised, gaping, costae colpi absent or weakly developed. Lumina 0.5-1.0 μm in diameter, circular to rounded polygonal in shape. Muri <0.5 μm thick.

Discussion: *Tricolpites* sp. A is more coarsely reticulate than *Tricolpites hians*, and less coarsely reticulate than *Retitrescolpites* spp.

Occurrence: Ypresian; 118 specimens observed (0.7%).

Botanical affinity: Eudicots, lower classification unknown.

Genus *Verrutricolpites* Pierce 1961

Discussion: *Verrutricolpites* includes all verrucate, tricolpate pollen.

Verrutricolpites sp. A
Plate 3.6, figure 1

Description: Tricolpate, verrucate, polar axis length 32 μm , equatorial diameter 17 μm . Colpi long, moderately incised. Exine ca. 1 μm thick, not visibly columellate. Prolate. Verrucae 1-2 μm in diameter, ≤ 0.5 μm tall, polygonal, separated by narrow interstitial depressions which form a negative reticulum. An ambiguously punctate sculpture is visible on the verrucae in phase contrast (Plate 3.6, fig. 1b).

Discussion: The type species of the genus, *Verrutricolpites sphaeroides* Pierce 1961, is spheroidal rather than prolate. *Verrutricolpites irregularis* González Guzmán 1967 has verrucae which are not nearly as low or rounded as this specimen. Jaramillo et al. (2007) describe a prolate type identified as *Verrutricolpites "gemmatus"* from the Upper Paleocene of Colombia, but in that morphotype the verrucae approach a gemmate sculpture.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower classification unknown.

Verrutricolpites sp. B
Plate 3.6, figure 2

Description: Tricolpate, verrucate, equatorial diameter 24 μm . Exine excluding verrucae <0.5 μm thick, not visibly columellate. Oblate, amb subcircular. Colpi extend ca. 3/5 the distance to

the poles, broadly gaping, with ragged margins, margins absent. Ornamentation in the form of densely arranged, rounded verrucae 0.5-3.0 μm wide and 0.5-1.5 μm high. A few of these verrucae approach a gemmate morphology.

Discussion: *Verrutricolpites* sp. A has verrucae with a different morphology and is prolate.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

3.4.4. Tricolporate Pollen (Plate 4, Plate 6, Plate 7, Plate 8, Plate 9)

Genus *Basopollis* Pflug 1953

Discussion: *Basopollis* is one of several genera collectively termed the Normapolles group (Tschudy 1975). *Basopollis* includes triaperturate grains with a triangular to concave-triangular amb. The apertures are slit-shaped, vestibulate, and complex. *Basopollis* is similar to *Choanopollenites* Stover 1966, but is distinguished by being vestibulate. The complex aperture structure is diagnostic and has been described as polyannulate (Tschudy 1975). Although Jardine (2011) described *Basopollis* as triporate, this study will follow Graham et al. (2000) and consider that the complex apertures are tricolporate.

Basopollis sp. A
Plate 3.7, figures 13-14

Description: Tricolporate, verrucate, equatorial diameter 19-24 μm . Amb triangular, angulaperturate. Exine thickness 1-2 μm in interapertural areas. Colpi short, annulate, vestibulate, pore morphology obscure. Vestibulum narrow and wide, covered by crescent-shaped endexinal flaps which form the annulus. Verrucae faint, 0.5-1.0 μm in diameter.

Discussion: This distinctive form has a close morphological similarity to pollen identified by Tschudy (1975) as “cf. *Choanopollenites* sp.,” by Areces-Mallea (1990) as *Basopollis krutzchi* Kedves 1974, by Graham et al. (2000) as “*Basopollis*/cf. *Choanopollenites* sp.,” and by Jarzen and Klug (2010) as “*Choanopollenites* sp.” In the original description for *Choanopollenites*, Stover et al. (1966) stated that *Choanopollenites* is not vestibulate, and is distinguished on this basis from *Basopollis*, which is vestibulate. The specimens in this study are interpreted as vestibulate, so they have been identified as *Basopollis*.

Occurrence: Ypresian; 7 specimens observed (<0.1%).

Botanical affinity: The botanical affinity is with the Normapolles group (Tschudy 1975). Normapolles pollen is similar to pollen from some modern taxa in the Myrtales, Saxifragales, and Fagales (Schönenberger et al. 2001).

Genus *Boehlensipollis* Krutzsch 1962 emend. Frederiksen in Frederiksen et al. 1983

Discussion: *Boehlensipollis* includes oblate, tricolporate pollen grains with a strongly triangular amb, narrow colpi that usually extend completely or nearly to the pole on at least one hemisphere, and large, distinctly atriate ora. Often the grains are heteropolar, with longer colpi on one hemisphere than the other.

Boehlensipollis? sp. A
Plate 3.9, figures 7-8; Plate 3.14, figure 15

Description: Tricolporate to tricolporoidate, verrucate to incipiently reticulate, equatorial diameter 35-(41)-46 μm . Exine thickness 1-3 μm , coarsely columellate. Oblate, specimens only seen in polar view, amb strongly triangular, mesocolpia more or less straight-sided. Colpi shallowly incised, often becoming obscure as the colpi approach the polar area. Some specimens appear syncolpate (Plate 3.9, fig. 8), while others do not (Plate 3.14, fig. 15). No visibly heteropolar grains were observed. Ora often obscure, shape indeterminate. Verrucae 1-3 μm in diameter, densely arranged, often overlapping or fused. In between the verrucae, lumina may be present, in some specimens approaching a reticulate sculpture (Plate 3.14, fig. 15).

Discussion: The generic identification of this taxon is somewhat questionable, as the pollen are not visibly heteropolar or atriate. The taxon has been tentatively assigned to *Boehlensipollis* based on its morphological similarity to *Boehlensipollis verrucata* Frederiksen 1988 and a type identified by Frederiksen (1983, Plate 17, figs. 26-28) as “*Boehlensipollis* sp. 2.” However, both these species are heteropolar, with one hemisphere syncolpate.

Occurrence: Ypresian; 354 specimens observed (2.2%). *Boehlensipollis* sp. A has a notably higher relative abundance in the PETM section than the later Ypresian.

Botanical affinity: Eudicots, possibly Elaeagnaceae (Frederiksen 1983).

Genus *Bombacacidites* Couper 1960 emend. Krutzsch 1970

Discussion: *Bombacacidites* includes brevitricolporate, planaperturate, reticulate pollen with a lenticular to sphaeroidal shape, similar to pollen found in the modern Bombacoideae. However, some pollen assigned to *Bombacacidites* may have been produced by other plant groups, formerly known as the families Sterculiaceae and Tiliaceae (Frederiksen 1983). In the APG IV classification, the Bombacaceae/Sterculiaceae/Tiliaceae groups have been subsumed into the family Malvaceae (Byng et al. 2016). Srivastava (1972a) emended *Bombacacidites*, restricting the genus to heterobrochate forms; this emendation will not be used because it excludes homobrochate species of *Bombacacidites*, for example *Bombacacidites nanobrochatus* Frederiksen 1983. *Intratriporepollenites* Pflug & Thomson in Thomson & Pflug 1953 is distinguished from *Bombacacidites* by being vestibulate (Nichols 2010).

Bombacacidites bombaxoides Couper 1960 sensu lato
Plate 3.7, figure 6; Plate 3.15, figure 1

Description: Brevitricolporate, micro-reticulate, equatorial diameter 27-(32)-36 μm . Exine 1-2 μm thick. Oblate, planaperturate, rounded subtriangular amb. Pores obscure, colpi short, gaping. Thickened colpi margins moderately well developed. Lumina greater than 0.5 μm and less than 1 μm in diameter at the apocolpium, gradually decreasing in size to <0.5 μm in diameter at the mesocolpium/grain edge. A single specimen observed in SEM (Plate 3.15, fig. 1) has often sinuous lumina.

Discussion: A broad species concept is used here, which includes specimens smaller than the range given by Couper (1960) of 41-44 μm equatorial diameter. *Bombacacidites bombaxoides* is distinguished from *Bombacacidites nacimientoensis* (Anderson 1960) Elsik 1968 by being more finely reticulate, with apocolpial lumina diameter <1 μm (Elsik 1968b; Frederiksen 1983), and is

distinguished from *B. nanobrochatus* by being more coarsely reticulate, with apocolpial brochi diameter $>0.5\ \mu\text{m}$ (Frederiksen 1983).

Occurrence: Ypresian; 52 specimens observed (0.3%). *Bombacacidites bombaxoides* is mainly known from the Cenozoic of New Zealand, Australia, and Antarctica, with scattered records from South America, North America, India, Europe, and Africa (Palynodata Inc. and White 2008).

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Bombacacidites brevis (Dueñas 1979) Muller et al. 1987

Plate 3.7, figures 2-3

Description: Brevitricolporate, micro-reticulate, equatorial diameter 23-(29)-37 μm . Exine ca. 1 μm thick, visibly columellate. Oblate, amb subcircular. Pores obscure, colpi short, gaping, incised ca. 3-5 μm deep in polar view. Thickened colpi margins moderately well developed. Lumina $<0.5\ \mu\text{m}$ in diameter, reticulum homobrochate.

Discussion: This species of *Bombacacidites* is distinguished by its small size, homobrochate reticulum, and circular amb.

Occurrence: Ypresian; 8 specimens observed ($<0.1\%$). *Bombacacidites brevis* has previously been identified exclusively from Eocene to Miocene strata in South America (Palynodata Inc. and White 2008).

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Ramírez-Arriaga, Prámparo, et al. (2014) gave the paleoecology of *Bombacacidites* as tropical deciduous forest.

Bombacacidites nacimientoensis (Anderson 1960) Elsik 1968

Plate 3.7, figures 7-8

Description: Brevitricolporate, reticulate, equatorial diameter 27-(33)-39 μm . Exine 1-2 μm thick. Oblate, planaperturate, rounded triangular amb. Pores obscure, colpi short, gaping. Thickened colpi margins moderately well developed. Lumina circular to irregularly rounded polygonal in shape, 1-3 μm in diameter at the apocolpium, gradually decreasing in size to $<0.5\ \mu\text{m}$ in diameter at the mesocolpium/grain edge.

Discussion: The original description for *Bombacacidites nacimientoensis* by Anderson (1960) did not state the size of the lumina, but Elsik (1968b) later provided a more detailed description, stating that the lumina size was 1-2 μm . Jaramillo and Dilcher (2001) included specimens with lumina up to 4 μm wide in *B. nacimientoensis*. *Bombacacidites bombaxoides* is similar, but more finely reticulate (Frederiksen 1983).

Occurrence: Ypresian; 37 specimens observed (0.2%). *Bombacacidites nacimientoensis* is a commonly identified species from the Paleogene Gulf of Mexico and North America (Palynodata Inc. and White 2008).

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Bombacacidites nanobrochatus Frederiksen 1983 sensu lato
Plate 3.7, figure 5

Description: Brevitricolporate, micro-reticulate, equatorial diameter 23-(29)-37 μm . Exine 0.5-1.5 μm thick. Oblate, planaperturate, rounded subtriangular amb. Pores obscure, colpi short, 2-3 μm wide, marginate. Lumina $<0.5 \mu\text{m}$ in diameter, homobrochate.

Discussion: A broad species concept is used here, which includes specimens larger than the size range given by Frederiksen (1983) of 18-30 μm . *Bombacacidites tilioides* Krutzsch 1970 is also finely reticulate, but is heterobrochate.

Occurrence: Ypresian; 16 specimens observed (0.1%). *Bombacacidites nanobrochatus* is known from the Paleogene of North America and the Miocene of Argentina (Palynodata Inc. and White 2008). Graham et al. (2000, p. 1532) describe a similar form, “*Bombacacidites* type 1,” from the Middle Eocene of Cuba, here considered conspecific with *B. nanobrochatus*.

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Bombacacidites sp. A
Plate 3.7, figure 1

Description: Brevitricolporate, reticulate, equatorial diameter 19-24 μm . Exine ca. 1 μm thick. Oblate, planaperturate, rounded subtriangular amb. Pores obscure, colpi short, marginate. Reticulum heterobrochate, lumina 1.0-1.5 μm in diameter at the apocolpium, gradually fining to $<0.5 \mu\text{m}$ in diameter at the mesocolpia. Lumina elliptical to rounded polygonal.

Discussion: This species is distinguished from other species of *Bombacacidites* in the IODP 364 assemblage by its small size and relatively coarse apocolpial reticulum. *Bombacacidites* sp. 2 of Frederiksen (1988, Plate 14, figs. 14-18) and *Bombacacidites* sp. of Ramírez-Arriaga, Prámparo, et al. (2014, fig. 3.23) are morphologically similar and may be conspecific.

Occurrence: Ypresian; 9 specimens observed (0.1%).

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Bombacacidites sp. B
Plate 3.7, figure 11

Description: Brevitricolporate, reticulate, equatorial diameter 45-56 μm . Nexine ca. 0.5 μm thick, sexine ca. 1-2 μm thick, columellate. Oblate, planaperturate, rounded subtriangular amb. Pores obscure, colpi short, marginate. Reticulum heterobrochate, lumina rounded polygonal in shape. Muri $<1 \mu\text{m}$ wide, lumina 3-8 μm in diameter at the apocolpia, fining to $<0.5 \mu\text{m}$ in diameter at the mesocolpia. An infragranulate texture is observable beneath the reticulum.

Discussion: *Bombacacidites* sp. B is easily distinguished by its large size and coarse reticulum.

Occurrence: Ypresian; 3 specimens observed ($<0.1\%$).

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Genus *Echitricolporites* van der Hammen 1956 ex Germeraad et al. 1968

Discussion: *Echitricolporites* includes echinate, tricolporate pollen grains. Despite the selection by Germeraad et al. (1968) of a fossil lectogenotype to validate the genus, Jansonius and Hills (1976) considered *Echitricolporites* a junior synonym of the modern genus *Baccharis* L.

Echitricolporites sp. A
Plate 3.9, figures 4-6

Description: Tricolporate, micro-echinate, equatorial diameter 17-(23)-28 μm . Exine ca. 1 μm thick, not visibly columellate. Oblate, amb subtriangular. Colpi not marginate, appearing as a thin slit. Pores lalongate, ca. 2x5 μm in equatorial view, occasionally vestibulate. Surface protrusions generally echinate, sometimes verrucate, ca. 0.5-1.0 μm tall.

Discussion: *Echitricolporites spinosus* van der Hammen 1956, the type species of the genus, is spherical, and much more coarsely echinate, with echinae 3-6 μm long (Germeraad et al. 1968). *Echitricolporites maristellae* Muller et al. 1987 is more robustly echinate, with a thicker exine, and highly costate pores.

Occurrence: Ypresian; 54 specimens observed (0.3%). FAD: 572.75 mbsf. 50.5-(51.34)-53.7 Ma.

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Ilexpollenites* Thiergart 1937 ex Potonié 1960

Discussion: *Ilexpollenites* is a form genus used for pollen similar to that produced by the modern genus *Ilex* L. (Caprifoliaceae). Modern *Ilex* pollen is tricolporate with poorly defined pores, and ornamented with conspicuous, generally free-standing, clavae and gemmae. These sculptural elements generally increase in size at the polar areas or intercolpia, although this is not a universal characteristic (Martin 1977). The generic description by Potonié (1960) restricts *Ilexpollenites* to forms in which the sculptural elements increase in size at the poles. However, fossil species of *Ilexpollenites* have been described which do not appear to have larger sculptural elements at the poles, for example several species described by McIntyre (1968). Also, although technically restricted to tricolporate types, *Ilexpollenites* grains may have obscure ora that are not clearly visible in light microscopy. *Ilexpollenites verrucatus* Pocknall & Mildenhall 1984, for example, was described as often lacking visible pores, and *Ilexpollenites clifdensis* McIntyre 1968 was described as tricolpate. A broad sense of *Ilexpollenites* is used in this study, which includes pollen with no significant size increase in sculptural elements towards the poles, as well as pollen with no visible ora.

Ilexpollenites cf. *I. verrucatus* Pocknall and Mildenhall 1984
Plate 3.9, figure 3

Description: Tricolporate or rarely tricolporoidate, clavate, gemmate, and/or verrucate, polar axis length 22-(25)-33 μm , equatorial diameter 14-(18)-25 μm , P/E ratio 1.15-(1.41)-1.67. Nexine 0.5-1.0 μm thick, sexine composed of usually free-standing clavae, gemmae, and/or verrucae, 0.5-1.5 μm in height. Colpi long, marginate. Pores usually prominent, occasionally

obscure, circular or slightly lalongate, ca. 3-5 μm in diameter. The exine does not exhibit a consistently observable tendency towards an increase in thickness at the poles.

Discussion: This species closely resembles *Ilexpollenites verrucatus*, although in *I. verrucatus* the exine is described as marginally thicker at the poles. A specimen identified as *Ilex* by Graham and Jarzen (1969) from the Oligocene of Puerto Rico is somewhat similar, but is more coarsely gemmate; also, the photographed grain is in polar view and possibly oblate, while *Gemmatricolporites* sp. A has been observed exclusively in equatorial view and is prolate.

Occurrence: Ypresian; 83 specimens observed (0.5%). The FAD of this species may be a useful regional biostratigraphic event. FAD: 582.78 mbsf. 50.5-(51.65)-53.7 Ma.

Botanical affinity: Eudicots, probably Aquifoliaceae.

Genus *Intratroporopollenites* Pflug & Thomson in Thomson & Pflug 1953 emend. Nichols 2010

Discussion: *Intratroporopollenites* includes tricolporate or tetracolporate, brevicolporate, vestibulate, annulate, oblate to peroblate pollen. The amb is circular to broadly rounded triangular, planaperturate in the triangular forms. The exine is tectate, superficially granulate, sometimes perforate or infrareticulate, and the size range is ca. 20-50 μm . Nichols (2010) provides an extensive discussion of the taxonomic nomenclature, concluding that the similar form genus *Tiliaepollenites* Potonié 1931 ex Potonié & Venitz 1934 is a junior synonym of the modern genus *Tilia* L.

Intratroporopollenites spp.

Plate 3.7, figures 9-10, 12

Description: Tricolporate, reticulate, equatorial diameter 20-(23)-26 μm . Exine 1-2 μm thick, visibly columellate. Oblate, amb subcircular to rounded triangular. Apertures short, vestibulate, the differentiation between pores and colpi sometimes ambiguous. A darkened area of thickened exine often surrounds the pores. Coarseness of reticulum variable, lumina <0.5 to ca. 2 μm in diameter, sometimes slightly heterobrochate. Reticulum usually appearing infrareticulate, in one specimen appearing supracreticulate (Plate 7, fig. 10).

Discussion: A range of morphologies have been grouped together here, which have not been described separately due to the low abundance of *Tiliaepollenites* spp. in the IODP 364 core. A single specimen (Plate 7, fig. 10) has a morphology transitional between *Tiliaepollenites* and *Bombacacidites*; it has been placed in *Tiliaepollenites* because the apertures appear marginally vestibulate. Some of these specimens resemble the “*Intratroporopollenites pseudinstructus* group” of Frederiksen (1988), and may be conspecific.

Occurrence: Ypresian; 12 specimens observed (0.1%). *Intratroporopollenites* is a common and widely distributed form genus in the Cenozoic (Palynodata Inc. and White 2008). Ramírez-Arriaga, Prámparo, et al. (2014, fig. 3.17) describe an “*Intratroporopollenites* sp.” which is similar to the IODP 364 specimens.

Botanical affinity: Probably Malvaceae, possibly a member of the former family Tiliaceae (Nichols 2010).

Paleoecology: Probably cloud forest. Ramírez-Arriaga, Prámparo, et al. (2014) gave the paleoecology of unspiciated *Intratroporopollenites* pollen as cloud forest.

Genus *Margocolporites* Ramanujam 1966 ex. Srivastava 1969 emend. Pocknall & Mildenhall 1984

Discussion: *Margocolporites* includes isopolar, oblate to sub-oblate, trimargocolporate pollen grains, with a reticulate, retipilate, scabrate, or psilate exine, and a psilate, granulate, or micro-reticulate margocolpus.

Margocolporites sp. A
Plate 3.8, figure 12

Description: Trimargocolporate, margocolpus faintly scabrate, remainder of exine micro-reticulate, equatorial diameter 32 μm . Exine ca. 1.0-1.5 μm thick, visibly columellate. Oblate, amb subcircular. Colpi long, widely gaping. Ora obscure. Lumina of reticulum ca. 0.5 μm in diameter.

Discussion: The single specimen of this type is quite similar to *Margocolporites vanwijhei* Germeraad et al. 1968, but the reticulum is finer, and the margocolpus is faintly scabrate. This specimen is also similar to a fossil Florida pollen form identified by Corbett (2004) as *Gleditsia* (Fabaceae) and by Jarzen et al. (2010) as *Margocolporites* sp., although Jarzen et al. (2010) described that form as more coarsely reticulate (lumina up to 8 μm in longest dimension).

Occurrence: Ypresian; one specimen observed (<0.1%).

Botanical affinity: Eudicots, probably the subfamily Caesalpinioideae (Fabaceae), based on the similarity to *Margocolporites vanwijhei*.

Paleoecology: Possibly lowland tropical forest, based on the similarity with *Margocolporites vanwijhei* Germeraad et al. 1968.

Margocolporites sp. B
Plate 3.8, figures 15-16

Description: Trimargocolporate, margocolpus psilate, remainder of exine micro-reticulate to reticulate, equatorial diameter 20-27 μm . Exine thickness 0.5-1.5 μm , visibly columellate outside of margocolpus. Oblate, amb subcircular to rounded subtriangular. Colpi gaping, deeply incised. Margocolpus 2-4 μm wide. Pore present, sometimes obscure, shape indeterminate in polar view. Reticulum with lumina usually 0.5-1.0 μm in diameter, occasionally slightly over 1 μm in diameter.

Discussion: *Margocolporites* sp. A is larger and more finely reticulate, *Margocolporites?* sp. C is rugulate, and *Margocolporites vanwijhei* is larger and more coarsely reticulate, with a baculate margocolpus.

Occurrence: Ypresian; 4 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Margocolporites? sp. C
Plate 3.8, figure 14

Description: Trimargocolporate, margocolpus scabrate, remainder of exine rugulate-striate, equatorial diameter 29 μm . Exine thickness ca. 1 μm . Exine not visibly columellate, the edges of

the grain appearing corrugated due to the rugulate sculpture. Oblate, amb rounded subtriangular. Colpi extend nearly full length of grain, with scabrate margocolpus and colpus membrane. Pores conspicuous, ca. 6-7 μm wide in polar view. Exine excluding margocolpus rugulate-striate, the raised ridges ca. 0.5 μm in diameter, anastomosing but roughly parallel to the polar axis.

Discussion: This species is distinguished by possessing a margocolpus and having a rugulate sculpture. The rugulate-striate sculpture technically falls outside of the emended description of *Margocolporites* given by Pocknall and Mildenhall (1984).

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Margocolporites vanwijhei Germeraad et al. 1968 sensu lato
Plate 3.8, figures 11, 13; Plate 3.14, figure 14

Description: Trimargocolporate, margocolpus baculate, remainder of exine reticulate, equatorial diameter 31-(35)-39 μm . Exine 1-3 μm thick, visibly columellate. Oblate, amb subcircular. Colpi widely gaping, deeply incised. Pores usually obscure, lolongate when visible (Plate 3.8, fig. 11). Reticulum with subcircular to rounded polygonal lumina, 1-4 μm in diameter, reticulum slightly finer at poles. Margocolpus indistinctly baculate in LM. In SEM, a psilate border ca. 1.5-2.0 μm wide between the coarse reticulum and the baculate margocolpus is visible, and the baculae are stacked perpendicularly to the grain surface (Plate 3.14, fig. 14b).

Discussion: A broad species concept is used here, which includes specimens falling outside the size ranges for *Margocolporites vanwijhei* given in the original description by Germeraad et al. (1968). The IODP 364 specimens are generally smaller than the protologue specimens; also, the pores in the protologue specimens were described as round, not lolongate. Ramírez-Arriaga, Prámparo, et al. (2014) describe a “*Margocolporites* aff. *vanwijhei*” from the Late Eocene-Early Oligocene of Puebla, Mexico, which is quite similar to the IODP 364 specimens, particularly in having lolongate pores.

Occurrence: Ypresian; 68 specimens observed (0.4%). Germeraad et al. (1968) gave the known range of *Margocolporites vanwijhei* in the Caribbean as Middle Eocene to present.

Margocolporites vanwijhei is fairly common and widely distributed in the Cenozoic (Palynodata Inc. and White 2008). These Ypresian specimens represent the earliest published occurrence of *M. vanwijhei* in Mexico, Central America, or the Caribbean (Graham 2010).

Botanical affinity: Eudicots, probably the subfamily Caesalpinioideae of the Fabaceae, possibly *Caesalpinia* L. (Germeraad et al. 1968).

Paleoecology: Possibly lowland tropical forest. Germeraad et al. (1968) noted that modern *Caesalpinia* species producing similar pollen inhabit both coastal habitats and dry thorn forests in Central America. Modern *Caesalpinia* is also found in shrubland/chaparral-woodland-savanna and lower to upper montane broad-leaved forests in Central America (Graham 2010). Ramírez-Arriaga, Prámparo, et al. (2014) classified their “*Margocolporites* aff. *vanwijhei*” pollen as tropical deciduous forest representatives. Correa-Metrio et al. (2011) grouped the Caesalpinioideae with tropical seasonal forest.

Genus *Psilatricolporites* van der Hammen 1956 ex van der Hammen & Wymstra 1964

Discussion: *Psilatricolporites* includes all psilate, tricolporate pollen. *Cupuliferoipollenites* Potonié 1951 ex Potonié 1960 is a form genus for tricolporate pollen that is psilate or faintly scabrate with a more or less faint infratexture, but *Cupuliferoipollenites* is reserved for pollen that is morphologically comparable to modern *Castanea* pollen (Jansonius and Hills 1976); also, although not stated in the original description, Jardine (2011) considered that *Cupuliferoipollenites* is restricted to small pollen grains.

Psilatricolporites sp. A

Plate 3.6, figure 8

Description: Tricolporate, psilate, polar axis length 32-42 μm , equatorial diameter 18-29 μm , P/E ratio 1.45-1.94. Exine 1-2 μm thick, not visibly columellate. Prolate, poles broadly rounded. Colpi long, thickened margins absent. Pores circular, lalongate, or lolongate, 3-6 μm in diameter, costae pori absent.

Discussion: *Psilatricolporites* sp. A is easily distinguished from most other tricolporate species by its large size and psilate sculpture. The shape of the pores is quite heterogenous, but not enough specimens have been observed to justify splitting this type.

Occurrence: Ypresian; 4 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Punctatricolporites* Kedves 2000 emend.

Emended description: Punctate, tricolporate pollen.

Discussion: As originally described by Kedves (2000), *Punctatricolporites* included punctate, tricolporate pollen grains which possess cavernae or fastigia. Because the genus name was formed using the artificial nomenclature system developed by van der Hammen (1954b, 1956) and Pierce (1961), the circumscription of *Punctatricolporites* is here broadened to follow their morphological classification.

Punctatricolporites sp. A

Plate 3.6, figure 11

Description: Tricolporate, punctate, polar axis length 37 μm , equatorial diameter 30 μm . Exine ca. 2 μm thick, visibly columellate. Prolate, poles moderately tapered. Colpi long, marginate. Pores conspicuous. Punctae <0.5 μm in diameter, more clearly visible in phase contrast.

Discussion: The single observed specimen of this type differs from the other species of *Punctatricolporites* described by Kedves (2000) in lacking cavernae/fastigia.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Retitricolporites* van der Hammen 1956 ex Van der Hammen & Wymstra 1964

Discussion: *Retitricolporites* includes all reticulate, tricolporate pollen grains. This wide circumscription is clearly in conflict with many other genera, and is best reserved for reticulate,

tricolporate pollen which can not be more narrowly placed in another existing genus. Jansonius and Hills (1976) considered *Retitricolporites* invalid, although van der Hammen and Wymstra (1964) argued that, if necessary, *Retitricolporites guianensis* Van der Hammen & Wymstra 1964 could be used as lectogenotype to validate the genus. Pollen arguably assignable to *Caprifoliipites* Wodehouse 1933, *Horniella* Traverse 1955, and/or *Rhoipites* Wodehouse 1933 have instead been placed in *Retitricolporites*. The reasoning for this decision is explained below.

Caprifoliipites as originally described included very small, ellipsoidal, coarsely reticulate, tricolporate pollen. The colpi are long and pointed, with conspicuous internally projecting furrow rims and pore rims. *Rhoipites* as originally described included finely reticulate, ellipsoidal, tricolporate pollen with long and pointed colpi. The furrow and pore thickenings are conspicuous and project deeply inwards. According to Nichols (2010), *Caprifoliipites* and *Rhoipites* are distinguished based on size and the coarseness of the reticulum, although these distinctions have not been quantitatively defined. The differentiation of *Caprifoliipites* and *Rhoipites* based on size has not been consistent in the literature. For example, *Caprifoliipites incertigrandis* Frederiksen 1980 has a polar axis length of 26-38 μm , *Caprifoliipites longus* Stanley 1965 has a polar axis length of 37-49 μm , *Rhoipites cryptoporus* Srivastava 1972 has a polar axis length of 27-36 μm , and *Rhoipites retiformis* Pocknall & Mildenhall 1984 has a polar axis length of 17-26 μm . Distinctions based on the coarseness of the reticulum are also inconsistent in the literature. For example, *Caprifoliipites longus* Stanley 1965 has lumina ca. 0.5 μm in diameter, *Caprifoliipites paleocenicus* Pocknall & Nichols 1996 has lumina ca. 1.0-1.5 μm in diameter, *Rhoipites capax* Frederiksen 1988 has lumina ca. 3-4 μm in diameter, and *Rhoipites guianensis* (van der Hammen & Wymstra 1964) Jaramillo & Dilcher 2001 has lumina ca. 4 μm in diameter.

Horniella is a similar form genus. As originally described, it included tricolporate pollen with long, wide colpi and transverse furrows (i.e., pores) that appear as lateral extensions of the colpi. The coarseness of the reticulum was not specified, but the muri were described as very high. According to Frederiksen (1983) and Jardine (2011), *Horniella* is distinguished from *Rhoipites* by having narrower or absent thickened margins, although this is not apparent from the original generic description by Traverse (1955); in fact, the type species, *Horniella clavaticosta* Traverse 1955, was described as having very prominent longitudinal costae. Finally, there is the issue that Traverse (1955) clearly intended for *Horniella* to be restricted to pollen with botanical affinity to the family Rutaceae.

Other form genus names have been proposed for reticulate, tricolporate pollen, which are arguably synonymous at least in part with *Rhoipites*, for example *Araliaceoipollenites* Potonié 1951 ex Potonié 1960, *Cistacearumpollenites* Nagy 1969, *Euphorbiacites* Sung & Leen in Sung et al. 1976, *Tricolporites* Cookson 1947 emend. Stover & Partridge 1973, and *Tricolporopollenites* Pflug in Thomson & Pflug 1953 (Pocknall and Crosbie 1982; Nichols 2010). Due to the uncertainties about differentiating these genera, reticulate, tricolporate pollen which can not be more narrowly placed in another form genus have been placed in *Retitricolporites*.

Retitricolporites sp. A
Plate 3.8, figures 1-2

Description: Tricolporate, micro-reticulate to reticulate, polar axis length 23-(30)-40 μm , equatorial diameter 14-(19)-28 μm , P/E ratio 1.15-(1.61)-2.36 (25 specimens measured). Exine 0.5-2.0 μm thick, visibly columellate. Prolate, polar ends of grain in equatorial view broadly

tapered to sharply pointed. Colpi extending nearly to ends of grain, with weakly to strongly developed thickened margins. Pore shape often difficult to determine, pore observable mainly as an equatorial gap in the colpi margins. Pore shape and size variable. Lumina nearly perfectly circular in some specimens, in other specimens irregularly polygonal, sometimes exhibiting a weak tendency towards elongation parallel to the polar axis. Lumina 0.5-2.0 μm in diameter, maximum lumina diameter $<4\ \mu\text{m}$.

Discussion: This species is quite variable in exine thickness, P/E ratio, size of pores, degree of development of colpi margins, shape of lumina, and coarseness of reticulation. These morphological parameters appear to form a continuum. A detailed morphometric study would probably be necessary to determine if this morphotype could be meaningfully subdivided.

Occurrence: Ypresian; 1,997 specimens observed (12.3%).

Botanical affinity: Eudicots, lower affinity unknown.

Retitricolporites sp. B

Plate 3.8, figures 3-4

Description: Tricolporate, micro-reticulate to reticulate, equatorial diameter 17-26 μm . Exine thickness ca. 1.0-1.5 μm , visibly columellate. Oblate, amb rounded subtriangular. Colpi extending nearly full length of grain, almost syncolpate, weakly marginate. Pores roughly circular, 2-4 μm in diameter, marginate, sometimes marginally vestibulate, resulting in a beak-shaped appearance around the pores. Lumina irregularly rounded polygonal in shape, 0.5-1.0 μm in greatest dimension, occasionally exceeding 1 μm .

Discussion: *Retitricolporites* sp. A and *Retitricolporites* sp. D are prolate; *Retitricolporites* sp. C has shorter colpi which are not marginate.

Occurrence: Ypresian; 9 specimens observed (0.1%).

Botanical affinity: Eudicots, lower classification unknown.

Retitricolporites sp. C

Plate 3.8, figure 6

Description: Tricolporate or tricolporoidate, micro-reticulate, approximately spherical, diameter 21-(27)-34 μm . Exine thickness 0.5-1.5 μm , visibly columellate. Spherical to oblate, amb subcircular. Colpi shallowly incised, short, margins absent. Pores often obscure, circular to lalongate, ca. 2-4 μm in diameter, often with thickened margins. Lumina 0.5-1.0 μm in diameter, circular to irregularly rounded polygonal in shape.

Discussion: *Retitricolporites* sp. B has longer colpi which are marginate.

Occurrence: Ypresian; 225 specimens observed (1.4%).

Botanical affinity: Eudicots, lower classification unknown.

Retitricolporites sp. D

Plate 3.8, figure 5

Description: Tricolporate, coarsely reticulate, polar axis length 34-46 μm , equatorial diameter 20-38 μm , P/E ratio 1.16-1.65. Exine 2-5 μm thick, visibly columellate. Prolate, ends of grain moderately to well tapered. Colpi long, deeply incised, with costae colpi; pores elliptical, circular to lalongate, diameter ca. 3-6 μm . Reticulum simplibaculate, muri 1-2 μm wide, lumina rounded

irregular polygonal or sinuous in shape, 2-5 μm in diameter, rarely up to 8 μm . Maximum lumina diameter $>4\ \mu\text{m}$.

Discussion: *Retitricolporites* sp. D is more coarsely reticulate than *Retitricolporites* sp. A. Aside from being tricolporate, this species closely resembles *Retitricolporites* sp. C.

Occurrence: Ypresian; 8 specimens observed ($<0.1\%$).

Botanical affinity: Eudicots, lower classification unknown.

Genus *Rhuspollenites* Thiele-Pfeiffer 1980

Discussion: *Rhuspollenites* includes tricolporate pollen with a striate-reticulate exine, pointed poles, and long equatorial colpi, resembling pollen from the modern genus *Rhus* L.

(Anacardiaceae). *Ailanthipites* Wodehouse 1933 as originally described is quite similar to *Rhuspollenites*. According to Nichols (2010), *Ailanthipites* is distinguished by being foveolate rather than reticulate, although in both genera the lumina are linearly arranged.

Rhuspollenites sp. A

Plate 3.8, figures 8-9

Description: Tricolporate or tricolporoidate, retistriate, polar axis length 24-(30)-43 μm , equatorial diameter 15-(19)-28 μm , P/E ratio 1.08-(1.55)-2.00. Exine thickness 0.5-1.5 μm , columellae usually obscure. Prolate. Colpi long, with variably developed margins. Pores obscure to conspicuous, 2-5 μm in diameter, circular to lalongate. Lumina $<0.5\ \mu\text{m}$ wide, elongated parallel to the polar axis, forming a retistriate sculpture. Muri approximately as wide as lumina.

Discussion: These specimens appear similar to pollen grains of *Ailanthipites berryi* Wodehouse 1933 photographed by Nichols (2010, Plate 16, figs. 7-10), although the sculpture of *A. berryi* was described as foveolate. *Rhuspollenites carbogena* (Traverse 1955) Traverse 1994 was described as having colpi which are ca. 2/3 the length of the grain and of nearly constant width, as well as having lalongate pores which form a "...distinct Latin cross" with the colpi (Traverse 1955, p. 56). The *Rhuspollenites* specimens in this study do not strongly or consistently exhibit either described feature. Ramírez-Arriaga et al. (2017) provide photographs but no descriptions of *Rhuspollenites* specimens with affinity to the Anacardiaceae which appear generally similar to *Ailanthipites* sp. A.

Occurrence: Ypresian; 220 specimens observed (1.4%).

Botanical affinity: Eudicots, possibly Anacardiaceae.

Genus *Rugutricolporites* González Guzmán 1967

Discussion: *Rugutricolporites* includes rugulate, tricolporate pollen grains.

Rugutricolporites aff. *R. felix* González Guzmán 1967

Plate 3.9, figure 2

Description: Tricolporate to tricolporoidate, rugulate, polar axis length 26-(30)-35 μm , equatorial diameter 14-(19)-24 μm , P/E ratio 1.42-(1.60)-1.86. Exine 0.5-1.5 μm thick, usually thicker at poles than equator. Not visibly columellate, grain outline crenate. Prolate. Colpi long,

with weakly to moderately developed thickened margins. Pores mainly visible as equatorial gaps in the colpi margins, often obscure, shape variable, roughly circular. Rugulae about 0.5 µm wide, anastomosing, with only a slight tendency toward alignment parallel to the polar axis.

Discussion: This type is quite similar to *Rugutricolporites felix*, which differs from *Rugutricolporites* aff. *R. felix* mainly in being more coarsely rugulate (rugulae width ca. 1 µm). Also, these grains are on average smaller than the size range given for *R. felix* (35-50 µm).

Occurrence: Ypresian; 40 specimens observed (0.2%).

Botanical affinity: Eudicots, lower affinity unknown.

Rugutricolporites sp. A

Plate 3.9, figure 1

Description: Tricolporate, rugulate-striate, equatorial diameter 28-36 µm. Exine 0.5-1.5 µm thick, not visibly columellate. Oblate, amb subtriangular, sides slightly convex. Pores annulate, slightly vestibulate, ca. 1-4 µm wide in polar view. Colpi narrow, shallowly incised, extending nearly full length of grain, almost syncolporate. Rugulae roughly parallel to polar axis, sinuous, anastomosing, <0.5 µm wide. The rugulae are barely observable in brightfield microscopy, but slightly more visible in phase contrast.

Discussion: An alternative generic assignment for this species would be to *Striatricolporites* Leidelmeyer 1966, if the sculptural elements are considered striae rather than rugulae.

Occurrence: Ypresian; 4 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Scabratricolporites* Roche & Schuler 1976

Discussion: *Scabratricolporites* includes all scabrate, tricolporate grains. *Siltaria* Traverse 1955 is partly synonymous with *Scabratricolporites*, but according to the original definition is restricted to scabrate tricolporate pollen with long colpi, large lalongate pores, and features intermediate between *Quercus* and *Castanea* pollen. None of the species in this study fit this strict definition of *Siltaria*, although Frederiksen (1980b, p. 52) defined *Siltaria* broadly, including tricolporate grains with a sculpture that is "...too fine for one to say that the grains are either reticulate or granulate." *Araliaceoipollenites* Potonié 1951 ex Potonié 1960 is similar in being granulate, a term that is partly synonymous with scabrate (Punt et al. 2007). The generic description of *Araliaceoipollenites* by Potonié (1960) translated by Jansonius and Hills (1976) states that at the poles the exoexine is thicker than the intexine, but they are equally thick at the equator. The outline is crenate. The pores are internally lalongate and externally more or less circular.

Scabratricolporites sp. A

Plate 3.6, figure 9

Description: Tricolporate, scabrate to granulate, polar axis length 21-(29)-46 µm, equatorial diameter 9-(17)-29 µm, P/E ratio 1.21-(1.77)-2.33. Exine 0.5-2.0 µm thick, usually visibly columellate. Prolate. Colpi extend nearly full length of grain, with weakly to strongly developed thickened margins. Pores barely visible to conspicuous, circular to lalongate, 1-4 µm in diameter. Sculpture indistinctly scabrate to clearly granulate.

Discussion: This heterogenous form species accommodates prolate, tricolporate grains which have surface sculpture ranging from indistinctly scabrate to clearly granulate.

Occurrence: Ypresian; 378 specimens observed (2.3%).

Botanical affinity: Eudicots, lower classification unknown.

Scabratricolporites sp. B

Plate 3.6, figure 10

Description: Tricolporate, scabrate, equatorial diameter 20-31 μm . Exine 1.0-1.5 μm thick, columellae present but somewhat obscure. Oblate, amb rounded subtriangular, nearly subcircular. Colpi extend nearly full length of grain, with absent to weakly developed margins. Pores present, shape indeterminate.

Discussion: This species is distinguished from *Scabratricolporites* sp. A by being oblate.

Occurrence: Ypresian; 3 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Striatricolporites* Leidekmeyer 1966

Discussion: *Striatricolporites* includes all striate, tricolporate pollen grains.

Striatricolporites aff. *S. conspicuus* Muller 1968

Plate 8, figure 7

Description: Tricolporate, truly striate, polar axis length 28-(31)-35 μm , equatorial diameter 13-(18)-20 μm , P/E ratio 1.45-(1.79)-2.38. Exine thickness ca. 1 μm , not visibly columellate.

Prolate, ends of grain moderately to sharply tapered. Colpi long, moderately to deeply incised, sometimes with thickened margins. Pores usually indistinct, rarely prominent, circular to lalongate, 2-4 μm in diameter. Striae <0.5 μm wide, roughly parallel to polar axis, sinuous.

Discussion: This species is similar to *Striatricolporites conspicuus*, differing mainly in having less parallel striae. Also, although in the original description by Muller (1968), the striae are described only as less than 1 μm broad, the IODP 364 specimens do appear more coarsely reticulate than the holotype specimen of *S. conspicuus*. *Striatopollis catatumbus* (González Guzmán 1967) Takahashi & Jux 1989 is larger (49-56 μm in length) and has a thicker exine (ca. 3 μm). However, these specimens are probably conspecific with pollen identified as “*Striatricolporites cataumbus* [sic] González Guzmán” by Graham et al. (2000, p. 1531) from the Middle Eocene of Cuba. *Striatricolporites* aff. *S. conspicuus* is also similar to Cenozoic Central American fossil pollen grains identified as the modern genus *Crudia* (Fabaceae) by Graham (1988, 1989, 1991, 1999), although the IODP 364 specimens are generally more prolate and smaller, with a thinner exine and finer striae. Finally, *Striatricolporites* aff. *S. conspicuus* is similar to and probably conspecific with an unnamed species of *Striatricolporites* described by Ramírez-Arriaga, Prámparo, et al. (2014, fig. 5.8-9). *Striatricolporites* aff. *S. conspicuus* is quite similar to *Striatopollis grahamii* sp. nov., differing only in possessing visible pores.

Occurrence: Ypresian; 279 specimens observed (1.7%).

Botanical Affinity: Eudicots, probably Fabaceae, possibly *Crudia*.

Paleoecology: The similarity of these specimens to modern *Crudia* pollen, a genus today found primarily in tropical lowlands and riverine environments of the Amazon (Graham 1991, 2003),

suggests that *S. conspicuus* may be indicative of tropical lowland environments. Additionally, Ramírez-Arriaga, Prámparo, et al. (2014) describe similar pollen grains of *Striatricolporites* as indicating a tropical deciduous forest paleoenvironment.

Striatricolporites sp. A
Plate 3.8, figure 10

Description: Tricolporate, striate, polar axis length 34-36 μm , equatorial diameter 20-28 μm , P/E ratio 1.29-1.70. Exine ca. 2-3 μm thick, sexine thicker than nexine, visibly columellate. Colpi extend nearly to ends of grain, with well developed thickened margins. Pores present but somewhat obscure, visible as a gap in the colpi margins. The striate pattern is quite distinctive, the striae ca. 0.5-0.7 μm wide, resembling long strands of spaghetti, roughly parallel with the polar axis, sinuous, the individual striae appearing virtually continuous throughout the length of the grain. An infragranulate pattern is observable below the striate sculpture, formed by the bases of the columellae.

Discussion: This species is distinguished from *Striatricolporites conspicuus* by its distinctive striae, its infragranulate pattern, and its thicker exine. *Striatricolporites minor* Muller 1968 is somewhat similar in having an infragranulate pattern beneath the striate sculpture, but has a thinner (<1 μm thick) exine and indistinctly bordered colpi. Additionally, the distinctive spaghetti-like striae are not visible.

Occurrence: Ypresian; 2 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Syncolporites* van der Hammen 1954

Discussion: *Syncolporites* includes all syncolporate pollen; parasyncolporate pollen have also been included in this genus, for example *Syncolporites minimus* Leffingwell 1970. *Syncolporites* was published in the same year as two other commonly identified form genera for syncolporate pollen, *Cupanieidites* Cookson & Pike 1954 ex Potonié 1960 and *Myrtaceidites* Cookson & Pike 1954 ex Potonié 1960. *Syncolporites* is arguably overly broad; the genus can be functionally split by the creation of new genera using the artificial nomenclature system of van der Hammen (1954, 1956), for example *Retisyncolporites* González Guzmán 1967. However, for the purposes of this study it was considered preferable to use the more inclusive *Syncolporites*.

As originally described, *Cupanieidites* was distinguished from *Myrtaceidites* by being clearly reticulate. Stover and Partridge (1973) considered that *Cupanieidites* and *Duplopollis* Krutzsch 1959 should be synonymized. Later emendations of *Cupanieidites* and *Myrtaceidites* complicate the taxonomy. Krutzsch (1969) emended *Cupanieidites* substantially, allowing pollen with non-reticulate sculpture to be included, and excluding pollen with well developed polar islands. Chmura (1973) also emended *Cupanieidites*; this emendation is rejected as overly broad, because non-syncolporate pollen are included in the generic diagnosis. Potonié (1960) emended *Myrtaceidites*, without substantially altering the original definition of the genus; both definitions specify that the amb should be triangular, not circular or subcircular, and that the sculpture should never be clearly reticulate. Many but not all of the species in these syncolporate form genera probably have a botanical affinity with the Myrtaceae and the Sapindaceae, roughly corresponding to the form genera *Myrtaceidites* and *Cupanieidites*, respectively (Thornhill and Macphail 2012).

Syncolporites sp. A
Plate 3.6, figure 12

Description: Parasyncolporate, faintly scabrate, equatorial diameter 23 μm . Exine ca. 1.5 μm thick, columellae barely visible. Oblate, amb subcircular. Colpi bifurcate near poles to form a triangular polar island ca. 5 μm across. Pores ca. 4-5 μm wide, shape indeterminate.

Discussion: An alternative generic assignment for these specimens is *Myrtaceidites*; however, *Myrtaceidites* is triangular to subtriangular in polar view (Thornhill and Macphail 2012).

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, possibly Myrtaceae.

Syncolporites? sp. B
Plate 3.6, figure 13

Description: Tricolporoidate, ambiguously syncolporate, micro-reticulate, equatorial diameter 21 μm . Exine ca. 1 μm thick, visibly columellate. Oblate, amb subtriangular, sides slightly convex. Colpi shallowly incised, visibly mainly as a darkened streak, ambiguously syncolpate. Ora present, shape indeterminate. Reticulum with lumina $\leq 0.5 \mu\text{m}$ in diameter.

Discussion: The assignment of this single specimen to *Syncolporites* is somewhat tentative due to the weakly developed colpi. *Syncolporites* sp. A is scabrate, and clearly parasyncolporate.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

3.4.5. Stephanocolpate Pollen (Plate 9)

Genus *Clavastephanocolpites* van der Hammen & Wymstra 1964

Discussion: *Clavastephanocolpites* includes clavate, stephanocolpate pollen.

Clavastephanocolpites sp. A
Plate 3.9, figures 13-14

Description: Stephanocolpate, clavate to baculate, diameter 25-(32)-40 μm . Nexine usually $\leq 1 \mu\text{m}$ thick, sexine composed of free-standing clavae, or occasionally baculae, 0.5-2.0 μm long. Oblate, amb subcircular. Pollen usually 5-colpate, occasionally 4-colpate or 6-colpate. Colpi moderately incised, margins absent. In one specimen (Plate 3.9, fig. 13) the surface sculpture has a croton pattern.

Discussion: *Clavastephanocolpites crotonoides* van der Hammen & Wymstra 1964 differs from this type by possessing a thicker exine (4 μm), shorter colpi, and costae colpi. Also, only 6-colpate specimens are mentioned in the original description for *C. crotonoides*, and the croton pattern is a diagnostic character. *Gemmastephanocolpites gemmeus* van der Hammen & Garcia 1966 is similar to *Clavastephanocolpites* sp. A, but the elements are composed of gemmae rather than clavae or baculae. A single specimen with a visible croton pattern has not been speciated separately because it otherwise closely resembles the common morphotype.

Occurrence: Ypresian; 27 specimens observed (0.2%).

Botanical affinity: Eudicots, lower affinity uncertain. The croton pattern found in one specimen of this species is also found in modern pollen from the families Buxaceae, Callitrichaceae, Euphorbiaceae, Icacinaceae, Orobanchaceae, and Thymelaeaceae (de Souza et al. 2016). The majority of specimens lacking a visible croton pattern are also quite similar to a 5-colpate, densely gemmate specimen of *Bauhinia tomentosa* L. (Fabaceae) imaged by Banks and Lewis (2018, fig. 4A).

Genus *Psilastephanocolpites* Leidekmeyer 1966

Discussion: *Psilastephanocolpites* includes psilate, stephanocolpate pollen.

Psilastephanocolpites sp. A
Plate 3.9, figure 11

Description: Stephanocolpate, psilate, equatorial diameter 21-24 μm . Exine 1-2 μm thick, columellae faintly visible. Oblate, amb subcircular. 4-colpate, colpi deeply incised, with ragged edges, margins absent.

Discussion: These specimens are probably conspecific with *Psilatricolpites* sp. A, but are identified separately because they fall outside the generic circumscription of *Psilatricolpites*.

Occurrence: Ypresian; 2 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Polygalaceae? type A
Plate 3.9, figures 9-10

Description: Stephanocolpate or stephanocolporoidate, punctate, polar axis length 25-(32)-37 μm , equatorial diameter 20-(27)-32 μm . Exine ca. 1 μm thick, not visibly columellate. Suboblate to prolate, pollen usually observed in equatorial view. Approximately 10-14 colpi extend nearly the full length of the grain, forming thin slits, 2-3 μm wide. Colpi margins absent. Pores not clearly visible. Punctae <0.5 μm in diameter are scattered evenly but somewhat irregularly across the surface.

Discussion: Polygalaceae? type A is easily distinguished from other stephanocolpate pollen in the assemblage by its punctate sculpture.

Occurrence: Ypresian; 30 specimens observed (0.2%). The FAD of this species may be a useful regional biostratigraphic event. FAD: 569.50 mbsf. 50.2-(50.47)-50.5 Ma.

Botanical affinity: Eudicots, possibly Polygalaceae. Kapp et al. (2000) note that the pores in *Polygala* L. pollen may be obscure, and it is possible that *Punctastephanocolpites polygaloides* gen. et sp. nov. is stephanocolporoidate rather than stephanocolpate. Punctate sculpture is present in the modern pollen of several genera in the Polygalaceae (Banks et al. 2008).

Genus *Retistephanocolpites* Leidekmeyer 1966

Discussion: *Retistephanocolpites* includes all reticulate, stephanocolpate pollen. According to Leidekmeyer (1966), *Stephanocolpites* van der Hammen 1954 is distinguished from *Retistephanocolpites* by possessing equatorial costae, but this appears to be contradicted by the

generic description of *Stephanocolpites* given in van der Hammen (1956), which, as the name implies, includes all pollen with more than three meridional colpi.

Retistephanocolpites sp. A
Plate 3.9, figure 12

Description: Stephanocolpate, micro-reticulate, equatorial diameter 24 μm . Exine ca. 1.5 μm thick, columellae barely visible. Oblate, amb subcircular. Colpi extending majority of grain length, moderately incised, margins absent, edges of colpi slightly ragged. Micro-reticulate, the lumina approximately circular, ca. 0.5 μm in diameter.

Discussion: The type species of the genus, *Retistephanocolpites angeli* Leidekmeyer 1966, is larger and more coarsely reticulate.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

3.4.6. Stephanocolporate Pollen (Plate 10)

Genus *Psilastephanocolporites* Leidekmeyer 1966

Discussion: *Psilastephanocolporites* includes all psilate, stephanocolporate grains.

Psilastephanocolporites hammenii sp. nov.
Plate 3.10, figures 1-4

Selected synonymy:

Psilastephanocolporites "cedrelloides" Jaramillo et al. 2014, figs. 262, 263

Holotype: The specimen in Plate 3.10, fig. 2 (597.10 mbsf, slide 1, EFS P38/1).

Repository: CENEX, LSU, Baton Rouge, Louisiana, USA.

Type locality: IODP 364 Site M0077, Chicxulub impact crater, Mexico.

Derivation of name: The specific name is in honor of Dr. Thomas van der Hammen. His system of pollen and spore nomenclature (e.g., van der Hammen 1954b, 1956) has been used to construct several genera used in this study, including *Psilastephanocolporites*. The informal name given by Jaramillo et al. (2014) for this species has not been used, in case the botanical affinity is not with the modern genus *Cedrela* Browne (Meliaceae).

Description: Tetracolporate, psilate, faintly scabrate, to punctate, polar axis length 22-(31)-42 μm , equatorial diameter 18-(23)-32 μm , P/E ratio 1.15-(1.34)-1.58 (20 specimens measured). Exine ca. 1-2 μm thick, not visibly columellate. Prolate, poles broadly rounded. Colpi variable in length, shallowly incised, margins absent. Pores prominent, circular to lalongate, with moderately thickened costae pori, diameter or major axis length ca. 3-8 μm .

Discussion: The IODP 364 specimens are considered conspecific with *Psilastephanocolporites "cedrelloides"* from the Miocene of Panama, although the IODP 364 are exclusively tetracolporate, while the Panama specimens are tetracolporate or 5-colporate (Carlos Jaramillo, personal communication, October 31, 2019). Similar tetracolporate pollen types from the Late Oligocene-Early Miocene of Chiapas, Mexico were identified by Graham (1999) as *Cedrela*. If considered useful in the future, tetracolporate and 5-colporate specimens could be identified separately as subspecies of *Psilastephanocolporites hammenii* sp. nov. Specimens with scabrate

or punctate sculpture, but otherwise similar to the psilate types, have been included within *Psilastephanocolporites hammenii* sp. nov., using a loose interpretation of the generic circumscription.

Occurrence: Ypresian; 141 specimens observed (0.9%). The modern genus *Cedrela* is found in Mexico, Central America, some islands in the Caribbean, and northern South America. Fossil and genetic evidence indicates *Cedrela* originated in North America in the early Paleogene and spread to South America in the Oligocene or early Miocene (Muellner et al. 2010).

Botanical affinity: Meliaceae, probably *Cedrela* (Graham 1999; Jaramillo et al. 2014).

Paleoecology: Probably lowland tropical forest. The two most common modern species of *Cedrela* in Mexico, *Cedrela odorata* L. and *Cedrela angustifolia* Sessé & Moc. ex C.DC., both grow at low to moderate elevations, and mostly in tropical moist and premontane wet forests (Graham 1999).

Stephanocolporate type A

Plate 3.10, figures 5-7; Plate 3.15, figure 4

Description: Tricolporate or stephanocolporate (3 to 6-colporate), verrucate and echinate, polar axis length 41-(50)-57 μm , equatorial diameter 13-(21)-28 μm , P/E ratio 1.51-(2.04)-3.98. Exine 1.5-2.5 μm thick. Shape prolate, polar extremities inflated. Colpi extend nearly full length of grain, thickened colpi margins well developed. Pores usually prominent, circular to lolongate, 2-4 μm in diameter. The positive sculptural elements are 0.5-1.0 μm in height, and appear verrucate to conate/echinate in light microscopy. In SEM the protrusions are broadly conical with blunt tips (i.e., echinate) or verrucate. Small punctae are also visible in SEM, sometimes approaching a micro-reticulate sculpture. The bulbous polar ends of the grain appear scabrate or perhaps baculate in light microscopy. In SEM, the polar ends are more clearly visible as ridges or baculae which form an irregular reticulum.

Discussion: This taxon bears some resemblance to the genera *Bulbopollis* Potonié 1968 emend. Elsik 1974 and *Chlonovaia* Elsik 1975 in possessing bulbous protrusions at the polar ends of the grain. However, *Bulbopollis* has more prominent bulbs, with plurifurcate anastomosing bacula or columellae, and *Chlonovaia* was described as colpate, not colporate (Jansonius and Hills 1976).

Occurrence: Ypresian; 16 specimens observed (0.1%). The FAD of Stephanocolporate type A in the Ypresian may be a useful biostratigraphic event, although there is some uncertainty due to the rarity of the species. FAD: 572.75 mbsf. 50.5-(50.74)-53.7 Ma.

Botanical affinity: Eudicots, lower affinity unknown.

3.4.7. Monoporate Pollen (Plate 10)

Genus *Milfordia* Erdtman 1960 emend. Partridge in Stover and Partridge 1973

Discussion: *Milfordia* includes monoporate pollen with a distinctly punctate or foveolate exine. *Monulcipollenites* Fairchild in Stover et al. 1966 and *Restioniidites* Elsik 1968 are junior synonyms of *Milfordia* as emended (Stover and Partridge 1973).

Milfordia hungarica (Kedves 1965) Krutzsch & Vanhoorne 1970
Plate 3.10, figure 9

Description: Monoporate, clearly punctate, diameter 31-(34)-37 μm . Exine ca. 1 μm thick, not visibly columellate. Oblate, amb subcircular. Pore 3-6 μm in diameter, with weakly to moderately thickened annulus 1-2 μm wide surrounding pore. Exine covered in circular punctae <0.5 μm in diameter, but clearly visible in light microscopy.

Discussion: *Milfordia minima* is distinguished from *Milfordia hungarica* (Kedves 1965) Krutzsch & Vanhoorne 1970 purely on the basis of size; *M. minima* is less than 30 μm in diameter. Frederiksen (1983) considered that *Milfordia geiseltalensis* Krutzsch 1970 might be synonymous with *M. hungarica* due to the lack of any significant morphological differences between the two species. The differentiation between *M. hungarica* and *M. minima* was justified by Frederiksen (1983) on the basis that, in the Gulf and Atlantic Coastal Plains, *M. minima* has a known range from the lower Paleocene to the lower Oligocene, while *M. hungarica* has only been observed in the Middle Eocene.

Occurrence: Ypresian; 73 specimens observed (0.4%). *Milfordia hungarica* is a globally distributed species in the Cenozoic (Palynodata Inc. and White 2008), although Central American and Caribbean occurrences of this species are lacking (Graham 2010). The occurrence of *M. hungarica* in Ypresian strata in this core represents a significant downward range extension of this species in Central America relative to the northern Gulf of Mexico. FAD: 597.10 mbsf. 50.5-(52.95)-53.7 Ma.

Botanical affinity: Probably Restionaceae. Frederiksen (1983) considered that the botanical affinity of this genus was possibly with the Restionaceae or *Joinvillea* (Joinvilleaceae). Akkiraz et al. (2008) considered that *Milfordia* belongs to the Restionaceae.

Paleoecology: Probably estuarine. Frederiksen (1985) provides a detailed discussion of the paleoenvironmental preferences of *Milfordia*, which are noted as wet environments; it is often abundantly found in brackish and coastal-plain environments, although some modern species of the Restionaceae can be found in upland environments. Akkiraz et al. (2008) consider that *Milfordia hungarica* indicates back-mangrove paleoenvironments.

Milfordia minima Krutzsch 1970
Plate 3.10, figure 10

Description: Monoporate, punctate, diameter 24-(27)-29 μm . Exine ca. 1 μm thick, not visibly columellate. Oblate, amb subcircular. Pore 4-7 μm in diameter, with weakly to moderately thickened annulus ca. 1-2 μm wide surrounding pore. Exine covered in circular punctae <0.5 μm in diameter, but clearly visible in light microscopy.

Discussion: *Milfordia minima* is distinguished from the otherwise similar *M. hungarica* by being less than 30 μm in diameter (Frederiksen 1983).

Occurrence: Ypresian; 553 specimens observed (3.4%). *Milfordia minima* is a common and widely distributed species in the Cenozoic; however, Central and South American occurrences are lacking (Palynodata Inc. and White 2008), except for a Paleogene occurrence from the Central Andes (Horton et al. 2001).

Botanical affinity: Probably Restionaceae.

Paleoecology: Probably estuarine.

Genus *Monoporopollenites* Meyer 1956

Discussion: *Monoporopollenites* as originally described by Meyer (1956) included all monoporate pollen. Potonié (1960) emended the genus, restricting it to psilate, monoporate pollen. Multiple other form genera for monoporate pollen exist. *Graminidites* Cookson 1947 ex Potonié 1960 emend. Krutzsch 1970 is another commonly used form genus. As emended by Krutzsch (1970), *Graminidites* includes all monoporate pollen with psilate sculpture or finely scabrate sculpture. *Monoporopollenites* and *Graminidites* are arguably synonymous; more detailed discussion of the taxonomy can be found in Jansonius and Hills (1976, card 5383) and Srivastava (2011). *Monoporopollenites* is interpreted here to include psilate, scabrate, or faintly punctate (i.e., micropitted) monoporate pollen, following Jaramillo and Dilcher (2001).

Monoporopollenites annulatus (van der Hammen 1954) Jaramillo & Dilcher 2001
Plate 3.10, figure 8

Description: Monoporate, psilate, faintly scabrate, or faintly punctate, diameter 24-(30)-36 μm . Exine $<0.5 \mu\text{m}$, not visibly columellate. Shape approximately spherical, usually folded. Pore 3-5 μm in diameter, weakly or strongly annulate, circular to elliptical.

Discussion: This species is quite similar to specimens of *Graminidites gramineoides* (Meyer 1956) Krutzsch 1970 described by Frederiksen (1980b) and Graham et al. (2000), particularly in being psilate, scabrate, or faintly punctate. Jaramillo and Dilcher (2001) identified similar monoporate pollen grains 25-40 μm in size, with psilate, scabrate, or punctate (i.e., micropitted) sculpture, as *Monoporopollenites annulatus*. Ramírez-Arriaga, Prámparo, et al. (2014) describe an unnamed species of *Monoporopollenites*, which they distinguish from *M. annulatus* on the basis of having scabrate rather than psilate sculpture. Those specimens are conspecific with *M. annulatus* as defined here.

Occurrence: Ypresian; 89 specimens observed (0.5%). Fossil pollen referable to the Poaceae may be found very rarely in the Cretaceous, is generally rare in the Paleocene, and becomes more common in the lower Eocene (Muller 1981).

Botanical affinity: Probably Poaceae (i.e., Gramineae) (Frederiksen 1980b), although Macphail and Hill (2002) cautioned that similar monoporate pollen with minute punctae can be produced by other families, including the Restionaceae.

Paleoecology: Possibly arid tropical scrub (Ramírez-Arriaga, Prámparo, et al. 2014), although Macphail and Hill (2002) state that in the Paleocene-Eocene the Poaceae initially occurred in regions dominated by evergreen wet forests in paratropical conditions. Correa-Metrio et al. (2011) did not find any definite association of modern Poaceae with any particular vegetation type, which may be a result of recent human disturbance. If the botanical affinity is with the Restionaceae rather than the Poaceae, this would indicate an estuarine habitat.

3.4.8 Triporate Pollen (Plate 10, Plate 11, Plate 12)

Betulaceae/Myricaceae type sensu Jardine (2011)
Plate 3.10, figures 12-13

Description: Triporate, scabrate, equatorial diameter 23-(26)-31 μm . Exine 1-2 μm thick, not visibly columellate. Oblate, amb subtriangular. Pores aspidate, ca. 3 μm wide in equatorial view.

Pores usually visibly atriate, although sometimes the atria are obscure. Sculpture faintly scabrate, possibly granulate.

Discussion: Pollen grains of this type are similar to pollen produced by plants of the families Betulaceae and Myricaceae. Often, pollen with this morphology is assigned to the form genera *Triporopollenites* Pflug & Thomson in Thomson & Pflug 1953 or *Triatriopollenites* Pflug in Thomson & Pflug 1953, which are distinguished by the presence or absence of an atrium. Jardine (2011) considered that recognizing the presence of an atrium consistently is difficult in light microscopy, so he grouped *Triporopollenites* and *Triatriopollenites* specimens with affinity to the Betulaceae and Myricaceae into a single informal taxon.

Occurrence: Ypresian; 47 specimens observed (0.3%).

Botanical affinity: Eudicots, probably Betulaceae or Myricaceae (Pocknall and Nichols 1996; Jardine 2011)

Betula? sp. A
Plate 3.10, figure 11

Description: Triporate, psilate to faintly scabrate, equatorial diameter 22-24 μm . Exine ca. 1 μm , not visibly columellate. Amb subcircular. Pores circular, annulate, annulus ca. 1-2 μm wide, pores ca. 3 μm in diameter.

Discussion: The two observed grains of this type are morphologically similar to modern *Betula nana* L. pollen, which may have a nearly perfectly circular amb, for example a pollen grain photographed by Karlsdóttir et al. (2008, fig. 1a). *Triatriopollenites* and *Trivestibulopollenites* do not have a subcircular amb. *Casuarinidites* Cookson and Pike 1964 is visibly columellate (Frederiksen 1978).

Occurrence: Danian-Ypresian; 2 specimens observed (<0.1%).

Botanical affinity: Probably Betulaceae, possibly *Betula* L.

Genus *Brosipollis* Krutzsch 1968

Discussion: *Brosipollis* is a form genus used for triporate or brevitricolporate grains with equatorially protruding pores, often with botanical affinity to the Burseraceae (e.g., Graham et al. 2000, Jardine 2011, Ramírez-Arriaga, Prámparo, et al. 2014). Jardine (2011) also included tetraporate forms in *Brosipollis*. The original description lists the sculpture types in *Brosipollis* as psilate, punctate, or striate, but the type species *Brosipollis salebrosus* (Pflug in Thomson & Pflug 1953) Krutzsch 1968 is intrarugulate, *Brosipollis solidus* Song 1996 is scabrate to finely granulate, and an unnamed species of *Brosipollis* described by Ramírez-Arriaga, Prámparo, et al. (2014) is reticulate-striate. The protruding pores may be either vestibulate or atriate, with prominent annuli. In polar view they may appear beak-shaped. *Corsinipollenites* Nakoman 1965 is similar in being triporate and strongly annulate, but in *Corsinipollenites* the pore structure is different, and the botanical affinity is with the Onagraceae (Jansonius and Hills 1976; Traverse 2007).

Brosipollis aff. *B. striata* Frederiksen 1988
Plate 3.12, figure 4

Description: Triporate, striate, equatorial diameter 19-(25)-28 μm . Exine 0.5-1.5 μm thick. Oblate, amb subspherical. Vestibulate, strongly annulate. Pores approximately circular, 3-4 μm in diameter. Coarse striae parallel to anastomosing, sometimes separating from the exine into hairlike strands, 0.5-1.0 μm wide.

Discussion: This type is similar to *B. striata*, but more coarsely striate; as originally described, the striae in *B. striata* are ca. 0.3 μm wide.

Occurrence: Ypresian; 46 specimens observed (0.3%).

Botanical affinity: Burseraceae, probably *Bursera* Jacq. ex L.

Paleoecology: Probably lowland tropical forest. Ramírez-Arriaga, Prámparo, et al. (2014) gave the affinity for *Brosipollis* spp. with affinity to *Bursera* as lowland tropical deciduous forest. The genus *Bursera* is common in both rainforests and tropical deciduous forests of modern Mexico (Rzedowski 2006). Correa-Metrio et al. (2011) assigned modern *Bursera* to tropical seasonal forest.

Brosipollis reticulatus sp. nov.
Plate 3.12, figures 5-6

Holotype: The specimen in Plate 12, fig. 6 (547.42 mbsf, slide 2, EFS L25/2).

Repository: CENEX, LSU, Baton Rouge, Louisiana, USA.

Type locality: IODP 364 Site M0077, Chicxulub impact crater, Mexico.

Derivation of name: The species name is in reference to the reticulate or striate-reticulate sculpture.

Description: Triporate, reticulate to reticulate-striate, equatorial diameter 24-(28)-32 μm . Exine 0.5-1.0 μm thick. Oblate, amb subtriangular to subcircular. Pores equatorial, circular, 3-6 μm in diameter, vestibulate, annulate, the annulae strongly protruding, in polar view beak-shaped. Sculpture irregularly reticulate to retistriate, the lumina <0.5 μm to ca. 1 μm in diameter, circular, elliptical, or rounded polygonal in shape. Striae 0.3-0.5 μm wide, simplicolumellate, the striae elongate, hairlike, often layered on top of each other, sometimes forming a partially striate pattern, but without any clear orientation relative to the polar axis.

Discussion: *Brosipollis reticulatus* sp. nov. is similar to other *Brosipollis* species observed in this study, differing mainly in its finely reticulate or reticulate-striate sculpture. A “*Brosipollis* sp.” described by Ramírez-Arriaga, Prámparo, et al. (2014, fig. 5.14-15) is also retistriate, but is tricolporate.

Occurrence: Ypresian; 10 specimens observed (0.1%)

Affinities: Burseraceae, probably *Bursera*. *Brosipollis reticulatus* is similar to the reticulate-striate triporate pollen of *Bursera simaruba* Sargent (Willard et al. 2004).

Paleoecology: Probably lowland tropical forest.

Brosipollis striata Frederiksen 1988
Plate 3.12, figures 2-3

Description: Triporate, striate, equatorial diameter 18-(23)-29 μm . Exine 1-2 μm thick, the striae forming ridges and valleys at the edge of the grain. Grains oblate to subspherical, amb

subtriangular. Vestibulate, strongly annulate. Pores more or less circular, diameter 2-4 μm . Fine striae parallel to anastomosing, $<0.5 \mu\text{m}$ wide.

Discussion: *Brosipollis* aff. *striata* is similar but more coarsely striate (striae $\geq 0.5 \mu\text{m}$ wide). *Brosipollis striatobrosus* (Kruttsch 1961) Kruttsch 1968 is also striate, but is tricolporate (Frederiksen 1988).

Occurrence: Ypresian; 124 specimens observed (0.8%). Graham et al. (2000) described a “*Brosipollis* cf. *B. striata*” from the Middle Eocene of Cuba, and Frederiksen (1988) described *B. striata* from the Eocene of Alabama. Elsik (1974) described similar pollen with affinity to *Bursera* from the Eocene of the Gulf Coastal Plain.

Botanical affinity: Burseraceae, probably *Bursera* (Frederiksen 1988).

Paleoecology: Probably lowland tropical forest.

Genus *Caryapollenites* Raatz 1937 ex Potonié 1960 emend. Kruttsch 1961

Discussion: *Caryapollenites* includes pollen grains referable to the Juglandaceae, resembling modern *Carya* pollen. *Caryapollenites* is triporate, with at least one pore in a subequatorial position. *Caryapollenites* has an area of thinned exine (i.e., solution-field) around the proximal polar area, which can be circular, triangular, or developed as a ring. A vestibulum is absent. The exine is usually finely granulate (Nichols and Ott 1978), but may also be psilate or scabrate. *Momipites* Wodehouse 1933 emend. Nichols 1973 is a similar form genus for fossil pollen with affinity to Juglandaceae, and is distinguished by having equatorial pores. *Subtriporopollenites* Thomson & Pflug 1953 emend. Kruttsch 1961 is distinguished by differences in exine structure and pore morphology, but perhaps most importantly by lacking an area of thinned exine (Jansonius and Hills 1976; Nichols and Ott 1978). *Platycaryapollenites* Nagy 1969 emend. Frederiksen & Christopher 1978 is a form genus for pollen resembling modern *Platycarya* pollen, and is distinguished from *Caryapollenites* by possessing pseudocolpi.

Caryapollenites veripites (Wilson & Webster 1946) Nichols & Ott 1978

Plate 3.11, figure 9

Description: Triporate, faintly granulate, diameter 27-30 μm . Exine 1-2 μm thick, not visibly columellate. Pores 2-3 μm in diameter, atria obscure in two specimens, barely visible in a third specimen. Oblate, rounded subtriangular amb. All three pores are clearly subequatorial. A circumpolar ring of thinned exine is faintly visible in phase contrast, but not clearly visible in transmitted light.

Discussion: *Caryapollenites veripites* is distinguished from other members of the genus by the circumpolar ring of thinned exine. *Caryapollenites inelegans* Nichols & Ott 1978 lacks this circumpolar ring, but is otherwise morphologically indistinguishable. The size range of these specimens matches well with the modal diameter of 29 μm for *C. veripites* given in Nichols and Ott (1978), who also noted that the atria are often obscure in polar view.

Occurrence: Ypresian; 1 specimen observed ($<0.1\%$). Two additional specimens were observed after quantitative counts were finished. *Caryapollenites veripites* has many occurrences in the Paleogene of North America, but Central and South American occurrences are lacking (Palynodata Inc. and White 2008).

Botanical affinity: Juglandaceae, probably *Carya* Nutt. (Nichols and Ott 1978).

Paleoecology: Probably montane forest. Ramírez-Arriaga, Prámparo, et al. (2014) described the paleoecology of an unnamed species of *Caryapollenites* as cloud forest. The modern range of *Carya* in Mexico is mainly restricted to mountainous and arid regions of northeastern Mexico (Manning 1949).

Genus *Corsinipollenites* Nakoman 1965

Discussion: The most obvious diagnostic feature of this triporate genus is its strongly annulate pores (Traverse 2007). *Bagelopollis* Carroll 1999 is similar to this genus, and in fact its type species, *B. verrucatus* (Frederiksen 1988) Carroll 1999, was originally placed in *Corsinipollenites*. *Bagelopollis* is distinguished by having pseudo-annuli that are elements of ectexinal ornamentation, rather than thickenings of the endexine as in *Corsinipollenites*. *Jussitriporites* Gonzalez 1967 is a junior synonym of *Corsinipollis* 1987 in references. *DMJllenites* according to Jaramillo and Dilcher (2001). Frederiksen (1983) discusses in detail possible synonymies with *Corsinipollenites*, for example *Onagraceapollis* Kedves & Adorján 1966 and *Onagracites* Martynova in Agranovskaya et al. 1960. *Brosipollis* is also triporate with strongly annulate pores, but the pore structure is different, often giving the pores a beak-shaped appearance. The botanical affinity is probably with the family Onagraceae, particularly if viscin threads are present on the grain (Frederiksen 1983; Zetter and Keri 1986; Pocknall and Jarzen 2009).

Corsinipollenites oculusnoctis (Thiergart 1940) Nakoman 1965

Plate 3.11, figure 15

Description: Triporate, psilate to faintly scabrate in light microscopy, equatorial diameter 43-54 µm. Exine 1-2 µm thick, not visibly columellate. Oblate, amb strongly triangular, sides of grain significantly convex, bulging. Pores 5-8 µm in diameter. Annuli strongly protruding, donut-shaped, labrum angle high (Frederiksen 1983). Viscin threads present in one specimen. Sculpture in SEM microscopy finely granulate.

Discussion: *Corsinipollenites parviangulus* Frederiksen 1983 is distinguished by having a lower labrum angle. *Corsinipollenites oculusnoctis* is similar to some informally named species identified by Ramírez-Arriaga, Prámparo, et al. (2014) with affinity to the modern genera *Epilobium* L. and *Ludwigia* L.

Occurrence: Ypresian; 2 specimens observed (<0.1%). One additional specimen in SEM was observed outside of the quantitative counts. *Corsinipollenites oculusnoctis* has a wide paleogeographic distribution in the Cenozoic (Palynodata Inc. and White 2008).

Botanical affinity: Onagraceae, possibly *Epilobium* or *Ludwigia* (Frederiksen 1983; Ramírez-Arriaga, Prámparo, et al. 2014).

Corsinipollenites parviangulus Frederiksen 1983 sensu lato

Plate 3.11, figure 13

Description: Triporate, psilate to faintly scabrate in light microscopy, equatorial diameter 33-(50)-69 µm. Exine 1-2 µm thick, not visibly columellate. Oblate, amb subtriangular. Pores 4-6 µm in diameter, prominently annulate, the annuli. Labrum angle low (Frederiksen 1983).

Sculpture in SEM granulate to irregularly rugulate. Viscin threads occasionally present, in SEM resembling coiled ropes.

Discussion: The presence of viscin threads in some specimens indicates a probable affinity with the Onagraceae. *Corsinipollenites psilatus* Jaramillo & Dilcher 2001 is smaller ($<40\text{ }\mu\text{m}$) than all but one of these specimens, and was not described as being scabrate or granulate.

Corsinipollenites scabratus Silva-Caminha et al. 2010 is more clearly scabrate and possesses verrucae. A broad species concept for *C. parviangulus* is used here, which includes specimens smaller than the size range of $42\text{--}72\text{ }\mu\text{m}$ given in the original description. Ramírez-Arriaga, Reyes-Salas, et al. (2014) described several species of *Corsinipollenites* informally identified by number, but gave no differential diagnosis with previously described species of *Corsinipollenites*. The species they listed with affinity to *Hauya* DC. appear most similar to *Corsinipollenites parviangulus*.

Occurrence: Ypresian; 8 specimens observed ($<0.1\%$). Although it appears that only Frederiksen (1983, 1988, 1989) has published occurrences of *C. parviangulus*, the genus *Corsinipollenites* has a wide paleogeographic distribution in the Cenozoic (Palynodata Inc. and White 2008). Some species described by Ramírez-Arriaga, Reyes-Salas, et al. (2014) may be conspecific with *C. parviangulus*, and similar grains with affinity to *Hauya* have been identified from the Oligocene of Puerto Rico (Graham and Jarzen 1969).

Botanical affinity: Onagraceae, possibly *Hauya* or *Circaea* Tourn ex. L. (Frederiksen 1983).

Paleoecology: Possibly montane forest. Modern *Hauya* pollen is today found in moist middle elevation vegetation, below the pine belt and above the drier tropical deciduous vegetation, in southern Mexico and Central America (Graham and Jarzen 1969).

Genus *Cranwellipollis* Martin & Harris 1974 emend. Dettmann & Jarzen 1996

Discussion: Martin and Harris (1974) emended *Proteacidites* Couper 1953, restricting its circumscription, and created a new genus, *Cranwellipollis*, which includes some species originally assigned to *Proteacidites*. Dettmann and Jarzen (1996) later emended *Cranwellipollis* to exclude forms with a differentially sculptured exine and forms with a nexine solution at the pore margins. As emended, *Cranwellipollis* includes triporate oblate pollen grains with triangular to subcircular ambis and simple pores. The columellate exine is undifferentiated between the apoporal and mesoporal regions, and is either uniform in thickness or gradually thinning towards the pore margins. The sculpture is pilate, granulate, verrucate, echinate, rugulate, or reticulate according to Dettmann and Jarzen (1996). In *Lewalanipollis* Dettmann & Jarzen 1996, a zone of nexine solution is present at the apertural margins; in *Propylipollis* Martin & Harris 1974, the nexine is thickened at the pore margins; in *Proteacidites* Cookson 1950 ex Couper 1953, the exine thins near the pores and the sculpture varies between the apoporal and mesoporal regions (Dettmann & Jarzen 1996).

Cranwellipollis? sp. A

Plate 3.11, figure 14

Description: Triporate, punctate, equatorial diameter $27\text{--}29\text{ }\mu\text{m}$. Exine ca. $1\text{ }\mu\text{m}$ thick, approximately the same thickness throughout the grain, visibly columellate, sexine approximately as thick as nexine. Amb strongly triangular, more or less straight-sided. Pores $3\text{--}5\text{ }\mu\text{m}$ wide, pore shape indeterminate (all specimens seen in polar view), pore structure obscure. Exine densely

punctate, the punctae $<0.5\ \mu\text{m}$ in diameter. The sculpture does not vary between the apoporal and mesoporal regions.

Discussion: The generic identification is somewhat uncertain, because generic identification of proteaceous grains following Dettmann and Jarzen (1996) relies on fine details of pore morphology which were not clearly identifiable in the two observed specimens of this type. These specimens are similar to *Cranwellipollis subpalisadus* (Couper 1953) Martin & Harris 1974 in having punctate (i.e., finely pitted) to finely pitted-reticulate sculpture, but *C. subpalisadus* has a less strongly triangular amb. *Proteacidites rectus* Pocknall & Mildenhall 1984 is also punctate (i.e., perforate) with relatively straight sides, but the exine is thicker (1.5-3.5 μm) and the grains are larger (32-49 μm).

Occurrence: Ypresian; 2 specimens observed ($<0.1\%$).

Botanical affinity: Eudicots, possibly Proteaceae, although similar morphologies are found outside the Proteaceae (Dettmann and Jarzen 1996).

Genus *Cricotriporites* Leidekmeyer 1966

Discussion: *Cricotriporites* includes triporate pollen with a circular amb. The pores are circular to oval, with an annulus and/or costae pori. The sculpture is psilate to finely scabrate.

Annutriporites González Guzmán 1967 is a similar form genus for triporate pollen grains with a psilate-microverrucate exine, a circular amb, circular to elliptical pores, and a thickened annulus which is not conspicuously protruding. Microverrucate sculpture is a type of scabrate sculpture according to Punt et al. (2007), so both *Cricotriporites* and *Annutriporites* include psilate and scabrate types. *Annutriporites* is here considered a junior synonym of *Cricotriporites*.

Scabratriporites van Hoeken-Klinkenburg 1964 includes all triporate pollen with a scabrate exine. *Psilatetriporites* Hoorn 1993 includes all psilate, triporate pollen. Both *Psilatetriporites* and *Scabratriporites* have overlapping circumscriptions with *Cricotriporites*, but the three genera are not synonymous. *Thomsonipollis* Krutzsch 1960 is distinguished by its complex pores and exine structure (Jansonius and Hills 1976; Jardine 2011).

Cricotriporites sp. A

Plate 3.11, figures 1-2

Description: Triporate, psilate, equatorial diameter 18-(21)-25 μm . Exine ca. 0.5 μm thick, not visibly columellate. Oblate to subspherical, amb subcircular. Grains often folded. Pores 2-4 μm wide, roughly circular, annulus moderately developed to nearly absent.

Discussion: This species is quite similar to the informally named *Celtis tshudyi* group of Frederiksen (1988). Jardine (2011) further discussed the nomenclature and morphology of this group. Similar specimens have also been identified as *Thomsonipollis sabinetownensis* Elsik 1974 by Ramírez-Arriaga, Prámparo, et al. (2014). *Thomsonipollis sabinetownensis* was later transferred to *Celtis* L. by Frederiksen (1988) and lumped into his *Celtis tshudyi* group. This species has not been placed in *Thomsonipollis* because it lacks the complex laminated exine structure found in that genus, and has not been placed in *Celtis* (Cannabaceae) because the botanical affinity with the modern genus is somewhat uncertain. *Annutriporites rotundus* Frederiksen 1983 is distinctly granulate and columellate. A similar species, *Triporopollenites plektosus* Anderson 1960, was described as slightly scabrate and annulate. *Scabratriporites*

redundans van Hoeken-Klinkenburg 1964 differs mainly in being more clearly scabrate or granulate.

Occurrence: Ypresian; 21 specimens observed (0.1%).

Botanical affinity: Eudicots, lower affinity unknown, but possibly the Cannabaceae.

Genus *Echitriporites* van der Hammen 1956 ex van Hoeken-Klinkenburg 1964

Discussion: *Echitriporites* includes all echinate, triporate pollen.

Echitriporites sp. A
Plate 3.12, figures 8-9

Description: Triporate, echinate, equatorial diameter 23-(28)-33 μm . Exine ca. 0.5 μm thick, not visibly columellate. Shape subspherical, grains usually folded. Pores 3-5 μm in diameter, slightly aspidate. Surface sculpture faintly scabrate with scattered echinae 0.5-2.0 μm in length, with broad bases and pointed tips.

Discussion: *Echitriporites trianguliformis* van Hoeken-Klinkenburg 1964 and *Echitriporites guianensis* Leidekmeyer 1966 both have triangular amb, with thicker exines and longer spines. *Echitriporites irregularis* Muller 1968 differs from *Echitriporites* sp. A in having echinae with rounded rather than pointed tips, but is otherwise similar, with a spherical shape and a thin, easily folded exine.

Occurrence: Ypresian; 8 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Echitriporites sp. B
Plate 3.12, figure 10

Description: Triporate, micro-echinate, equatorial diameter 21 μm . Exine ca. 0.5 μm thick, not visibly columellate. Oblate, amb subcircular. Zonoporate, pores ca. 1.5 μm in diameter, prominently aspidate, the aspides forming a ring of thickened exine ca. 3-4 μm wide around the pores. Positive sculptural elements ≤ 0.5 μm in diameter and length scattered across the whole surface of the grain, some of which are low and rounded and best described as granulate, others which are long and pointed and best described as micro-echinate.

Discussion: *Echitriporites* sp. A has larger echinae and less pronounced aspides.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Gemmatriporites* Méon 1991

Discussion: *Gemmatriporites* includes all gemmate, triporate pollen.

Gemmatriporites sp. A
Plate 3.12, figure 7

Description: Triporate, gemmate, equatorial diameter 24-29 μm . Exine thickness somewhat difficult to observe due to the gemmate ornamentation, probably ca. 2 μm thick including the

gemmae. Shape subspherical, amb subcircular. Pores circular or slightly lolate, equatorial. Ornamentation in the form of gemmae densely and evenly distributed over the grain, ca. 1 μm in width and height.

Discussion: The type species of the genus, *Gemmatriporites ogwashiensis* Méon 1991, has a convex triangular rather than subcircular amb.

Occurrence: Ypresian; 3 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Momipites* Wodehouse 1933 emend. Nichols 1973

Discussion: This genus of triporate pollen is referable to the Juglandaceae. The emendation of *Momipites* by Frederiksen and Christopher (1978) is rejected, following Jardine (2011).

Momipites includes triporate pollen with equatorial, circular to lolate, atriate pores. Thinned areas of exine or folds may or may not be present. Wodehouse (1933) described the surface texture as smooth. Nichols (1973) described the exine as psilate, faintly scabrate, or foveolate. Frederiksen and Christopher (1978), in their emended description of *Momipites*, described the exine as usually granulate. Jardine (2011) described the exine as smooth or evenly granulate. *Platycaryapollenites* is distinguished from *Momipites* by possessing pseudocolpi.

Caryapollenites has subequatorial pores. *Momipites* is distinguished from the Betulaceae/Myricaceae type sensu Jardine (2011) by having less strongly annulate or tumescent pores, and by being less densely granulate.

Momipites amplius (Leffingwell 1970) Nichols 1973

Plate 3.11, figure 8

Description: Triporate, finely and evenly granulate, equatorial diameter 31 μm . Exine ca. 1 μm thick except near the annulate pores, where the exine is thickened to ca. 1.5 μm . Exine not visibly columellate. Oblate, amb subtriangular, sides slightly convex. Pores equatorial, atriate, probably circular in shape, ca. 2 μm in diameter. An irregular circumpolar ring of thinned exine surrounds a polar island ca. 8 μm in diameter.

Discussion: *Momipites amplius* is distinguished from most other species of *Momipites* by possessing a circumpolar ring of thinned exine, and by having a subtriangular amb with convex sides. *Momipites anellus* Nichols & Ott 1978 is similar but smaller, with a size range of 18-27 μm . *Caryapollenites veripites* also possesses a circumpolar ring of thinned exine, but in that species the pores are subequatorial.

Occurrence: Ypresian; 1 specimen observed (<0.1%). *Momipites amplius* has mainly been described from the Paleocene of North America, although there are a few younger occurrences, as well as some occurrences in China. This is the first published occurrence of *M. amplius* in Central America, the Caribbean, or South America (Palynodata Inc. and White 2008; Graham 2010).

Botanical affinity: Juglandaceae (Nichols 1973).

Paleoecology: Possibly montane forest. Ramírez-Arriaga, Prámparo, et al. (2014) considered that two species of *Momipites*, with presumably similar paleoecologies to *M. amplius*, represented cloud forest. On the other hand, Akkiraz et al. (2008) describe the habitat of two other species of *Momipites* as lowland-riparian. The ecological preferences of the plants producing these pollen types were apparently broader in the Early Tertiary than they are now (Frederiksen 1985).

Momipites coryloides Wodehouse 1933 sensu lato
Plate 3.11, figures 6-7

Description: Triporate, finely and evenly granulate, diameter 17-(22)-29 μm . Exine ca. 1 μm thick, not visibly columellate. Oblate, amb subtriangular to nearly subcircular, sides convex. Pores equatorial, atriate, probably circular in shape, 2-3 μm in diameter. No clearly defined area of thinned exine or regular folding is present.

Discussion: Some specimens have a more circular amb than *M. coryloides* as originally described, but are otherwise similar to *M. coryloides* and are here considered conspecific. *Momipites coryloides* and *Momipites wyomingensis* Nichols & Ott 1978 are distinguished from other species of *Momipites* by the lack of polar modification and a convex subtriangular amb. In the original description for *M. wyomingensis*, the size range was given as 19-27 μm . Nichols and Ott (1978) stated that *M. coryloides* is identical to *M. wyomingensis* except in its larger size. However, the original description of *M. coryloides* by Wodehouse (1933) provided a size range of 21-33.1 μm in diameter. Presumably, Nichols and Ott (1978) restricted *M. coryloides* to specimens >27 μm in diameter, although this was not clearly stated, and technically this definition would require *M. coryloides* to be emended. According to Nichols and Ott (1978) there is some biostratigraphic utility in separating this morphological type by size class, because in the Wind River Basin the smaller forms (*M. wyomingensis*) are restricted to the Paleocene, and the larger forms (*M. coryloides*) first appear in the Eocene. However, in the IODP 364 section, only a single specimen (Plate 11, fig. 6) exceeded 27 μm in diameter, so it was not considered useful to subdivide this type based on size. If forms similar to *M. coryloides* are split on the basis of size, either informal terminology should be used (e.g., *M. coryloides* <27 μm), or *M. coryloides* should be emended to define an appropriate size range for *M. coryloides* which does not overlap with *M. wyomingensis*.

Occurrence: Ypresian; 26 specimens observed (0.2%). *Momipites coryloides* is a common and globally distributed species in the late Cretaceous and Paleogene, although South American occurrences are lacking (Palynodata Inc. and White 2008), and has been identified from the Eocene and Oligocene of Mexico (e.g., Ramírez-Arriaga, Prámparo, et al. 2014; Ramírez-Arriaga and Reyes-Salas 2014).

Botanical affinity: Juglandaceae, probably *Alfaroa* or *Engelhardtia* (Nichols and Ott 1978).

Paleoecology: Possibly montane forest.

Momipites triradiatus Nichols 1973
Plate 3.11, figure 10

Description: Triporate, indistinctly granulate, equatorial diameter 24 μm . Exine ca. 0.7 μm thick except in the vicinity of the pores, where it thickens to ca. 1.2 μm . Exine not visibly columellate. Oblate, amb subtriangular, sides slightly convex. Pores equatorial, atriate, probably circular in shape, ca. 2.0-2.5 μm in diameter. A triradiate fold ca. 3 μm wide centered at one pole is present, with the three rays pointed toward the pores and extending ca. 1/2 the distance to the pores.

Discussion: The triradiate fold in this specimen is diagnostic. *Momipites wodehousei* Nichols 1973 is similar, but larger (>27 μm).

Occurrence: Ypresian; 1 specimen observed (<0.1%). *Momipites triradiatus* is widely distributed in the Paleocene and Eocene, although Central and South American occurrences are lacking (Palynodata Inc. and White 2008). However, Martínez-Hernández and Ramírez-Arriaga

(1999) identified *M. triradiatus* from the Paleocene of south-central Mexico, and provided a stratigraphic range chart for the Tepexi de Rodríguez region, which restricted the range of *M. triradiatus* and related forms to the Paleocene.

Botanical affinity: Juglandaceae (Nichols 1973).

Paleoecology: Possibly montane forest.

Genus *Psilatriporites* Hoorn 1993

Discussion: *Psilatriporites* includes all psilate, triporate pollen. *Cricotriporites* is partly synonymous with *Psilatriporites*, but is restricted to forms with circular amb and annulate pores.

Psilatriporites sp. A Plate 3.11, figures 11-12

Description: Triporate, psilate to faintly scabrate, diameter 20-(22)-27 μm . Exine ≤ 1 μm thick, not visibly columellate. Oblate, amb strongly triangular, sides slightly convex. Pores 2-5 μm in diameter, often with a frayed appearance. Vestibula absent, atria not visible. Annulus absent or only weakly developed.

Discussion: *Psilatriporites* sp. A is similar to grains identified as *Allophylus* L. (Sapindaceae) from the lower Miocene of Panama (Graham 1988), although the *Allophylus* specimens were costate, the exine was thicker (ca. 2 μm), and the sculpture was described as scabrate to micro-reticulate. A modern specimen of *Allophylus africanus* P. Beauv. photographed by Gosling et al. (2013) is similar in being triporate and strongly triangular, but is larger (ca. 40 μm) and granulate. The affinity therefore may be with the Sapindaceae. On the other hand, this species is similar to *Propylipollis subscabratus* (Couper 1960) Askin 2000, which was formerly placed in *Proteacidites*, as well as an undescribed and unspiciated specimen of *Proteacidites* photographed by Ramírez-Arriaga et al. (2017) from the Eocene of Mexico. *Psilatriporites* sp. A is also similar to the modern pollen of *Macadamia ternifolia* F. Muell. (Proteaceae) (Halbritter et al. 2018, p. 163).

Occurrence: Ypresian; 7 specimens observed ($<0.1\%$).

Botanical affinity: Eudicots, possibly Proteaceae or Sapindaceae (see discussion).

Genus *Retitriporites* Ramanujam 1966

Discussion: *Retitriporites* includes reticulate, triporate pollen grains. Van der Hammen (1956) first proposed *Retitriporites* as a subgenus using pollen of a modern species as the type specimen. Ramanujam (1966), González Guzmán (1967), and Muller (1968) all independently elevated *Retitriporites* to generic rank, but Ramanujam (1966) has priority. Jansonius and Hills (1976) considered *Retitriporites* illegitimate, because González Guzmán (1967) maintained the original nomenclatural type used by van der Hammen (1956), but Jansonius and Hills (1976) were apparently unaware that Ramanujam (1966) had earlier raised *Retitriporites* to generic rank, with a fossil type species, *Retitriporites curvimurati* Ramanujam 1966.

Retitriporites sp. A
Plate 3.12, figure 1

Description: Triporate, reticulate, equatorial diameter 22 μm . Exine ca. 1.5 μm thick, visibly columellate. Oblate, amb subtriangular, angulaperturate. Pores ca. 3 μm wide in equatorial view; annulus, atrium, vestibulum absent. Muri ca. 0.5 μm wide, lumina irregularly rounded polygonal in shape, ranging from 0.8-4.0 μm in diameter but mostly 1.5-2.5 μm in diameter.

Discussion: This specimen is similar to, but significantly smaller than, the holotype of *Retitriporites curvimurati* Ramanujam 1966, which has an equatorial diameter of 35 μm .

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, lower affinity uncertain, but *Retitriporites* sp. A is similar to pollen produced by the extant genus *Erythrina* L. (Fabaceae) (Hemsley and Ferguson 1985). Ramanujam (1966) also noted the similarity of *R. curvimurati* to *Erythrina*.

Genus *Scabratriporites* van Hoeken-Klinkenburg 1964

Description: *Scabratriporites* includes all scabrate, triporate pollen.

Scabratriporites redundans González Guzmán 1967 sensu lato
Plate 3.11, figure 3

Description: Triporate, scabrate to finely granulate, equatorial diameter 18-(21)-23 μm . Exine ca. 1 μm thick. Oblate, amb subcircular to rounded subtriangular. Pores 3-4 μm wide in polar view, annuli weakly to moderately developed.

Discussion: A broad species concept is used here, which includes specimens with a pore diameter >2.5 μm and an exine thickness ≥ 1 μm . *Annutriporites rotundus* Frederiksen 1983 is similar to *S. redundans*; Frederiksen (1983) considered that *A. rotundus* has a more distinct annulus than *S. redundans*. Since González Guzmán (1967) never described the annulus, beyond saying that an annulus is occasionally present in *S. redundans*, *A. rotundus* is arguably a junior synonym of *S. redundans*.

Occurrence: Ypresian; 178 specimens observed (1.1%). *Scabratriporites redundans* has mainly been observed in the Cenozoic of South America, with a single occurrence in West Africa (Palynodata Inc. and White 2008).

Botanical affinity: Eudicots, lower affinity unknown.

Genus *Subtriporopollenites* Pflug & Thomson in Thomson & Pflug 1953 emend. Krutzsch 1961

Discussion: *Subtriporopollenites* includes pollen referable to the Juglandaceae, resembling modern *Carya* pollen. *Subtriporopollenites* is triporate, with at least one pore in a subequatorial position. *Caryapollenites* is a similar form genus, but is distinguished by possessing an area of thinned exine (i.e., solution-field) around the proximal polar area. Krutzsch (1961) described the exine and atrium structure in some detail, but these characteristics are not always informative. Frederiksen (1980a, 1988), for example, described *Subtriporopollenites nanus* (Pflug & Thomson in Thomson & Pflug 1953) Frederiksen 1980 as having an indeterminate, apparently simple exine structure, without columellae. Also, *S. nanus* was described as never atriate by Frederiksen (1980a).

Subtriporopollenites cf. *S. nanus* (Pflug & Thomson in Thomson and Pflug 1953) Frederiksen
1980

Plate 3.11, figure 5

Description: Triporate, psilate to faintly granulate, diameter 18-(21)-23 μm . Exine 1.5-2.5 μm thick, not visibly columellate. Oblate, amb subcircular. Pores 1-3 μm in diameter, circular, atria sometimes visible but often obscure or absent. In some specimens one, two, or all three pores are clearly subequatorial, in other specimens the pores are ambiguously subequatorial, possibly para-isopolar. No area of thinned exine is visible.

Discussion: These specimens are similar to *S. nanus* in being $<25 \mu\text{m}$ in equatorial diameter, as well as in having an exine with obscure or absent collumellae. However, *S. nanus* was described as being never atriate, and atria are visible in some of these specimens. Also, the pores in these specimens are often substantially larger than those of *S. nanus* (ca. 1 μm diameter).

Occurrence: Ypresian; 48 specimens observed (0.3%).

Botanical affinity: Juglandaceae, probably *Carya*. *Subtriporopollenites* has a similar morphology to modern *Carya* pollen (Nichols and Ott 1978). *Subtriporopollenites* cf. *nanus* is similar to modern pollen of *Carya cardiformis* (Wangenh.) K. Koch, in which the pores are only slightly shifted to one side of the pollen grain (Bos and Punt 1991, Plate 2, Figs. 1-6).

Paleoecology: Possibly montane forest (see paleoecology section for *Caryapollenites veripites*).

Genus *Trivestibulopollenites* Pflug in Thomson and Pflug 1953

Discussion: *Trivestibulopollenites* includes triporate pollen with vestibulate, equatorial pores. An atrium is never present. The amb is more or less triangular, never circular. No interloculum, solution-wedge, oculus or praevestibulum is present. An annulus or labrum may be present. The original description by Thomson and Pflug (1953) did not restrict the sculpture types permissible in *Trivestibulopollenites*. The Betulaceae/Myricaceae type is not vestibulate.

Trivestibulopollenites sp. A

Plate 3.10, figure 14

Description: Triporate, faintly scabrate, equatorial diameter 24 μm . Exine ca. 1.5 μm thick, not visibly columellate. Oblate, amb subtriangular, sides slightly convex. Vestibulate, aspidate, pore canals ca. 2 μm wide in polar view.

Discussion: *Trivestibulopollenites betuloides* Thomson & Pflug 1953 was originally described as having a smooth exine. *Betula infrequens* Stanley 1965 is granulate, but the amb is approximately circular. *Betula infrequens* Stanley 1965 has a more circular amb.

Trivestibulopollenites fissuratus Frederiksen 1978 is coarsely granulate or verrucate and has a shallower vestibulum. Jardine (2011) did not speciate pollen in the genus *Trivestibulopollenites*.

Occurrence: Thanetian; 1 specimen observed ($<0.1\%$).

Botanical affinity: Probably Betulaceae, possibly *Betula* L. This specimen is similar to *Betula pubescens* Ehrhart, although this specimen is more clearly scabrate than *B. pubescens* (Blackmore et al. 2003). *Betula papyrifera* Marsh is also similar (Kapp et al. 2000).

3.4.9. Stephanoporate Pollen (Plate 12, Plate 13)

Genus *Alnus* Ehrhart

Discussion: Pollen grains of the genus *Alnus* are so distinctive that even Paleogene pollen grains of this type can be placed in the modern genus with reasonable confidence. The grains are stephanoporate, typically with 4-7 vestibulate pores placed at the angles of the grain, forming a polygonal amb. The presence of arcus and vestibula differentiates pollen grains of *Alnus* from other stephanoporate grains (Jardine 2011). The sculpture is scabrate or faintly granulate (Stanley 1965).

Alnus verus (Potonié 1931) Martin and Rouse 1966
Plate 3.12, figures 11-12

Description: Stephanoporate, psilate to faintly scabrate, equatorial diameter 20-29 μm . Exine ca. 1 μm thick, not visibly columellate. Oblate, amb pentagonal or hexagonal, depending on pore count, angulaperturate. Pores 5-6 in number, circular, annulate, vestibulate. Distinct arcus are present.

Discussion: Multiple form species have been designated to differentiate *Alnus* pollen on the basis of size or pore number. For example, *Alnus trina* Stanley 1965 and *Alnus quaternaria* Stanley 1965 possess three or four pores, respectively. Jardine (2011) provided detailed reasoning for using *A. verus* in a broad sense for *Alnus* pollen without a polar ring of thinned exine. Although Potonié (1931) gave a size range of 17-21 μm in the original description for *A. verus*, later authors expanded the species definition to include larger pollen; Thomson and Pflug (1953) gave a size range of 18-35 μm for *Polyvestibulopollenites verus* (Potonié 1934) Thomson & Pflug 1953, which is synonymous with *A. verus*. Some authors (e.g., Pocknall and Nichols 1996) use the form genus *Alnipollenites* Potonié 1931 rather than *Alnus*. An alternative spelling sometimes used in the literature is *Alnus vera* (e.g., Frederiksen 1980b; Ramírez-Arriaga, Prámparo, et al. 2014).

Occurrence: Danian-Ypresian; 5 specimens observed (<0.1%). Pollen similar to modern *Alnus* is common and widely distributed throughout the Northern Hemisphere in the Cenozoic, with some Cretaceous occurrences as well (Palynodata Inc. and White 2008). The migration of *Alnus* to South America appears to have occurred in the Pleistocene (Germeraad et al. 1968; D'Apolito et al. 2018).

Botanical affinity: *Alnus* (Betulaceae).

Paleoecology: Probably montane forest. Ramírez-Arriaga, Prámparo, et al. (2014) gave the paleoecology for *A. verus* as cloud forest, but Frederiksen (1985) noted that the presence of *Alnus* pollen may also indicate riparian or lowland freshwater swamp paleoenvironments. In modern Central America, *Alnus* is generally restricted to higher elevation forests (Tedersoo 2017). Germeraad et al. (1968) note that the presence of *Alnus* pollen in the tropics is related to the presence of substantial mountain ranges. Correa-Metrio et al. (2011) assigned *Alnus* to the high elevation *Quercus* and coniferous forests.

Genus *Malvacipollis* Harris 1965 emend. Krutzsch 1966

Discussion: Harris (1965) originally described *Malvacipollis* as including echinate, stephanoporate pollen grains with rimmed (i.e., annulate) pores. Krutzsch (1966) emended *Malvacipollis*, substantially altering the generic description to include pollen with a more or less circular amb and various numbers of small, circular pores, apparently including both stephanoporate and pantoporate pollen. The pores may or may not be annulate. *Malvacipollis* as emended by Krutzsch (1966) includes pollen with echinate sculpture as well as psilate, scabrate, and verrucate pollen. The botanical affinity of specimens assigned to *Malvacipollis* appears split between the Malvaceae and the Euphorbiaceae. In specimens of *Malvacipollis* with affinity to the Malvaceae, the sexine is thickened under the spines and the columellae extend into the base of the spines, and in specimens of *Malvacipollis* with affinity to the Euphorbiaceae, the spines are a simple extension of the outer homogenous exine layer (Martin 1974; Frederiksen 1983).

Malvaceidites Khan 1976 and *Malvacearumpollis* Nagy 1962 emend. Krutzsch 1966 are both reserved for larger (generally <100 microns in diameter) echinate pantoporate pollen grains, and are arguably junior synonyms of *Malvacipollis*, because no size restriction was given for *Malvacipollis*. *Malvacipolloides* Anzotégui & Garralla 1986 is tricolporate. *Compositoipollenites* Potonié 1951 ex Potonié 1960 is here considered a nomen ambiguum because the description is unclear as to whether the grains are triporate or tricolporate (Jansonius and Hills 1976, card 542). *Echistephanoporites* Leidelmeyer 1966 includes stephanoporate pollen grains with an echinate sculpture and annulate pores, and is partially synonymous with *Malvacipollis*. *Echiperiporites* van der Hammen and Wymstra (1964) includes echinate, pantoporate pollen grains, and is also partially synonymous with *Malvacipollis*.

Malvacipollis spp. (Euphorbiaceae type)
Plate 3.13, figures 1-3; Plate 15, figures 9-10

Description: Stephanoporate, echinate, equatorial diameter 19-(26)-32 μm (twenty specimens measured). Exine <1 μm thick, occasionally up to ca. 2 μm thick. Exine columellate, although the columellae are often obscure. The exine is not thickened beneath the spines, and the columellae do not extend into the base of the spines. Amb circular, shape approximately spherical, grains often folded. Generally, 5 to 7 approximately equatorial pores are present when the grains are observed in polar view and not folded, but more often the grain is folded and oriented in a manner where the position and number of pores is indeterminate. Annuli weakly developed or absent. Spines supratectal, 0.5-2.5 μm long, variable in shape, sometimes very thin and hairlike, sometimes with broad bases. The exine surrounding the spines is psilate or indistinctly scabrate in light microscopy. In SEM, the exine surrounding the spines is granulate to micro-verrucate, with interspersed punctae, and the spines are faintly striate. In SEM, as in light microscopy, pores are often not observable, and the grains appear inaperturate.

Discussion: There appears to be a morphological continuum in the size and distribution of the spines, as well as the exine thickness. Many of these specimens could be included within *Malvacipollis spinulosa* Frederiksen 1983, which includes oblate spheroidal, echinate, zonoporate pollen with generally 4-9 pores, although the pores are often obscure. In *M. spinulosa*, the spines are widely spaced, 1.2-1.5 μm long, and the exine is 0.5-1.0 μm thick. Frederiksen (1983) stated that *Malvacipollis tschudyi* (Frederiksen 1973) Frederiksen 1980 is distinguished from *M. spinulosa* by having a thicker exine (1.5 μm) than *M. spinulosa*. However,

M. tschudyi was originally described as being vestibulate, and vestibula are not visible in the IODP 364 specimens. According to Frederiksen (1983), *M. spinulosa* is distinguished from *Malvacipollis diversus* Harris 1965 emend. Stover & Partridge 1973 by being less densely conate and from *Malvacipollis subtilis* Stover in Stover & Partridge 1973 by having a thinner exine (<1 µm thick). According to Stover and Partridge (1973), *M. subtilis* is distinguished from *M. diversus* by having spines or spinules rather than conate projections, although these terms are often considered synonymous (Punt et al. 2007), as well as by having spines which tend to be more widely spaced. Attempts to speciate the *Malvacipollis* specimens in the IODP 364 core using these criteria were considered unproductive. *Malvacipollis?* sp. A is similar in being approximately spherical and echinate, but that species is only questionably porate, the spines are much more densely arranged, and the sexine is thickened under the spines.

Occurrence: Ypresian; 1605 specimens observed (9.9%). *Malvacipollis diversus* and *M. subtilis* are known almost exclusively from the Cenozoic Australasian and Antarctic floral provinces, with a few South American occurrences, while *M. tschudyi* has been most commonly identified from the northern Gulf of Mexico coastal plain (Palynodata Inc. and White 2008). *Malvacipollis spinulosa* was originally identified from the Eocene of California (Frederiksen 1983), but has also been identified from the Paleogene of Mexico (e.g., Martínez-Hernández and Ramírez-Arriaga 1999; Ramírez-Arriaga, Prámparo, et al. 2014) and the Cenozoic of South America (e.g., Romero Valeo 2014; Sá and Carvalho 2017). In addition to the northern Gulf of Mexico occurrences, *Malvacipollis tschudyi* has been identified from the Middle Eocene of Cuba (Graham et al. 2000) and Florida (Jarzen and Dilcher 2006).

Botanical affinity: Probably Euphorbiaceae. *Malvacipollis* spp. (Euphorbiaceae type) possesses spines which are a simple extension of the exine, suggesting a botanical affinity with the Euphorbiaceae; in the Malvaceae, the sexine is thickened under the spines and the columellae extend into the base of the spines (Martin 1974; Frederiksen 1983).

Paleoecology: Probably lowland tropical forest. Ramírez-Arriaga, Prámparo, et al. (2014) identified the paleoecology of *M. spinulosa* as tropical deciduous forest, and Romero Valero (2014) identified the paleoecology of *M. spinulosa* as lowland forest.

Malvacipollis? sp. A (Malvaceae type)
Plate 3.13, figures 4-5

Diagnosis: Ambiguously porate, possibly inaperturate, echinate, diameter 17-(26)-31 µm. Exine 1-2 µm thick, visibly columellate, the columellae extending into the base of the spines, the sexine thickened under the spines. Outline circular, shape probably approximately spherical. No apertures are clearly visible, although a few specimens appear to have faint irregular holes or thinned areas of exine, which may be pores. The spines are mostly 0.5-1.5 µm long, longer than they are wide, tapering to a point, very densely arranged.

Discussion: There is some uncertainty in the generic diagnosis, because it is unclear whether the grains are truly inaperturate, or whether they possess obscure apertures not clearly visible in light microscopy. If this species is truly inaperturate, a more appropriate form genus would be *Peltandripites* Wodehouse 1933 emend. Nichols 2010, which includes echinate, inaperturate pollen.

Occurrence: Ypresian; 187 specimens observed (1.2%). FAD: 574.35 mbsf. 50.5-(50.88)-53.7 Ma.

Botanical affinity: Eudicots, possibly Malvaceae. These grains are somewhat similar in appearance to *Malvacipollis diversus* Harris 1965, which is also approximately spherical and echinate, but in *M. diversus* and other species of *Malvacipollis* the grains are more clearly zonaporate or pantoporate. The thickened sexine at the base of the spines and the extension of the columellae into the base of the spines are reminiscent of echinate pollen in the Malvaceae (Martin 1974).

Scabrastephanoporites gen. nov.

Type species: *Scabrastephanoporites variabilis* gen. et sp. nov.

Description: Pollen with more than three equatorial pores and scabrate sculpture. The pores have no visible atrium.

Derivation of name: This name follows the artificial nomenclature system of van der Hammen (1954, 1956).

Discussion: *Polyatriopollenites* (Potonié 1931) Pflug 1953 has perhaps an overly broad circumscription according to the original description translated by Jansonius and Hills (1976), which includes all stephanoporate (and rarely triporate) pollen types with equatorial or sub-equatorial atriate pores. *Polyatriopollenites* is generally reserved for pollen with affinity to *Pterocarya* Nutt. ex Moq. (Juglandaceae) (Jardine 2011). Although the genus description for *Scabrastephanoporites* gen. nov. deviates from the artificial nomenclature system of van der Hammen (1954b, 1956) by restricting the genus to non-atrinate types, this was considered preferable to creating a new genus which would be partly synonymous with *Polyatriopollenites*. *Polyporopollenites* Pflug 1953 in Thomson & Pflug 1953 is a junior synonym of *Ulmipollenites* Wolff 1934 emend. Srivastava 1969, according to Jansonius and Hills (1976). *Polyvestibulopollenites* Pflug 1953 in Thomson & Pflug 1953 is a junior synonym of *Alnipollenites* Potonié 1931, according to Frederiksen and Ames (1979).

Scabrastephanoporites variabilis gen. et sp. nov.

Plate 3.12, figures 13-16

Holotype: The specimen in Plate 3.12, figure 15 (558.26 mbsf, slide 1, EFS S34/1).

Repository: CENEX, LSU, Baton Rouge, Louisiana, USA.

Type locality: IODP 364 Site M0077, Chicxulub impact crater, Mexico.

Derivation of name: The specific name is in reference to the variable morphology of the pores and exine sculpture.

Description: Zonoporate, indistinctly scabrate to granulate, equatorial diameter 21-(24)-28 μm . Exine ca. 1 μm thick, not visibly columellate. Oblate, amb circular. 4-5 roughly circular pores present, 2-3 μm in diameter, thickened annuli virtually absent to moderately developed.

Discussion: Some specimens of *S. variabilis* gen. et sp. nov. with granulate sculpture resemble *Ulmipollenites krempii* (Anderson 1960) Frederiksen 1979 emend., but the sculpture is never clearly verrucate in *S. variabilis* gen. et sp. nov. Other specimens are nearly psilate.

Occurrence: Ypresian; 305 specimens observed (1.9%).

Botanical affinity: Eudicots, possibly Cannabaceae or Ulmaceae. *Scabrastephanoporites variabilis* gen. et sp. nov. is somewhat similar to *Ulmipollenites krempii*, and also resembles modern pollen of *Planera aquatica* (Walt.) Gmel. (Ulmaceae), although *P. aquatica* pollen is larger (ca. 44 microns) (Kapp et al. 2000). An alternative botanical affinity for *S. variabilis* gen.

et sp. nov. is suggested by the resemblance to modern *Celtis* L. pollen (Kapp et al. 2000) and the *Celtis tschudyi* (Elsik 1974) Frederiksen 1980 group (Frederiksen 1988, Jardine 2011), although the detailed pore structure described by Frederiksen (1980b) for *C. tschudyi* has not been observed in *S. variabilis* gen. et sp. nov.

Genus *Ulmipollenites* Wolff 1934 emend. Srivastava 1969

Discussion: This form genus was erected for pollen similar to modern *Ulmus* L. pollen. The sculpture is either verrucate or rugulate, and the pollen grain is zonoporate, with three or more pores. Arcus may or may not be present. *Ulmoidepites* Anderson 1960 is a junior synonym of *Ulmipollenites* (Srivastava 1969).

Ulmipollenites krempii (Anderson 1960) Frederiksen 1979 emend.
Plate 3.12, figures 17-20; Plate 15, figure 11

Selected synonymy:

Ulmoidepites krempii Anderson 1960, plate 6, fig. 2

Ulmoidepites planeraeformis Anderson 1960, plate 4, fig. 1

Ulmoidepites tricostatus Anderson 1960, plate 4, figs. 20-21

Emended description: Verrucate pollen with 3-5 equatorial or slightly subequatorial, slightly annulate pores. Oblate to approximately spherical; circular or polygonal amb. Equatorial diameter usually 15-30 μm . Arcus may or may not be present.

Description of IODP 364 specimens: Zonoporate, verrucate, diameter 19-(24)-29 μm . Exine approximately 1-2 μm thick, not visibly columellate. Oblate, amb subcircular to polygonal. Usually four, rarely three or five, equatorial annulate pores. Pore diameter 1.5-3.0 μm . Verrucae 0.5-2.0 μm in diameter. Arcus more often absent or indistinct, occasionally distinct. In SEM microscopy, granules or papillae ca. 0.1 μm in length are also observable, densely covering the exine.

Discussion: The emendation of *Ulmipollenites krempii* given here formalizes a broad definition of the species used by Nichols and Brown (1992), which includes triporate, tetraporate, and 5-porate specimens, with or without arcus. Anderson (1960) originally gave the species name as *U. krempii*, but the proper latin spelling is *U. krempii*, and the name should be changed to the proper spelling, according to Article 60.8 of the Shenzhen code (Turland et al. 2018). *Ulmipollenites krempii* was originally described as having ulmoid sculpture, which is generally understood to mean verrucate sculpture (i.e., Pocknall and Nichols 1996, Jardine 2011). Either 3 or 4 annulate pores are present, the amb is circular to subcircular, and arcus are present. The size range originally given for *U. krempii* was 16-26 μm in diameter. *Ulmoidepites planeraeformis* was distinguished by having 5 pores and a pentagonal amb, and *Ulmoidepites tricostatus* was distinguished by having a more triangular outline with beaded (i.e., verrucate) arcus. Both *U. planeraeformis* and *U. tricostatus* are considered synonymous with *U. krempii* as here emended. *Ulmipollenites undulosus* Wolff 1934 and *U. thompsoniana* (Traverse 1955) Frederiksen 1988 are distinguished by being rugulate rather than verrucate. If it is considered desirable in future studies to split *U. krempii* based on pore count or the presence or absence of arcus, this could be accomplished either by naming subspecies or using informal terminology (e.g., *U. krempii* 4-porate, non-arcuate).

Occurrence: Ypresian; 704 specimens observed (4.3%). *Ulmipollenites krempii* has a wide paleogeographic distribution in the Cenozoic (Palynodata Inc. and White 2008).

Botanical affinity: Ulmaceae (Pocknall and Nichols 1996, Jardine 2011).

Paleoecology: Probably moist montane forest. Elsik (1968b) stated that *Ulmipollenites krempii* sensu stricto has affinity with *Planera aquatica*, which, as the name suggests, has a preference for wet environmental conditions. Ramírez-Arriaga, Prámparo, et al. (2014) gave the paleoecology of *Ulmipollenites* spp. as cloud forest. Correa-Metrio et al. (2011) assigned modern *Ulmus* to mountain mesophyllous forest.

3.4.10. Pantoporate Pollen (Plate 13)

Genus *Chenopodipollis* Krutzsch 1966

Discussion: *Chenopodipollis* is used for small, thick-walled pantoporate pollen grains with affinity to the Amaranthaceae. Formerly, Chenopodiaceae was considered a separate family, but is now relegated to the subfamily Chenopodioideae of the Amaranthaceae in the APG IV classification (Byng et al. 2016). According to the original description by Krutzsch (1966), *Chenopodipollis* includes spherical, pantoporate pollen grains. The pores are closely and evenly distributed over the grain, and partially closed by a thin membrane. The exine is approximately 1-2 μm thick, and the sculpture is punctate. *Caryophyllidites* Couper 1960 is differentiated by having a coarser wall structure and larger, less numerous pores. *Chenopodipollis* is similar to *Periporopollenites* Pflug and Thomson 1953, which as originally described included all pantoporate pollen. Krutzsch (1966) emended *Periporopollenites* and restricted the genus to forms with a micro-reticulate exine. Stover and Partridge (1973) reserved *Periporopollenites* for pantoporate pollen with 10-32 pores and a punctate, granulate, or finely reticulate exine. Specifically excluded in their circumscription of the genus are small, thick-walled forms assignable to *Chenopodipollis* and more ornamented forms like *Malvacipollis*. In practice, *Chenopodipollis* is often used for pollen with affinity to the Amaranthaceae, even if they do not have a punctate exine. Ramírez-Arriaga, Prámparo, et al. (2014), for example, described an unnamed species of *Chenopodipollis* with a finely reticulate exine, and Nichols and Brown (1992) described an unnamed species of *Chenopodipollis* with a granulate or perforate exine. Another genus that may be confused with *Chenopodipollis* is *Psilaperiporites* Regali et al. 1974 emend. Muller et al. 1987, which is a form genus for pantoporate pollen with a smooth to perforate (i.e., punctate) exine. Some specimens of *Psilaperiporites* have a botanical affinity with the Amaranthaceae, for example *Psilaperiporites minimus* Regali et al. 1974 (Jaramillo et al. 2014).

Chenopodipollis sp. A

Plate 3.13, figures 6-7; Plate 15, figure 12

Description: Pantoporate, psilate to faintly scabrate in LM. Spherical, diameter 21-(24)-28 μm . Exine 1.5-2.0 μm thick, columellate. Grain spherical. Using the C/D ratio, the number of pores is estimated to be 50-80 (Kapp et al. 2000). The pores are distributed evenly over the surface of the grain, from 1.0-1.5 μm in diameter. In SEM, the exine is evenly covered with small granulae and micro-echinae ca. 0.1-0.2 μm in diameter, as well as minute punctae ca. 0.03-0.05 μm in diameter. Granulae and echinae are also present in the pores.

Discussion: *Chenopodipollis* sp. A is quite similar to modern pollen of some species of Amaranthaceae, for example *Salicornia bigelovii* Torr. and *Amaranthus australis* (Gray) Sauer (Willard et al. 2004). The type species of the genus, *Chenopodipollis multiplex* Krutzsch 1966, differs from these specimens in being infrareticulate.

Occurrence: Danian-Ypresian; 71 specimens observed (0.4%). *Chenopodipollis* pollen is common and globally distributed in the Cenozoic (Palynodata Inc. and White 2008).

Botanical affinity: Amaranthaceae.

Paleoecology: Possibly estuarine. Ramírez-Arriaga, Prámparo, et al. (2014) describe an unnamed species of *Chenopodipollis*, differing from these specimens mainly in being micro-reticulate, and consider that it represents tropical arid scrub. Rzedowski (2006) noted the presence of Amaranthaceae in modern Mexican deserts, particularly in areas with salty soil. Many modern members of this family are xerophytes and halophytes, and may indicate estuarine environments, particularly salt marshes (Frederiksen 1985). Nichols and Traverse (1971) considered *Chenopodipollis multiplex* a diagnostic palynomorph in their Marine Influence Assemblage from the Late Paleocene-Early Eocene Wilcox Group of South Texas, and speculated that the parent plant lived in a coastal environment.

Genus *Psilaperiporites* Regali et al. 1974

Discussion: *Psilaperiporites* includes all psilate, pantoporate (i.e., periporate) pollen. *Periporopollenites* Thomson & Pflug 1953 as originally described included all pantoporate pollen, but Krutzsch (1966) emended *Periporopollenites* and restricted the genus to reticulate, pantoporate pollen similar to modern *Liquidambar* pollen (Jansonius and Hills 1976). Jordan and MacPhail (2003) used a broad definition of *Periporopollenites* which includes pollen previously assigned to *Caryophyllidites* Couper 1960, *Liquidambarpollenites* Raatz 1938 ex Potonié 1960, *Parsonidites* Couper 1960, *Periporites* van der Hammen 1956, and *Polyporina* Naumova 1939 ex Potonié 1960.

Psilaperiporites sp. A Plate 3.13, figure 9

Description: Pantoporate, psilate, diameter 67 μm . Exine ca. 2 μm thick, not visibly columellate. Shape spherical. Roughly 35-50 pores were originally present, extrapolating from the fully preserved half of the grain. Pores 5-10 μm in diameter, annuli absent, pore spacing irregular, margins irregular. A thin aperture membrane with a faintly granulate texture is visible on some pores in phase contrast.

Discussion: The single specimen of this type is much larger than all other pantoporate pollen grains in this study. *Periporopollenites polyoratus* (Couper 1960) Stover & Partridge 1973 is somewhat similar to *Psilaperiporites* in having non-annulate pores with irregular margins, but *P. polyoratus* is smaller and has clavate columellae with a punctate surface sculpture.

Caryophyllidites Couper 1960 included spherical pantoporate pollen with more than 20 pores, irregular non-annulate pore margins, and a thick, tectate exine. The botanical affinity for *Caryophyllidites* is the Caryophyllaceae (Couper 1960). *Psilaperiporites* sp. A could be accommodated within *Caryophyllidites*, except the exine is not visibly tectate, and arguably the exine is not thick relative to the equatorial diameter. Also, Stover and Partridge (1973) and Jordan and MacPhail (2003) consider *Caryophyllidites* a junior synonym of *Periporopollenites*.

Occurrence: Ypresian; 1 specimen observed (<0.1%).

Botanical affinity: Eudicots, possibly Caryophyllaceae. The non-annulate, irregular margins of the pores in *Psilaperiporites* sp. A are similar to pollen morphologies produced by modern Caryophyllaceae (Couper 1960), but modern pollen of the Caryophyllaceae is spinulose-punctate, scabrate-punctate, scabrate, or reticulate (Perveen and Qaiser 2006). Positive sculpture features in the apertures of this specimen, which appear granulate in LM, are similar to granulate or micro-echinate apertural protrusions in Caryophyllaceae specimens observed in SEM by Halbritter et al. (2018, fig. 22). Pantoporate pollen is also produced by Amaranthaceae, Convolvulaceae, Euphorbiaceae, Hamamelidaceae, Nyctaginaceae, Rivinaceae, and Papaveraceae (Jordan and Macphail 2003).

Psilaperiporites suarezi Vajda-Santivanez 1999 sensu lato
Plate 3.13, figures 10-11

Description: Pantoporate, psilate to faintly scabrate, equatorial diameter 22-26 µm. Exine 0.5-1.5 µm thick, columellae not clearly visible. Grains subspherical. Approximately 20-30 pores are irregularly distributed across the grain surface. The pores are circular to oval, 1.5-4.0 µm in diameter. Annuli are absent.

Discussion: *Psilaperiporites suarezi* was originally described as psilate, pantoporate, 20-38 µm in size, with 16-34 circular to slightly elliptical pores 2-3 µm in diameter (Vajda-Santivanez 1999). A broad sense of the species is used here to include specimens with pores slightly smaller than 2 µm, as well as faintly scabrate specimens. In *Chenopodipollis* sp. A, the pore count is higher and the pores are more regularly arranged. *Psilaperiporites robustus* Regali et al. 1974 is larger (45-48 µm). *Psilaperiporites minimus* Regali et al. 1974 is larger and has a higher pore count (Vajda-Santivanez 1999).

Occurrence: Ypresian; 3 specimens observed (<0.1%). *Psilaperiporites suarezi* was originally described from the Paleocene of Bolivia (Vajda-Santivanez 1999). No other occurrences are listed in Palynodata Inc. and White (2008).

Botanical affinity: Eudicots, lower affinity unclear. Pantoporate pollen is produced by the Amaranthaceae, Caryophyllaceae, Convolvulaceae, Euphorbiaceae, Hamamelidaceae, Nyctaginaceae, Rivinaceae, and Papaveraceae (Jordan and Macphail 2003).

3.4.11. Tetrad Pollen (Plate 13)

Genus *Retitetradites* Pierce 1961

Discussion: *Retitetradites* includes all reticulate, tetrad pollen.

Retitetradites sp. A
Plate 3.13, figure 8

Description: Tetrad, composed of tricolpate grains, reticulate, approximate diameter of tetrads 41-54 microns. Tetrads in the form of a tetrahedron. Exine thickness ca. 2-3 microns, clearly separated into ectexine and endexine of approximately equal thickness, prominently columellate, the columellae clavate. Colpi extending nearly full length of grain, with slightly thickened

margins. Lumina in reticulum subcircular to rounded polygonal in shape, 1-2 microns in diameter, the muri slightly thinner than the lumina.

Discussion: The type species of the genus, *Retitetradites monocolpatus* Pierce 1961, is monocolpate.

Occurrence: Ypresian; 3 specimens observed (<0.1%).

Botanical affinity: Eudicots, lower affinity unknown.

3.5. Discussion and conclusions

The diverse angiosperm assemblage in the IODP 364 core from Site M0077 includes 107 taxa. Of these, 25 taxa are previously described species, 77 taxa are identified using informal systematic terminology, and five taxa are newly described species. Many of the taxa identified using informal terminology may be worth naming as new species, but the naming of new species was considered conservatively. The palynological literature is vast, and regional practices in taxonomy, exacerbated by the publication of species names in multiple languages, in many cases practically prevent a comprehensive review of all named species in particular genera. For example, the database of Palynodata Inc. and White (2008) lists 405 varieties of *Tricolpites*, of which approximately 255 are formally named species. Therefore, in this study, new species were named only if a minimum of 10 specimens were observed, and if there was reasonable confidence that the new species was not conspecific with a previously named species. Further investigation of Paleogene pollen assemblages from the Yucatán Peninsula and nearby areas will help to clarify these taxonomic issues.

Existing plant spore and pollen taxa with reasonably well-established paleogeographic ranges in the literature (see supplementary material) suggest that the paleobotanical assemblage in the IODP 364 core has more taxa in common with North America than South America. Of these 40 Paleogene taxa, 20 occur in both North and South America, 15 occur in North America but not South America, three occur in South America but not North America, and two occur neither in North America nor in South America. *Hamulatisporis hamulatis* Krutzsch 1959 was present in Paleogene North America, but appears to have no published occurrences in Paleogene South America (Palynodata Inc. and White 2008; Graham 2010), although there is a record of *H. hamulatis* from the Cretaceous of Venezuela (Sinanoglu 1984). Pollen taxa with a botanical affinity to the Juglandaceae (*Caryapollenites* Raatz 1937 ex Potonié 1960 emend. Krutzsch 1961, *Momipites* Wodehouse 1933 emend. Nichols 1973), *Bursera* (*Brosipollis* Krutzsch 1968), and *Alnus* Ehrhart indicate a similarity to Paleocene–Eocene North American assemblages. *Bombacacidites brevis*, *Scabratrporites redundans* González Guzmán 1967, and *Spirosyncolpites spiralis* González Guzmán 1967 have published occurrences in South America but not North America. Two species, *Foveotrilletes crater* Stover & Partridge 1973 and *Undulatisporites mineri* (Singh & Kumar 1972) Smith et al. 2019, have previously only been described from Australasia and India, respectively (Palynodata Inc. and White 2008; Smith et al. 2019). Some of these differences may be due to regional taxonomic practices, or convergent morphologies, but the overall resemblance of the IODP 364 assemblage to contemporaneous assemblages from North America is clear. Possibly the most unique feature of the IODP 364 angiosperm assemblage generally is the high relative abundance of *Malvacipollis* spp. with affinity to the Euphorbiaceae, approximately 9.9% of the total pollen and plant spore count (see supplementary material). During the Paleocene and early Eocene, North and South America were widely separated, and the closest emergent landmass which could serve as a source for the pollen

in the IODP 364 core was probably in either the Yucatán Peninsula or mainland Mexico (Iturralde-Vinent and MacPhee 1999).

Unfortunately, despite a large number of high-resolution samples from the basal Paleocene strata above the impact breccia, the oldest observed terrestrial palynomorphs in the IODP 364 core were two fern spores of the genus *Deltoidospora* at 615.50 mbsf (Smith et al. 2019); the age of this sample depth is constrained by foraminiferal biostratigraphy to between 65.25 and 65.72 Ma. The oldest angiosperm pollen observed in the core, a single specimen of *Betula?* sp. A and four specimens of *Chenopodipollis* sp. A, occur at 615.03 mbsf; the estimated age of this sample is 65.15 Ma (see Supplementary material). Throughout the rest of the Paleocene section, pollen is either entirely absent or present in abundances too low to make any confident interpretations about the Paleocene assemblage. However, the high relative abundance of *Chenopodipollis* sp. A in the Paleocene may be evidence of a predominantly estuarine pollen source area. The near absence of palynomorphs generally in the Paleocene section stands in contrast to the calcareous microfossil record (Lowery et al. 2018; Jones et al. 2019). This indicates that the low abundance in the Paleocene section is probably the result of poor preservation of organic-walled microfossils. Gulick et al. (2019) note that based on paleogeographic reconstructions, the closest emergent land at the onset of the Paleocene (moment of impact) was 800 km westward across a relatively shallow shelf (ca. 100m water depth). Certainly, all regional vegetation would have been annihilated by the impact event itself, and there is strong evidence that the impact caused a global mass extinction in many terrestrial plant groups (Vajda et al. 2001; Vajda and Raine 2003; McElwain and Punyasena 2007). However, due to the near absence of pollen in the Paleocene part of the section, and the lack of information about Cretaceous pollen assemblages from the Yucatán Peninsula, it is not possible to quantitatively estimate the magnitude of the extinction event from the angiosperm pollen assemblage in the IODP 364 core.

The earliest well-preserved pollen assemblages in the IODP 364 core occur in a thin black shale at 607.06–607.27 mbsf deposited during the PETM (Gulick et al. 2017). *Malvacipollis* spp., here interpreted as representing a lowland tropical forest paleoenvironment, are particularly abundant in the PETM, and other species have their highest relative abundances during the PETM, specifically *Boehlensipollis?* sp. A, *Clavastephanocolpites* sp. A, and *Scabratricolpites* sp. A. Pollen abundances in the upper Ypresian section are variable, but generally increase upsection. Near the top of the IODP 364 core, abundances are generally very high and preservation is generally excellent. Taxa representative of lowland tropical forest are substantially more common than taxa representative of montane forest, arid tropical scrub, or estuarine paleoenvironments. Because the location of the IODP 364 core was at approximately 500–700 m paleo-water depth during the Eocene (Gulick et al. 2017), the pollen assemblage is probably a mix of nearby pollen source areas, perhaps from local highs on the crater rim, low-elevation carbonate islands on the Yucatán Peninsula, or estuarine settings in central Mexico. Taxa suggestive of montane forest taxa may represent a pollen source area from the Mexican highlands to the west and south. Future palynological analysis of more autochthonous pollen assemblages from regional paleotopographic highs may help to clarify and confirm these preliminary paleoecological interpretations. The taxonomy presented here, and in Smith et al. (2019), provides the first description of Paleogene pollen and spores from inside the Chicxulub impact crater, and is intended to serve as a useful reference for future palynologists studying coeval pollen assemblages from the Gulf Coast of Mexico and the Yucatán Peninsula.

3.6. Plates to Chapter 3

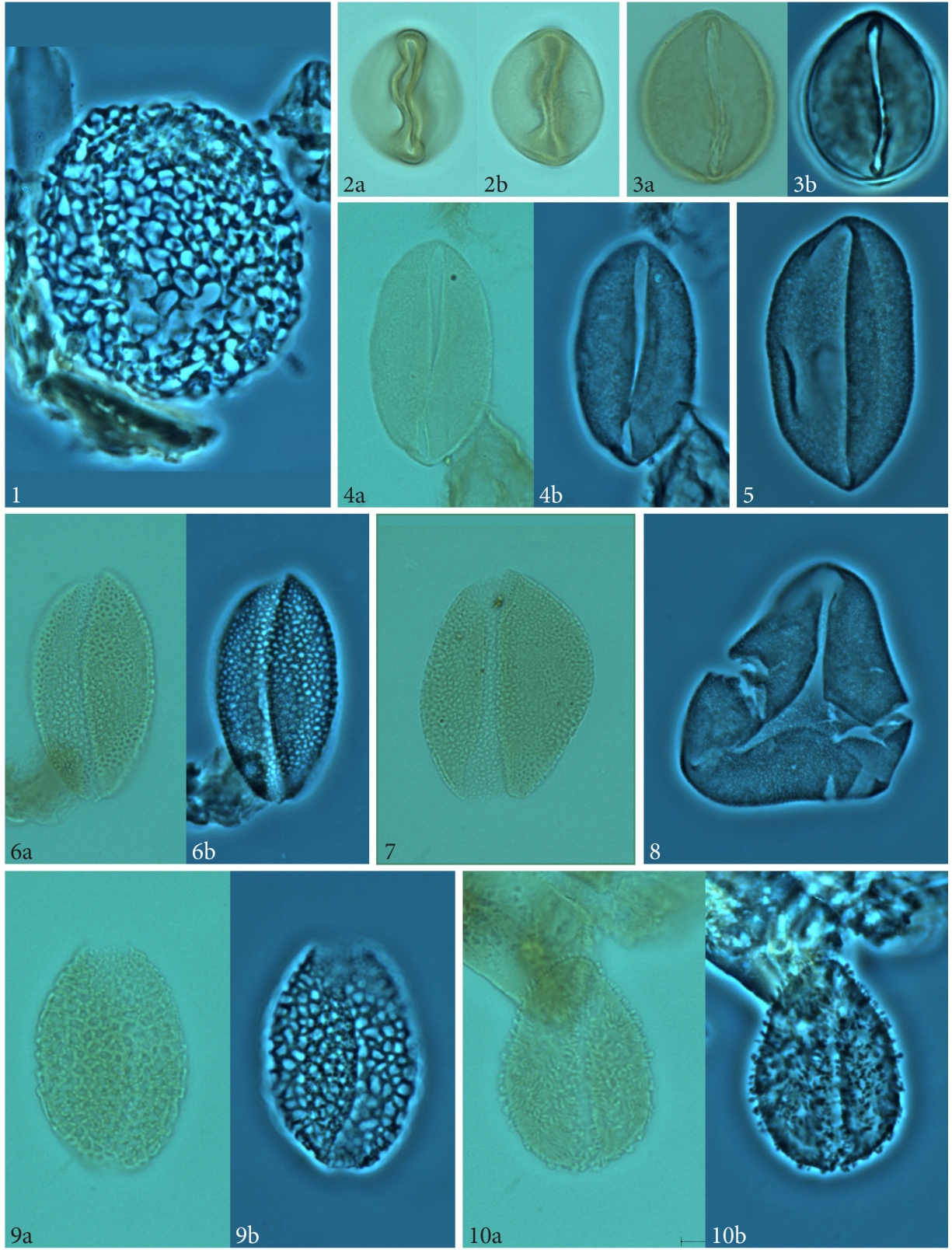


Plate 3.1

Plate 3.1. Inaperturate, monocolpate, and trichotomocolpate pollen from IODP (International Ocean Discovery Program) 364.

1. *Retipollenites?* sp. A, 559.91 mbsf (meters below seafloor), slide 1, EFS (England Finder Slide) M31/2.

2. *Monocolpopollenites* cf. *M. tranquilloides*, 539.43 mbsf, slide 1, EFS Q18/1.

3. *Monocolpopollenites tranquillus*, 572.75 mbsf, slide 1, EFS L38/1.

4. *Arecipites tenuixinous*, 539.43 mbsf, slide 1, EFS 043/1.

5. *Arecipites tenuixinous*, 520.79 mbsf, slide 1, EFS V30/2.

6. *Liliacidites variegatus*, 534.85 mbsf, slide 1, EFS P34/1.

7. *Liliacidites variegatus*, 569.50 mbsf, slide 1, EFS S39/1.

8. *Liliacidites* sp. B, 555.07 mbsf, slide 1, EFS G28/4.

9. *Liliacidites* sp. A, 553.54 mbsf, slide 1, EFS T39/1.

10. *Clavamonocolpites* sp. A, 516.00 mbsf, slide 1, EFS U15/0.

Scale bar=10 μm .

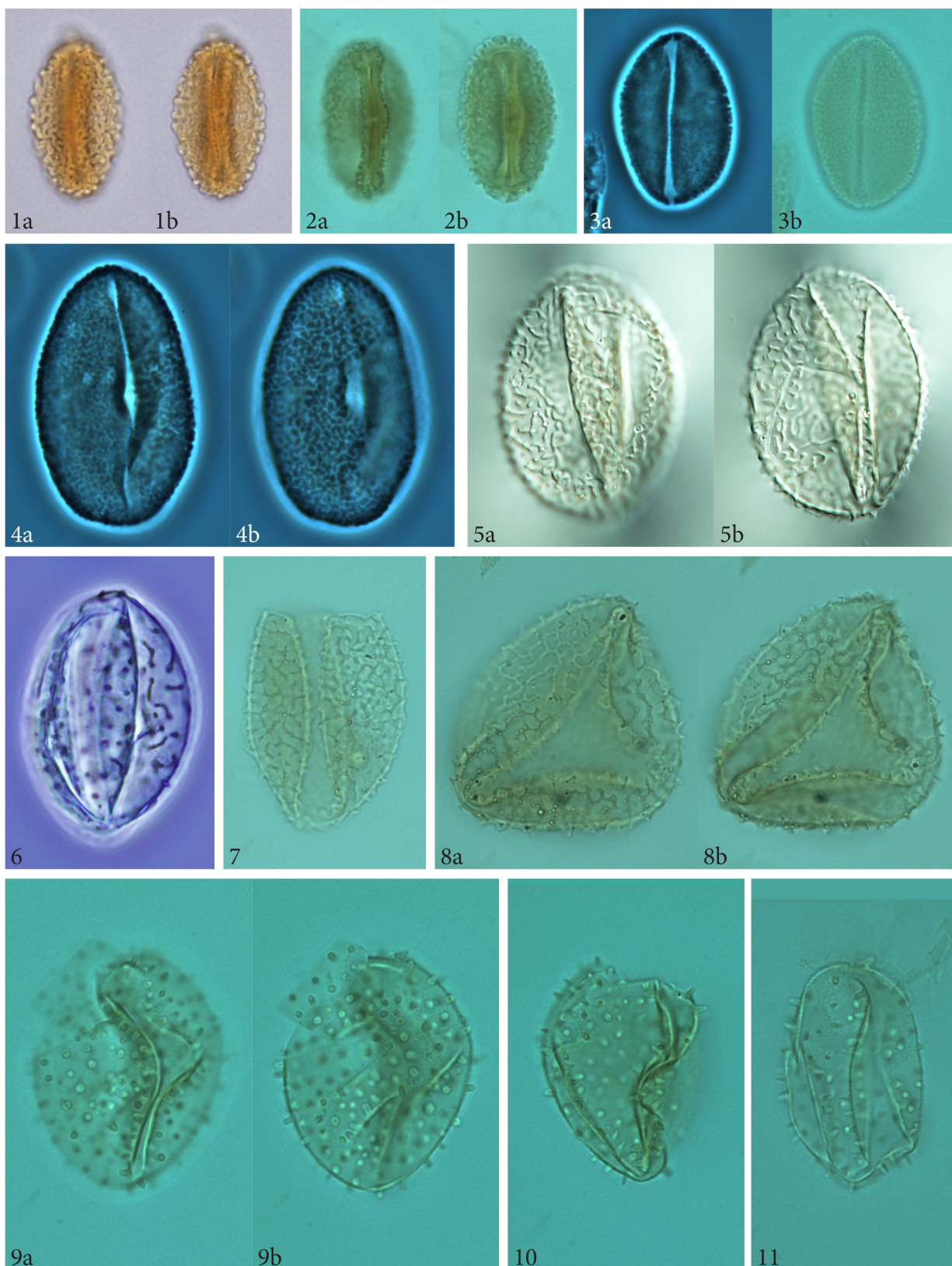


Plate 3.2

Plate 3.2. Monocolpate and trichotomocolpate pollen from IODP 364.

1. *Rugumonocolpites* sp. A, 577.73 mbsf, slide 2, EFS Q24/3.
2. *Rugumonocolpites* sp. A, 523.92 mbsf, slide 1, EFS Q36/1.
3. *Rugumonocolpites* sp. B, 527.08 mbsf, slide 1, EFS U16/1.
4. *Rugumonocolpites* sp. B, 607.22 mbsf, slide 2, EFS S46/0.
5. *Rugumonocolpites* sp. C, 505.88 mbsf, slide 1, EFS Q33/1.
6. *Rugumonocolpites* sp. C, 520.79 mbsf, slide 1, EFS L18/0.
7. *Rugumonocolpites* sp. C, 505.88 mbsf, slide 2, EFS P30/1.
8. *Rugumonocolpites* sp. C, 505.88 mbsf, slide 1, EFS N17/0.
9. *Echimonocolpites chicxulubensis*, sp. nov. (holotype), 523.92 mbsf, slide 1, EFS N18/0.
10. *Echimonocolpites chicxulubensis*, sp. nov., 563.29 mbsf, slide 1, EFS N41/0.
11. *Echimonocolpites chicxulubensis*, sp. nov., 561.48 mbsf, slide 1, EFS U30/2.

Scale bar=10 μ m.

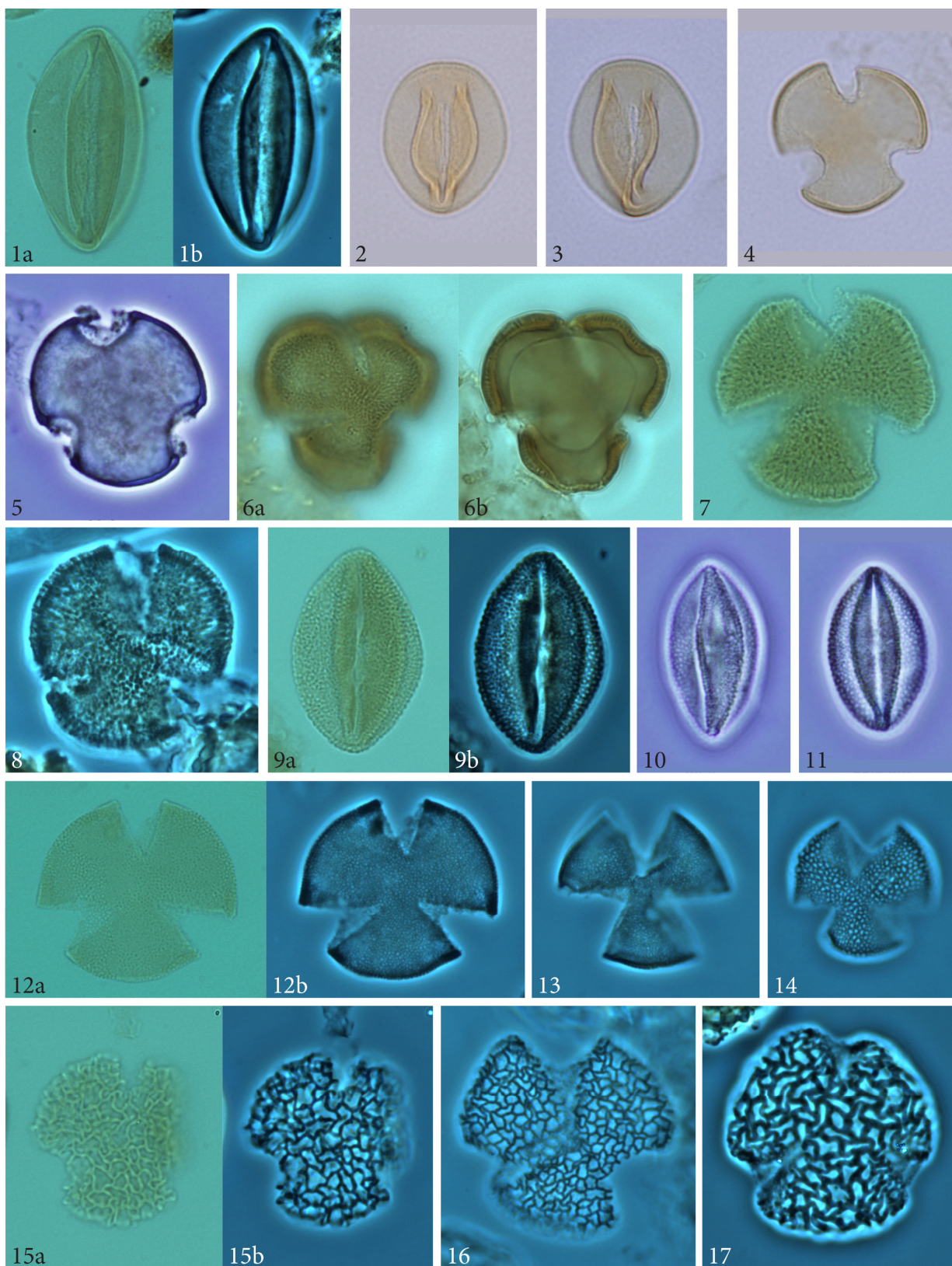


Plate 3.3

Plate 3.3. Tricolpate pollen from IODP 364.

1. *Cupuliferoidaepollenites* sp., 569.50 mbsf, slide 1, EFS L34/1.
2. *Eucommia?* sp. A, 519.31 mbsf, slide 1, EFS U19/0.
3. *Eucommia?* sp. A, 525.48 mbsf, slide 1, EFS H31/1.
4. *Psilatricolpites* sp. A, 577.73 mbsf, slide 2, EFS V26/0.
5. *Psilatricolpites* sp. A, 520.79 mbsf, slide 1, EFS R35/1.
6. *Scabratricolpites* sp. B, 606.61 mbsf, slide 2, EFS R34/2.
7. *Scabratricolpites* sp. A, 540.89 mbsf, slide 1, EFS S31/1.
8. *Scabratricolpites* sp. A, 548.96 mbsf, slide 1, EFS P43/0.
9. *Fraxinoipollenites* sp., 520.79 mbsf, slide 1, EFS S39/1.
10. *Fraxinoipollenites* sp., 509.17 mbsf, slide 2, EFS G29/0.
11. *Fraxinoipollenites* sp. 509.17 mbsf, slide 2, EFS K22/1.
12. *Tricolpites hians*. 564.86 mbsf, slide 1, EFS P37/1.
13. *Tricolpites hians*, 564.86 mbsf, slide 1, EFS P39/1.
14. *Tricolpites* sp. A, 531.75 mbsf, slide 1, EFS U44/1.
15. *Retitrescolpites anguloluminosus*, 520.79 mbsf, slide 1, EFS R27/2.
16. *Retitrescolpites anguloluminosus*, 547.42 mbsf, slide 2, EFS L27/2.
17. *Retitrescolpites* sp. A, 530.24 mbsf, slide 2, EFS Q13/1.

Scale bar=10 μ m.

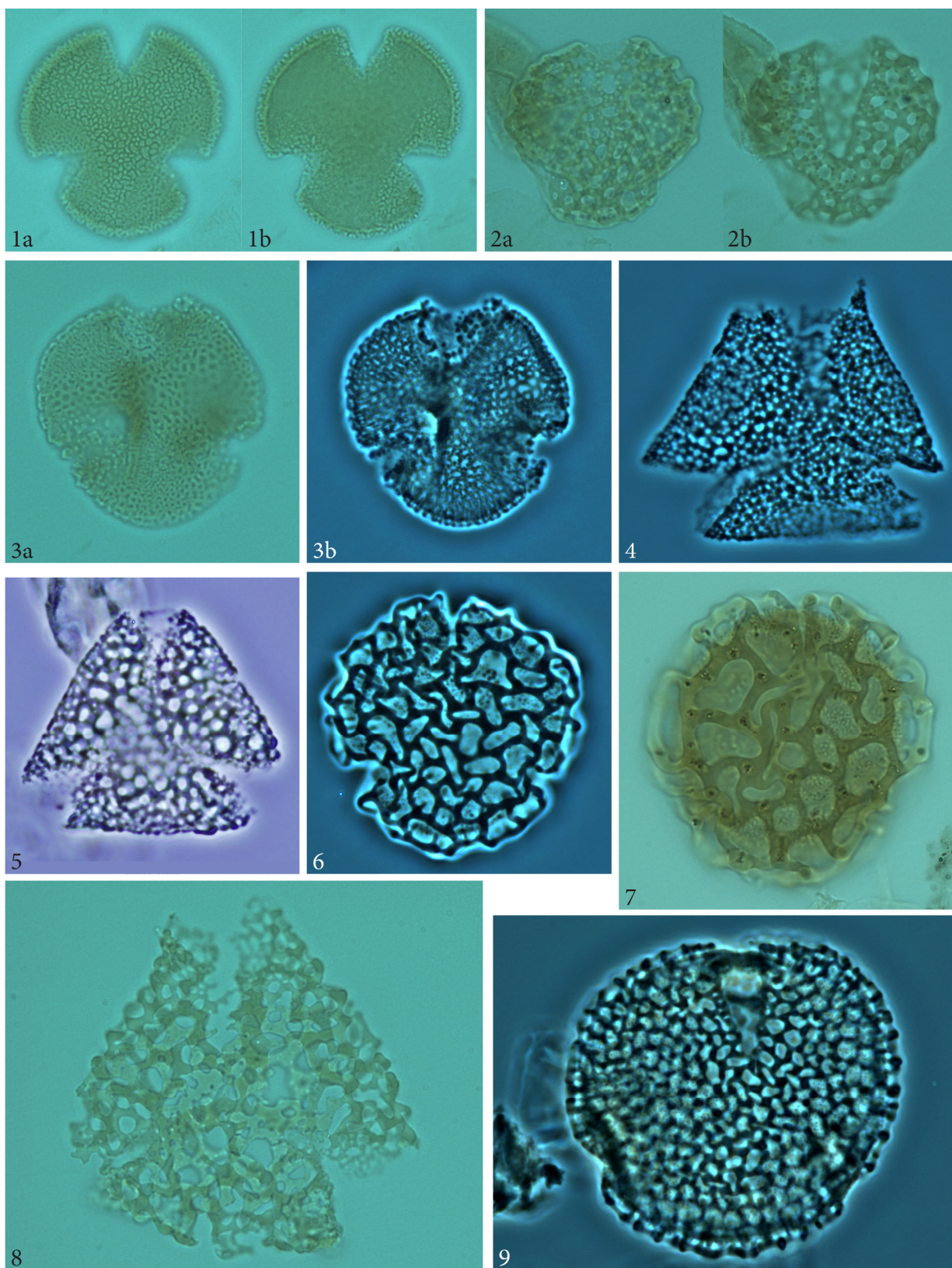


Plate 3.4

Plate 3.4. Tricolpate pollen from IODP 364.

1. *Retitrescolpites* sp. A, 558.26 mbsf, slide 1, EFS R13/1.
 2. *Retitrescolpites* sp. A, 561.48 mbsf, slide 1, EFS S40/1.
 3. *Retitrescolpites* sp. B, 516.00 mbsf, slide 1, EFS U12/1.
 4. *Retitrescolpites* sp. C, 561.48 mbsf, slide 1, EFS Q21/2.
 5. *Retitrescolpites* sp. C, 520.79 mbsf, slide 2, EFS O31/0.
 6. *Spirosyncolpites spiralis*, 561.48 mbsf, slide 1, EFS V10/1.
 7. *Spirosyncolpites spiralis*, 582.78 mbsf, slide 1, EFS T29/0.
 8. *Retitrescolpites* sp. C, 516.00 mbsf, slide 1, EFS Q32/1.
 9. *Spirosyncolpites spiralis*, 510.90 mbsf, slide 1, EFS O28/2.
- Scale bar=10 μ m.

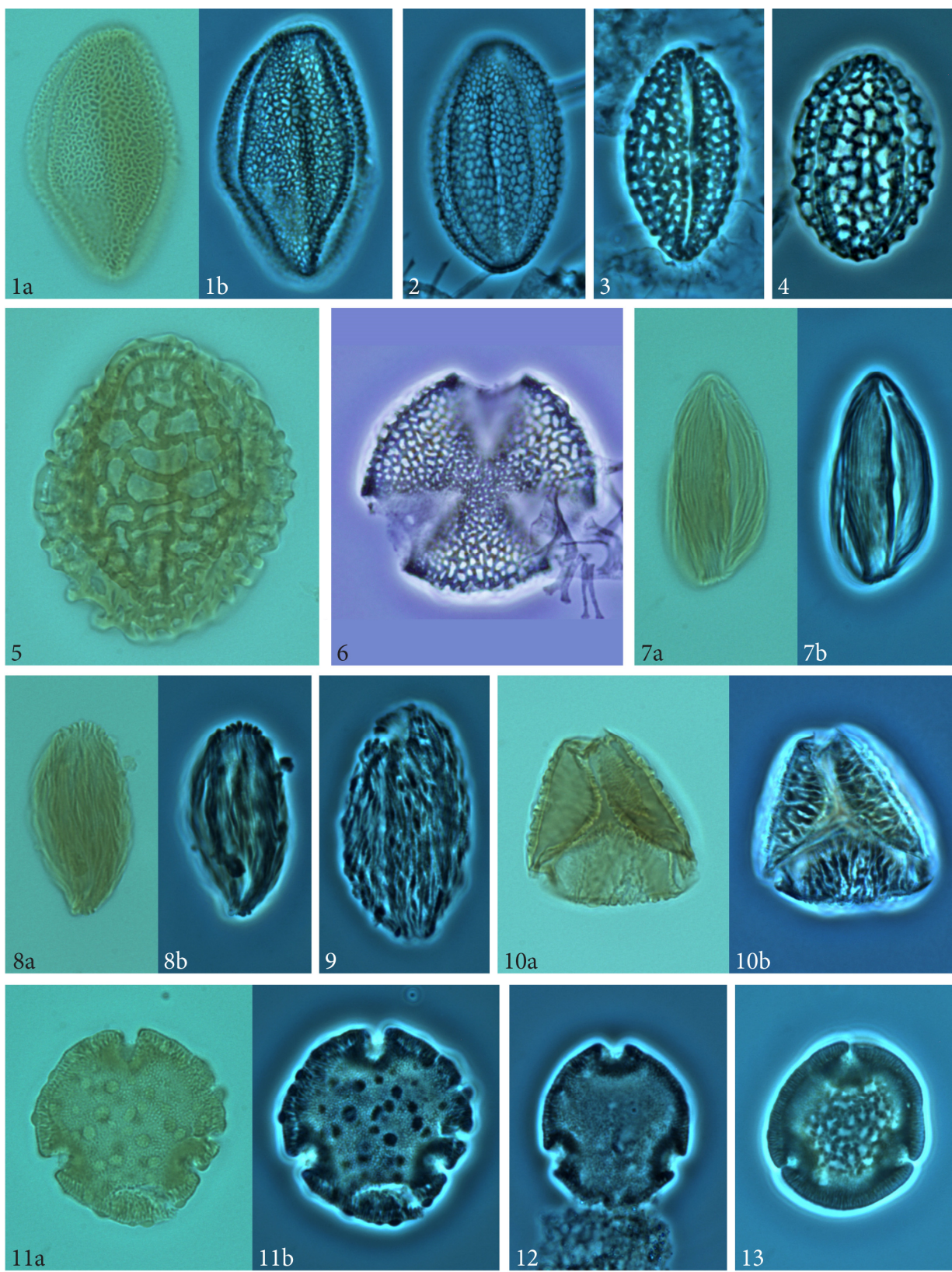


Plate 3.5

Plate 3.5. Tricolpate pollen from IODP 364.

1. *Retitricolpites* sp. A, 555.07 mbsf, slide 1, EFS R38/1.
2. *Retitricolpites* sp. A, 536.39 mbsf, slide 1, EFS T45/1.
3. *Retitricolpites* sp. B, 536.39 mbsf, slide 1, EFS Q20/0.
4. *Retitricolpites* sp. B, 505.88 mbsf, slide 2, EFS Q31/1.
5. *Retitricolpites* sp. C, 523.92 mbsf, slide 1, EFS P22/2.
6. *Rousea* sp. A, 520.79 mbsf, slide 1, EFS K19/0.
7. *Striatopollis grahamii*, sp. nov., 551.98 mbsf, slide 1, EFS T37/1.
8. *Striatopollis grahamii*, sp. nov. (holotype), 520.79 mbsf, slide 1, EFS S39/1.
9. *Striatopollis grahamii*, sp. nov., 520.79 mbsf, slide 1, EFS W23/2.
10. *Insulapollenites* aff. *I. rugulatus*, 606.61 mbsf, slide 1, EFS W42/1.
11. *Discoidites* sp. A, 520.79 mbsf, slide 1, EFS R 46/0.
12. *Discoidites* sp. A, 597.10 mbsf, slide 2, EFS U30/2.
13. *Discoidites* sp. A, 533.27 mbsf, slide 1, EFS Q28/1.

Scale bar=10 μ m.

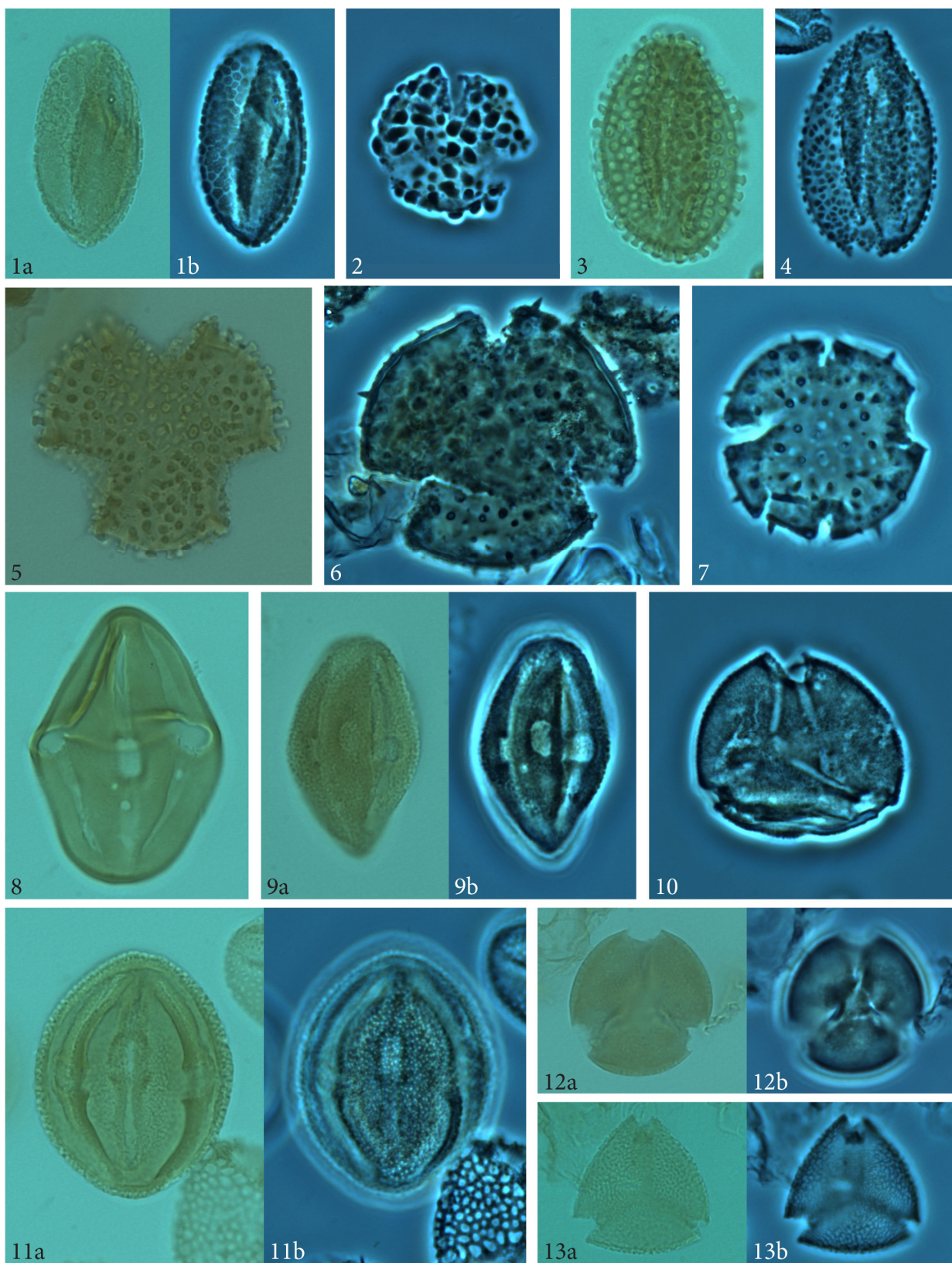


Plate 3.6

Plate 3.6. Tricolpate and tricolporate pollen from IODP 364.

1. *Verrutricolpites* sp. A, 542.61 mbsf, slide 2, EFS R38/1.
2. *Verrutricolpites* sp. B, 597.10 mbsf, slide 2, EFS S10/2.
3. *Clavatricolpites* aff. *C. gracilis*, 533.54 mbsf, slide 1, EFS S21/0.
4. *Clavatricolpites* aff. *C. gracilis*, 537.86 mbsf, slide 1, EFS Q26/2.
5. *Clavatricolpites* sp. A, 510.90 mbsf, slide 2, EFS O17/0.
6. *Echitricolpites* sp. A, 566.52 mbsf, slide 1, EFS N29/2.
7. *Echitricolpites* sp. A, 547.42 mbsf, slide 2, EFS M36/1.
8. *Psilatricolporites* sp. A, 555.07 mbsf, slide 1, EFS V36/1.
9. *Scabratricolporites* sp. A, 547.42 mbsf, slide 2, EFS V25/2.
10. *Scabratricolporites* sp. B, 572.75 mbsf, slide 2, EFS W29/2.
11. *Punctatricolporites* sp. A, 537.86 mbsf, slide 1, EFS S43/3.
12. *Syncolporites* sp. A, 606.61 mbsf, slide 1, EFS R23/2.
13. *Syncolporites?* sp. B, 523.92 mbsf, slide 1, EFS Q31/2.

Scale bar=10 μ m.

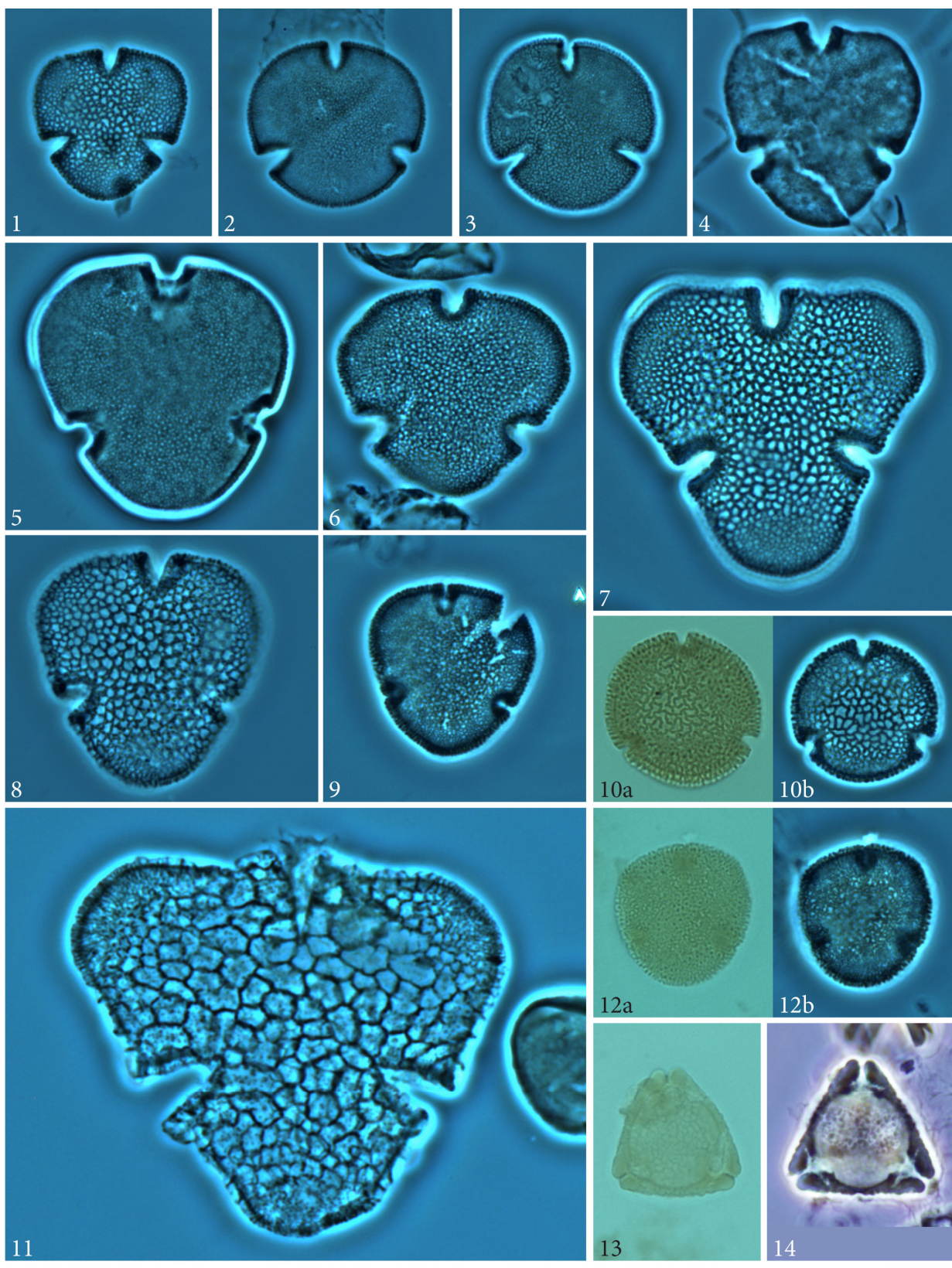


Plate 3.7

Plate 3.7. Tricolporate pollen from IODP 364.

1. *Bombacacidites* sp. A, 528.69 mbsf, slide 2, EFS T29/2.
2. *Bombacacidites brevis*, 537.86 mbsf, slide 1, EFS U38/0.
3. *Bombacacidites brevis*, 553.54 mbsf, slide 1, EFS Q14/1.
4. *Bombacacidites nanobrochatus*, 607.22 mbsf, slide 2, EFS F33/0.
5. *Bombacacidites nanobrochatus*, 527.08 mbsf, slide 1, EFS U14/0.
6. *Bombacacidites bombaxoides*, 512.24 mbsf, slide 2, EFS S28/2.
7. *Bombacacidites nacimientoensis*, 553.54 mbsf, slide 1, EFS Q25/2.
8. *Bombacacidites nacimientoensis*, 537.86 mbsf, slide 1, EFS T34/0.
9. *Tiliaepollenites* sp., 523.92 mbsf, slide 1, EFS S29/2.
10. *Tiliaepollenites* sp., 607.04 mbsf, slide 1, EFS S37/0.
11. *Bombacacidites* sp. B, 564.86 mbsf, slide 1, EFS F25/4.
12. *Tiliaepollenites* sp., 512.24 mbsf, slide 2, EFS N19/4.
13. *Basopollis* sp. A, 536.39 mbsf, slide 1, EFS U41/0.
14. *Basopollis* sp. A, 520.79 mbsf, slide 1, EFS P21/4.

Scale bar=10 μ m.

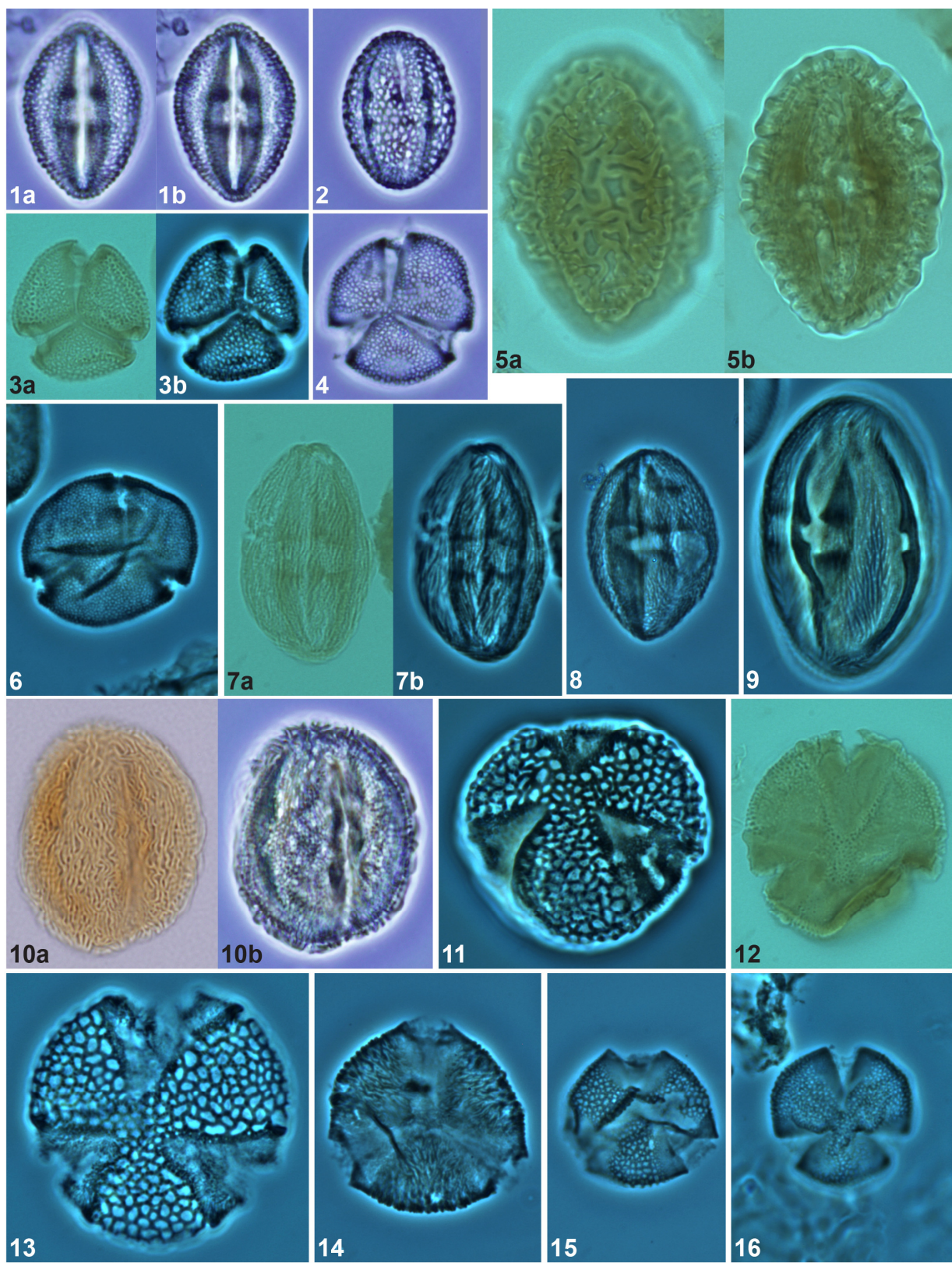


Plate 3.8

Plate 3.8. Tricolporate pollen from IODP 364.

1. *Retitricolporites* sp. A, 520.79 mbsf, slide 1, EFS H19/1.
2. *Retitricolporites* sp. A, 520.79 mbsf, slide 1, EFS M27/2.
3. *Retitricolporites* sp. B, 527.08 mbsf, slide 1, EFS T41/1.
4. *Retitricolporites* sp. B, 542.61 mbsf, slide 1, EFS U19/0.
5. *Retitricolporites* sp. D, 553.54 mbsf, slide 1, EFS U46/0.
6. *Retitricolporites* sp. C, 514.14 mbsf, slide 1, EFS T35/2.
7. *Striatricolporites* aff. *S. conspicuus*, 520.79 mbsf, slide 1, EFS S33/1.
8. *Rhuspollenites* sp., 607.22 mbsf, slide 2, EFS O39/1.
9. *Rhuspollenites* sp., 558.26 mbsf, slide 1, EFS R24/0.
10. *Striatricolporites* sp. A, 520.79 mbsf, slide 1, EFS J19/1.
11. *Margocolporites vanwijhei*, 520.79 mbsf, slide 1, EFS T44/0.
12. *Margocolporites* sp. A, 507.53 mbsf, slide 2, EFS S17/1.
13. *Margocolporites vanwijhei*, 523.92 mbsf, slide 1, EFS T35/1.
14. *Margocolporites?* sp. C, 607.22 mbsf, slide 2, EFS G28/4.
15. *Margocolporites* sp. B, 607.22 mbsf, slide 2, EFS G28/4.
16. *Margocolporites* sp. B, 528.69 mbsf, slide 2, EFS O38/0.

Scale bar=10 μ m.

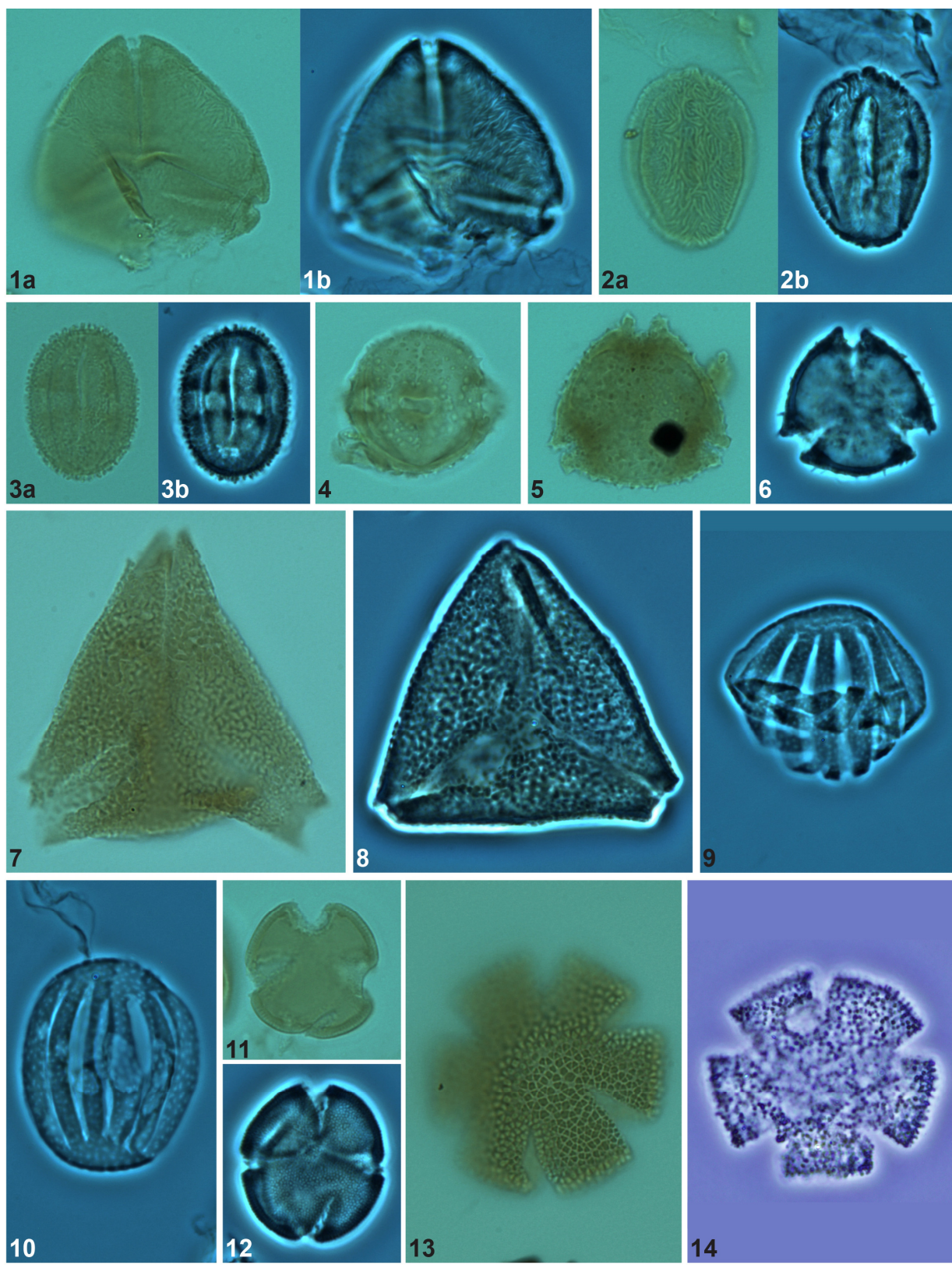


Plate 3.9

Plate 3.9. Tricolporate and stephanocolpate pollen from IODP 364.

1. *Rugutricolporites* sp. A, 569.50 mbsf, slide 1, EFS N27/1.
2. *Rugutricolporites* aff. *R. felix*, 512.24 mbsf, slide 2, EFS O30/1.
3. *Ilexpollenites* cf. *I. verrucatus*, 556.58 mbsf, slide 1, EFS U23/0.
4. *Echitricolporites* sp. A, 555.07 mbsf, slide 1, EFS Q17/2.
5. *Echitricolporites* sp. A, 569.50 mbsf, slide 1, EFS N34/3.
6. *Echitricolporites* sp. A, 523.92 mbsf, slide 1, EFS R24/2.
7. *Boehlensipollis* sp. A, 607.22 mbsf, slide 2, EFS T36/1.
8. *Boehlensipollis* sp. A, 607.22 mbsf, slide 2, EFS J46/1.
9. Polygalaceae? type A, 531.75 mbsf, slide 1, EFS L26/0.
10. Polygalaceae? type A, 509.17 mbsf, slide 1, EFS Q37/1.
11. *Psilastephanocolpites* sp. A, 551.98 mbsf, slide 1, EFS V24/2.
12. *Retistephanocolpites* sp. A, 606.61 mbsf, slide 2, EFS H28/2.
13. *Clavastephanocolpites* aff. *C. crotonoides*, 607.04 mbsf, slide 2, EFS K36/1.
14. *Clavastephanocolpites* aff. *C. crotonoides*, 607.22 mbsf, slide 1, EFS N24/0.

Scale bar=10 μ m.

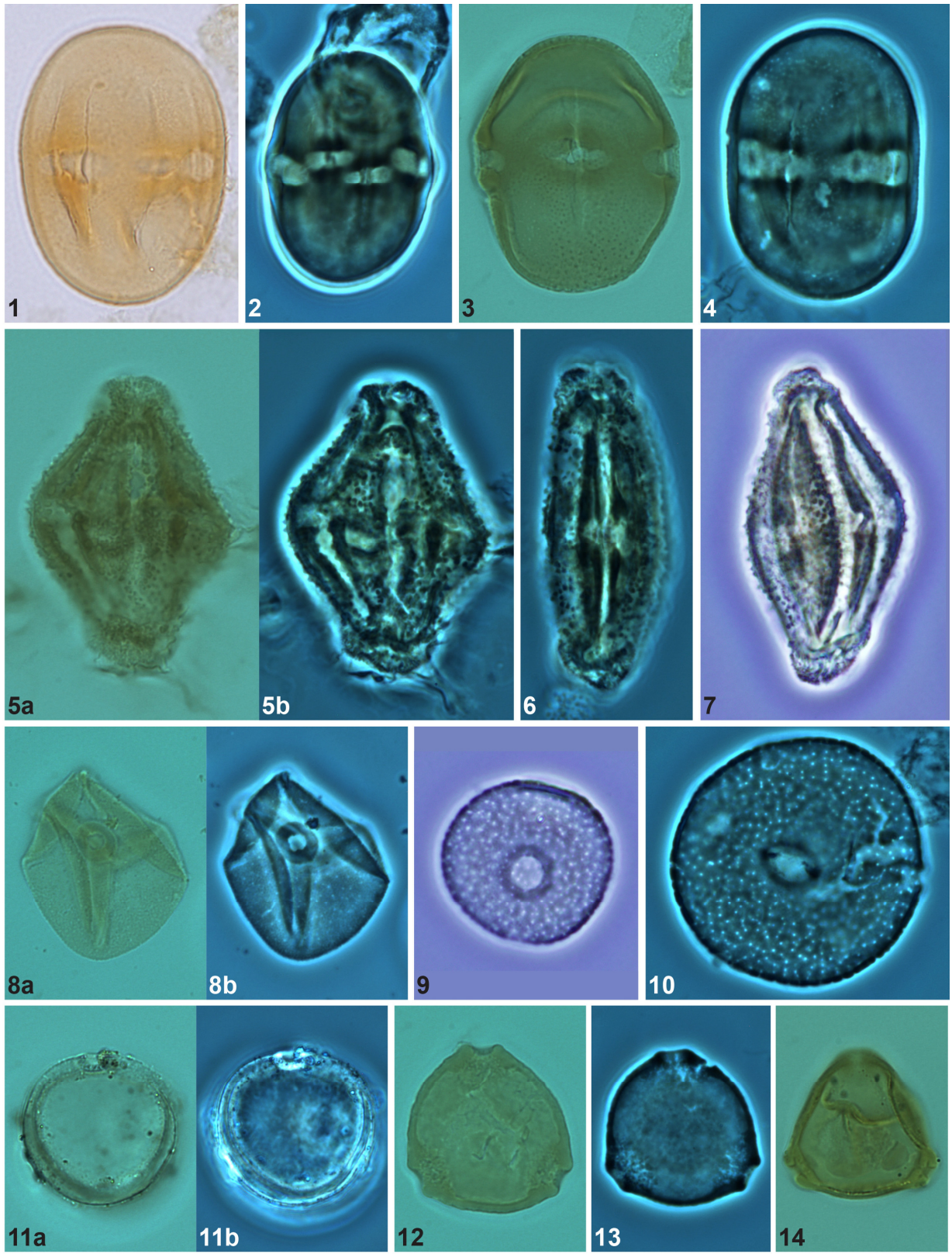


Plate 3.10

Plate 3.10. Stephanocolporate, monoporate, and triporate pollen from IODP 364.

1. *Psilastephanocolporites hammenii*, sp. nov., 577.73 mbsf, slide 2, EFS G19/4.
 2. *Psilastephanocolporites hammenii*, sp. nov. (holotype), 597.10 mbsf, slide 1, EFS P38/1.
 3. *Psilastephanocolporites hammenii*, sp. nov., 540.89 mbsf, slide 1, EFS P24/2.
 4. *Psilastephanocolporites hammenii*, sp. nov., 564.86 mbsf, slide 1, EFS P36/1.
 5. Stephanocolporate type A, 520.79 mbsf, slide 1, EFS X43/0.
 6. Stephanocolporate type A, 505.88 mbsf, slide 1, EFS O34/1.
 7. Stephanocolporate type A, 520.79 mbsf, slide 1, EFS N23/0.
 8. *Monoporopollenites annulatus*, 606.61 mbsf, slide 1, EFS G28/4.
 9. *Milfordia minima*, 525.48 mbsf, slide 1, EFS H33/1.
 10. *Milfordia hungarica*, 569.50 mbsf, slide 1, EFS O25/2.
 11. Betulaceae type A, 615.03 mbsf, slide 1, EFS R16/0.
 12. Betulaceae/Myricaceae type, 533.27 mbsf, slide 1, EFS S23/0.
 13. Betulaceae/Myricaceae type, 536.39 mbsf, slide 1, EFS U39/1.
 14. *Trivestibulopollenites* sp. A, 607.35 mbsf, slide 1, EFS S28/2.
- Scale bar=10 μ m.

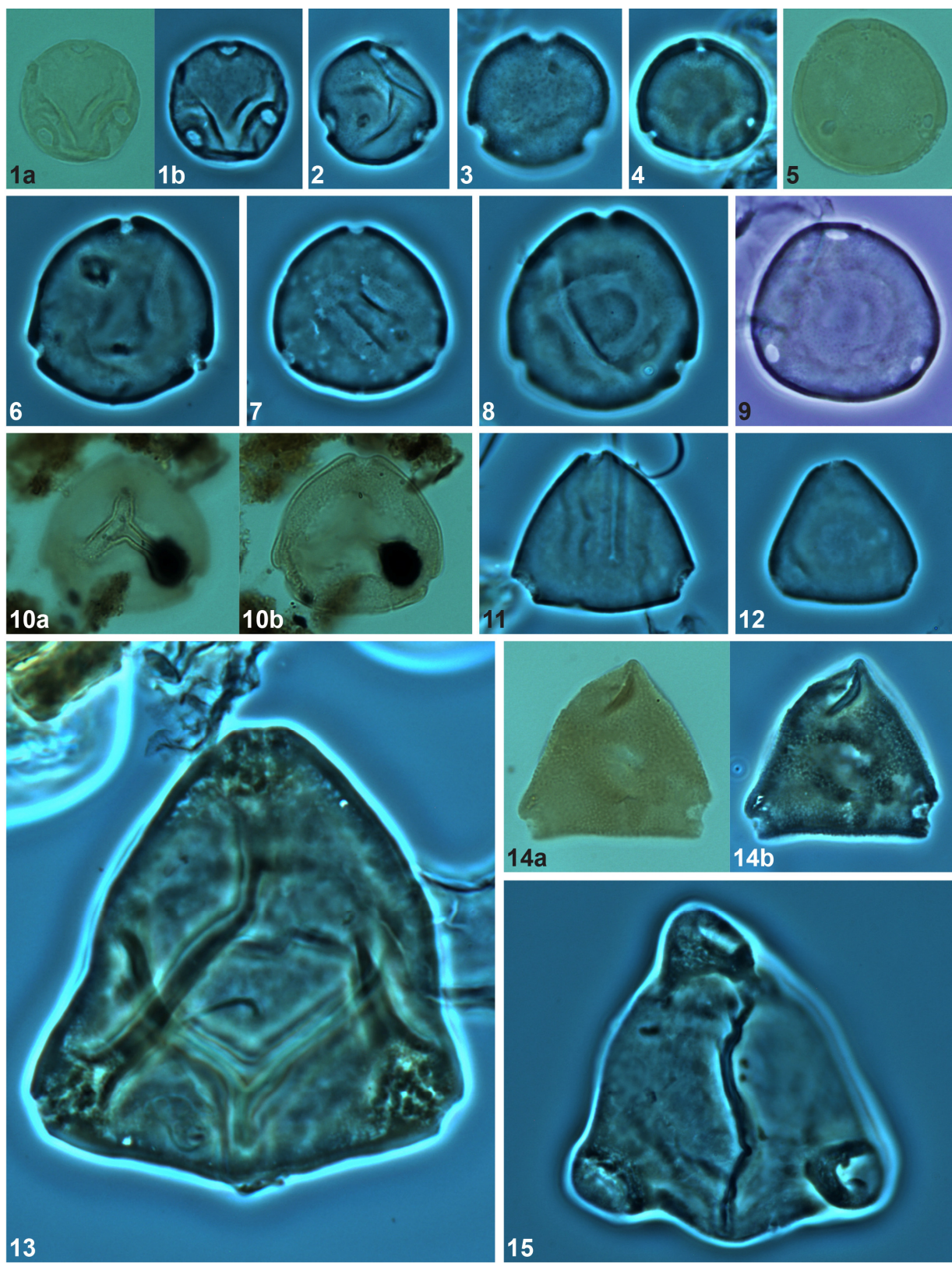


Plate 3.11

Plate 3.11. Triporate pollen from IODP 364.

1. *Cricotriporites* sp. A, 507.53 mbsf, slide 2, EFS W44/1.
 2. *Cricotriporites* sp. A, 512.24 mbsf, slide 2, EFS N38/1.
 3. *Scabratriporites redundans*, 514.14 mbsf, slide 1, EFS R36/1.
 4. *Subtriporopollenites* cf. *S. nanus*, 527.08 mbsf, slide 1, EFS U28/2.
 5. *Subtriporopollenites* cf. *S. nanus*, 536.39 mbsf, slide 1, EFS U41/0.
 6. *Momipites coryloides*, 520.79 mbsf, slide 1, EFS V35/1.
 7. *Momipites coryloides*, 553.54 mbsf, slide 1, EFS T33/1.
 8. *Momipites amplius*, 530.24 mbsf, slide 2, EFS Q29/1.
 9. *Caryapollenites veripites*, 509.17 mbsf, slide 2, EFS K23/0.
 10. *Momipites triradiatus*, 566.52 mbsf, slide 2, EFS P22/2.
 11. *Psilatriporites* sp. A, 527.08 mbsf, slide 1, EFS T41/0.
 12. *Psilatriporites* sp. A, 527.08 mbsf, slide 1, EFS R32/4.
 13. *Corsinipollenites parviangulus*, 606.61 mbsf, slide 2, EFS T17/0.
 14. *Cranwellipollis?* sp. A, 607.22 mbsf, slide 2, EFS O24/2.
 15. *Corsinipollenites oculusnoctis*, 561.48 mbsf, slide 1, EFS V17/1.
- Scale bar=10 μ m.

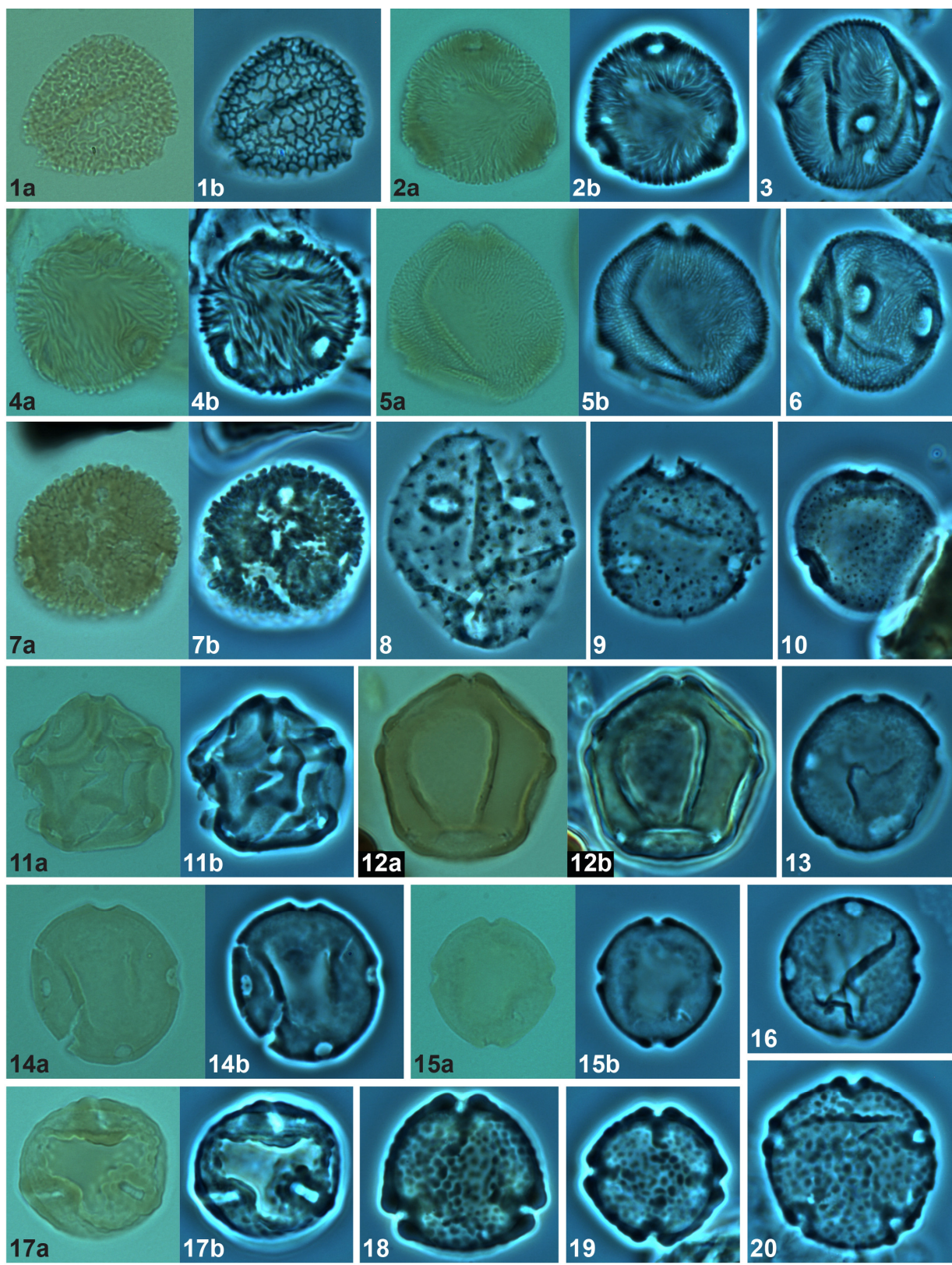


Plate 3.12

Plate 3.12. Triporate and stephanoporate pollen from IODP 364.

1. *Retitriporites* sp. A, 505.88 mbsf, slide 2, EFS P36/1.
2. *Brosipollis striata*, 559.91 mbsf, slide 1, EFS V33/1.
3. *Brosipollis striata*, 547.42 mbsf, slide 2, EFS R43/0.
4. *Brosipollis* aff. *B. striata*, 553.54 mbsf, slide 1, EFS Q20/2.
5. *Brosipollis reticulatus*, sp. nov., 558.26 mbsf, slide 1, EFS R24/0.
6. *Brosipollis reticulatus*, sp. nov. (holotype), 547.42 mbsf, slide 2, EFS L25/2.
7. *Gemmatriporites* sp. A, 607.22 mbsf, slide 2, EFS F17/3.
8. *Echitriporites* sp. A, 505.88 mbsf, slide 2, EFS Q46/0.
9. *Echitriporites* sp. A, 558.26 mbsf, slide 1, EFS R26/2.
10. *Echitriporites* sp. B, 597.10 mbsf, slide 2, EFS U33/1.
11. *Alnus verus*, 522.38 mbsf, slide 2, EFS S28/4.
12. *Alnus verus*, 607.15 mbsf, slide 1, EFS N39/1.
13. *Scabrastephanoporites* sp., 520.79 mbsf, slide 1, EFS U20/2.
14. *Scabrastephanoporites* sp., 569.50 mbsf, slide 1, EFS L36/1.
15. *Scabrastephanoporites* sp., 558.26 mbsf, slide 1, EFS S34/1.
16. *Scabrastephanoporites* sp., 516.00 mbsf, slide 1, EFS T34/2.
17. *Ulmipollenites krempii*, 569.50 mbsf, slide 1, EFS L47/0.
18. *Ulmipollenites krempii*, 607.06 mbsf, slide 1, EFS J31/3.
19. *Ulmipollenites krempii*, 512.24 mbsf, slide 2, EFS S21/2.
20. *Ulmipollenites krempii*, 523.92 mbsf, slide 1, EFS R17/2.

Scale bar=10 μ m.

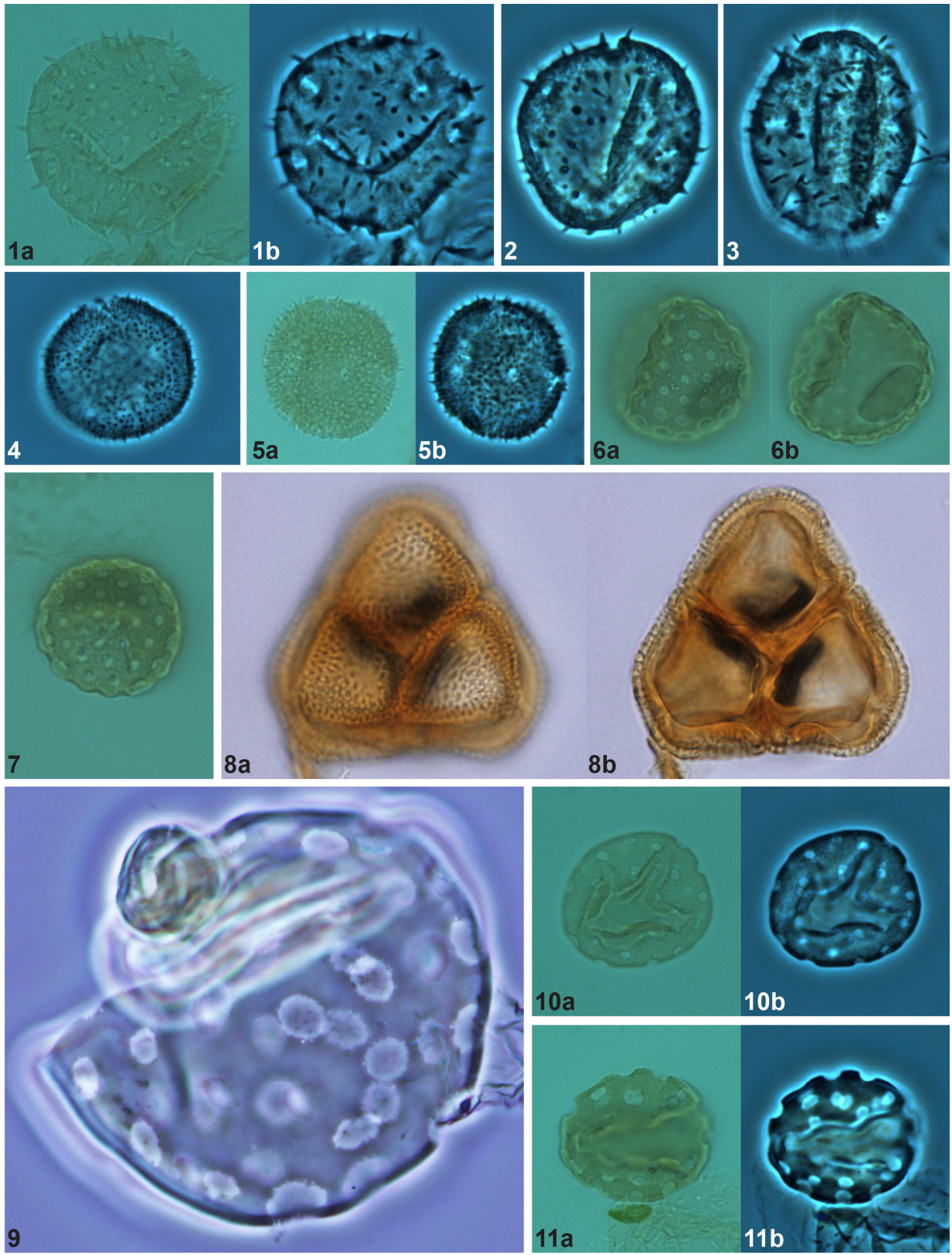


Plate 3.13

Plate 3.13. Stephanoporate and pantoporate pollen from IODP 364.

1. *Malvacipollis* sp. (Euphorbiaceae type), 536.39 mbsf, slide 1, EFS T42/0.
2. *Malvacipollis* sp. (Euphorbiaceae type), 520.79 mbsf, slide 1, EFS M31/0.
3. *Malvacipollis* sp. (Euphorbiaceae type), 527.08 mbsf, slide 1, EFS U24/2.
4. *Malvacipollis*? sp. A (Malvaceae type), 564.86 mbsf, slide 1, EFS N17/4.
5. *Malvacipollis*? sp. A (Malvaceae type), 556.58 mbsf, slide 1, EFS R15/2.
6. *Chenopodipollis* sp. A, 531.75 mbsf, slide 1, EFS K16/1.
7. *Chenopodipollis* sp. A, 531.75 mbsf, slide 1, EFS L29/3.
8. *Retitetradites* sp. A, 577.73 mbsf, slide 2, EFS S27/0.
9. *Psilaperiporites* sp. A, 597.10 mbsf, slide 1, EFS J34/2.
10. *Psilaperiporites suarezi*, 607.22 mbsf, slide 1, EFS T28/0.
11. *Psilaperiporites suarezi*, 579.39 mbsf, slide 1, EFS S33/1.

Scale bar=10 μ m.

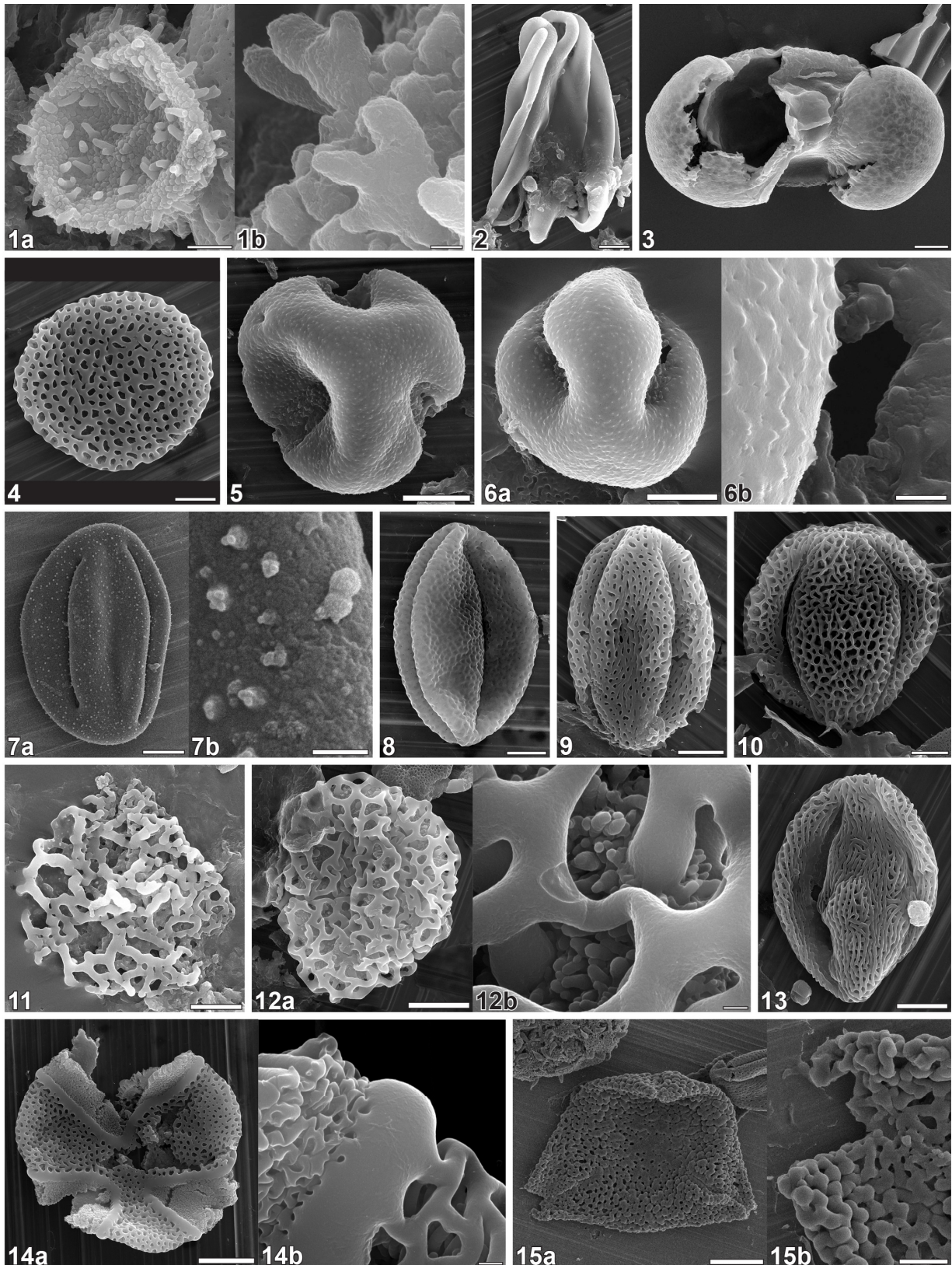


Plate 3.14

Plate 3.14. Scanning electron microscopy images of spores and pollen from IODP 364.

1. *Raistrickia* sp. A, 582.78 mbsf.
2. *Gnetaceaepollenites* sp. A, 577.73 mbsf.
3. Class Pinopsida, 607.18 mbsf.
4. *Retipollenites*? sp. A, 510.90 mbsf.
5. *Psilatricolpites* sp. A, 577.73 mbsf.
6. *Eucommia*? sp. A, 517.61 mbsf.
7. *Cupuliferoidaepollenites* sp., 510.90 mbsf.
8. *Fraxinoipollenites* sp., 505.88 mbsf.
9. *Retitricolpites* sp. A, 505.88 mbsf.
10. *Retitricolpites* sp. B, 505.88 mbsf.
11. *Retitrescolpites* sp. C, 517.61 mbsf.
12. *Spirosyncolpites spiralis*, 510.90 mbsf.
13. *Ailanthipites* sp. A, 542.61 mbsf.
14. *Margocolporites vanwijhei*, 510.90 mbsf.
15. *Boehlensipollis* sp. A, 510.90 mbsf.

Scale bars: 1a, 2, 4, 5, 6a, 7a, 8–10, 13= 5 μm ; 1b, 6b, 7b, 12b, 14b=0.5 μm ; 3, 11, 12a, 14a, 15a=10 μm ; 15b=2 μm .

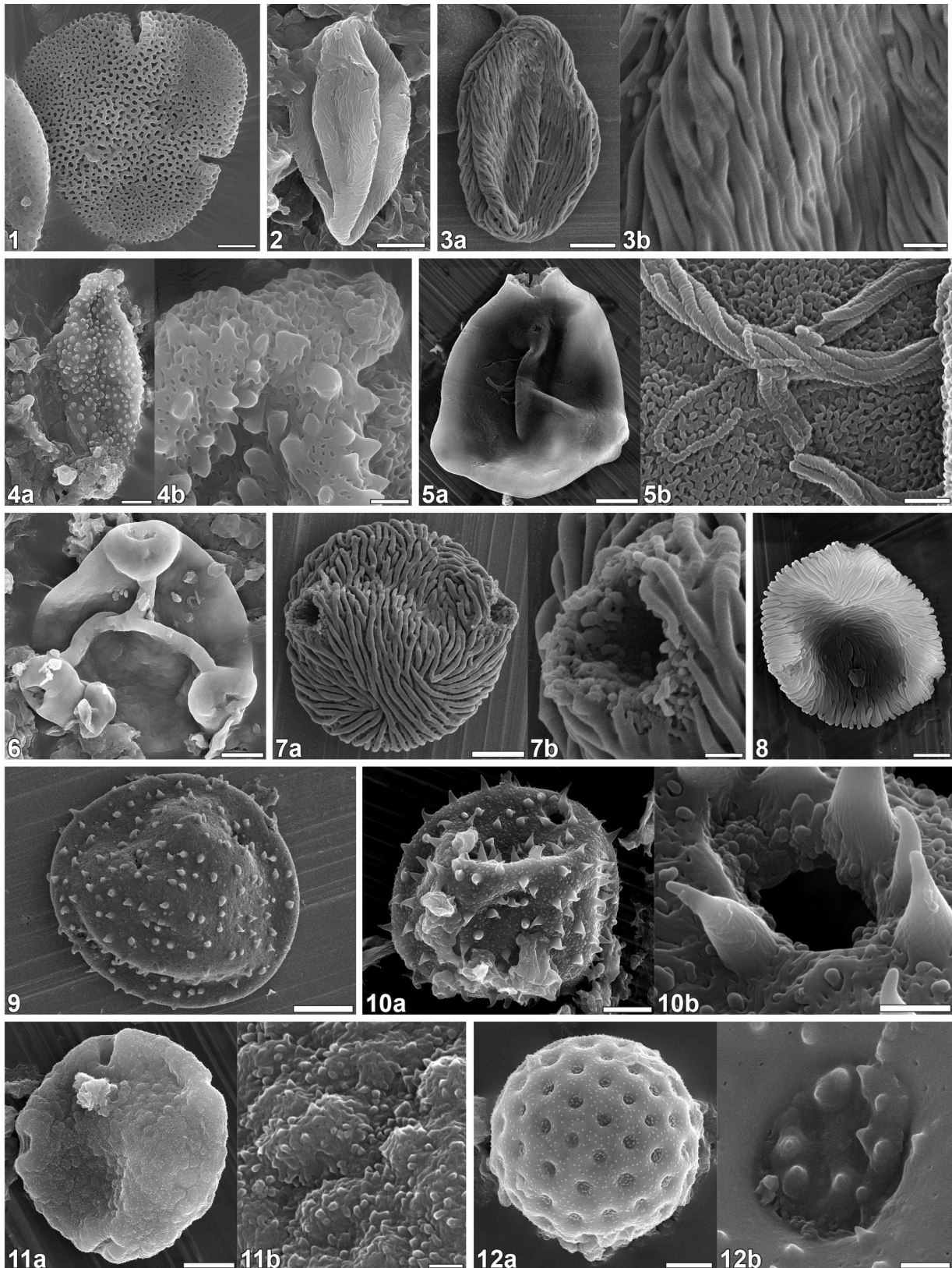


Plate 3.15

Plate 3.15. Scanning electron microscopy images of pollen from IODP 364.

1. *Bombacacidites bombaxoides*, 517.61 mbsf.
2. *Rugutricolporites* aff. *R. felix*, 548.96 mbsf.
3. *Striatopollis grahamii*, sp. nov., 510.90 mbsf.
4. Stephanocolporate type A, 517.61 mbsf.
5. *Corsinipollenites parviangulus*, 510.90 mbsf.
6. *Corsinipollenites oculusnoctis*, 517.61 mbsf.
7. *Brosipollis* aff. *B. striata*, 510.90 mbsf.
8. *Brosipollis striata*, 510.90 mbsf.
9. *Malvacipollis* sp. (Euphorbiaceae type), 510.90 mbsf.
10. *Malvacipollis* sp. (Euphorbiaceae type), 577.73 mbsf.
11. *Ulmipollenites krempii*, 597.10 mbsf.
12. *Chenopodipollis* sp. A, 510.90 mbsf.

Scale bars: 1, 2, 3a, 4a, 7a, 8, 9, 10a, 11a, 12a=5 μm ; 3b, 4b, 5b, 7b, 10b=1 μm ; 5a, 6=10 μm ; 11b, 12b=0.5 μm .

CHAPTER 4. LIFE AND DEATH IN THE CHICXULUB IMPACT CRATER: A RECORD OF THE PALEOCENE-EOCENE THERMAL MAXIMUM

4.1. Introduction and geologic setting

The Paleocene-Eocene Thermal Maximum was a period of global warming associated with ocean acidification, an intensified hydrological cycle, reductions in marine dissolved oxygen concentrations, eustatic sea level rise, and ecological shifts (e.g., Zachos et al. 2003; Gingerich 2006; Dickson et al. 2014; Sluijs et al. 2014; Carmichael et al. 2017). Recent age estimates place the PETM at approximately 55.93-55.71 Ma (Westerhold et al. 2017; Hollis et al. 2019). The onset of the PETM is marked by a global negative carbon isotope excursion (CIE) (Dickens et al. 1997; Gradstein et al. 2012). Possible sources of this isotopically light carbon include methane clathrates, combustion of organic matter, thermogenic methane, desiccation of epicontinental seas, and organic matter released from permafrost (McInerney and Wing 2011). Sea surface temperatures during the PETM in some low-latitude regions exceeded 35 °C, resulting in heat stress for eukaryotic plankton (e.g., Frieling et al. 2018). In contrast, the few existing PETM records of low-latitude terrestrial plant assemblages indicate an increase in diversity (e.g., Jaramillo et al. 2010; Srivastava and Prasad 2015; Prasad et al. 2018). Here, we established a new multiproxy record of the response of marine and terrestrial biota to the PETM in the western Caribbean/Gulf of Mexico at International Ocean Discovery Program (IODP) Expedition 364 Site M0077. This includes the first published pollen and spore PETM assemblage from tropical North America (Smith et al. 2019; Smith, Warny, Jarzen, et al. 2020). These data allow us to determine the extent of marine and terrestrial heat stress from the understudied region and determine how they compare with other PETM sections.

Site M0077 targeted the peak ring of the Chicxulub impact crater in the Yucatán Peninsula, México (Fig. 1) (Morgan et al. 2017). The crater was a marine depositional basin in the Paleogene, with mainly pelagic and outer-platform sediment deposition (Lefticariu et al. 2006). Immediately after impact, some of the rim may have been subaerially emergent (Morgan et al. 1997), but, if so, would have been quickly eroded. During the PETM, only isolated areas of the crater rim were still emergent, given the existence of an embayment into the crater to the north and northwest (Gulick et al. 2008). Although PETM records from the Gulf of Mexico are scarce, another site in the Chicxulub crater, the Yaxcopoil-1 (Yax-1) core, contains a PETM section identified by a negative carbon isotope excursion, deposited during a period of maximum flooding (Whalen et al. 2013) (Fig. 1). The PETM has also been identified on the Mississippi paleoshelf (Fig. 1), where evidence indicates increased TEX₈₆^H-based sea surface temperatures (SSTs), photic zone euxinia, and sea level rise (Sluijs et al. 2014).

4.2. Methods

Quantitative palynological abundances are expressed in terms of specimens per gram, using a *Lycopodium* spike. Species counts, descriptions, and paleoecological interpretations can be found in Smith et al. (2019) and Smith, Warny, Jarzen, et al. (2020). The D/S ratio between dinoflagellate cysts and pollen/plant spores is described in Warny et al. (2003). The degree of bioturbation has been quantified using the Bioturbation Index (BI) (Taylor and Goldring 1993).

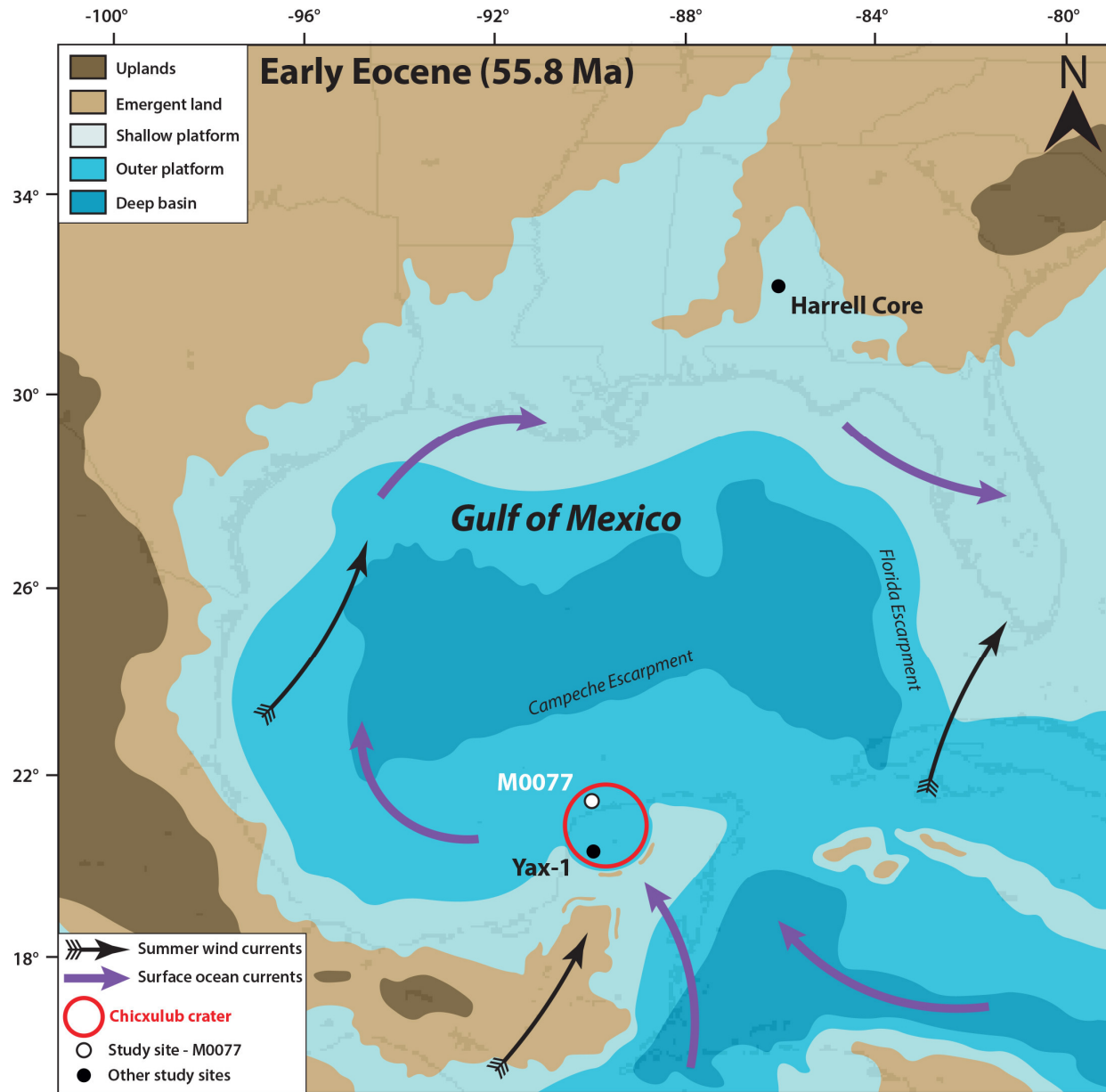


Figure 4.1. Paleocene-Eocene Thermal Maximum (55.8 Ma) paleogeography of the Gulf of Mexico and surrounding regions, modified from Scotese and Wright (2018), with locations of Site M0077 (IODP 364), Yax-1 (Whalen et al. 2013), and the Harrell Core in east-central Mississippi (Sluijs et al. 2014). The Harrell Core location has been adjusted to match the paleo-latitude/longitude at the PETM. Surface ocean currents and summer wind fields from Winguth et al. (2010).

Samples for $\delta^{15}\text{N}_{\text{bulk}}$ and $\delta^{13}\text{C}_{\text{TOC}}$ ($n = 51$) analyses were prepared by acidifying approximately 0.5 g subsamples of powdered material with an excess of 1 M HCl. The acid-insoluble residues were neutralized, freeze-dried and analyzed for their carbon and nitrogen contents as well as stable isotope compositions using a Costech Elemental Analyzer (ECS 4010) and a Delta+XP mass spectrometer. Typical instrumental precision of the isotope measurements is $<0.2\text{‰}$. Clay mineral assemblages were identified by X-ray diffraction on oriented mounts of non-calcareous clay-sized particles ($<2\text{ }\mu\text{m}$). SSTs were estimated using the $\text{TEX}_{86}^{\text{H}}$ calibration of Kim et al. (2010). Additional methods are provided as supplementary materials along with all data.

4.3. Results

IODP drilling at Site M0077 recovered Paleocene to early Eocene post-impact sedimentary rocks between 617.33-505.70 meters below seafloor (mbsf) (Fig. 2). The PETM section (607.27-607.06 mbsf) is a laminated black to dark gray shale, separated from an upper Paleocene carbonate hardground by an unconformity, and grading upwards into a burrowed lower Eocene packstone. Bioturbation is absent to minimal in the PETM, with rare *Chondrites* ichnofossils, except at the top of the interval (607.11-607.06 mbsf) where *Planolites* burrows are observed, infilled with sediment from the overlying packstone. The clay mineral assemblages are dominated by R0 random illite/smectite mixed layers (up to 90%), and also contains traces of chlorite, illite, and palygorskite. The latter is rare in the upper Paleocene, and increases in abundance through the PETM, reaching a peak at 607.08 mbsf. The PETM interval is characterized by a marked increase in magnetic susceptibility, anhysteretic remanent magnetization (ARM), and isothermal remanent magnetization (IRM). The average values increase by a factor of 15.7, 5.8, and 12.4 for χ , ARM, and IRM, respectively, compared to the average values over the analyzed pre-PETM interval (607.67-607.27 mbsf) (see supplementary materials).

Total organic carbon (TOC) is low above and below the PETM (Fig. 2), with unusually high concentrations ($>10\%$ rock weight) in the upper PETM. $\delta^{13}\text{C}_{\text{TOC}}$ is -28.4‰ at the base of the PETM section, and generally becomes more negative upsection, with the most depleted values of ca. -30‰ in the upper PETM. Above 607.07 mbsf, $\delta^{13}\text{C}_{\text{TOC}}$ values become more positive, then stabilize at ca. -27.5‰ at 607.03 mbsf. $\delta^{15}\text{N}_{\text{bulk}}$ is 5.3‰ at the base of the PETM, with more depleted values through the PETM, reaching a minimum around -2‰ at 607.21 mbsf. The PETM $\delta^{15}\text{N}_{\text{bulk}}$ record is marked by two negative excursions with values below 0‰ , separated by an interval of positive $\delta^{15}\text{N}_{\text{bulk}}$ values between 607.17-607.13 mbsf. Above 607.10 mbsf, $\delta^{15}\text{N}_{\text{bulk}}$ values become more positive, reaching $\sim 1\text{‰}$ at the top of the analyzed interval (Fig. 2).

$\text{TEX}_{86}^{\text{H}}$ -based SSTs rose from $\sim 34\text{ }^{\circ}\text{C}$ in the late Paleocene section to $\sim 38\text{ }^{\circ}\text{C}$ in the PETM section, then decreased slightly in the early post-PETM section (Fig. 2). Green and purple sulfur bacteria biomarkers (chlorobactane, okenane, and isorenieratane) reach their highest concentrations near the bottom of the PETM section, with low concentrations through the rest of the event (Fig. 2). Nannofossil abundances decrease through the PETM section and become rare in the post-PETM section. Foraminifera at Site M0077 are frequent to abundant in the upper Paleocene section but are absent to very rare in the PETM section, with evidence of reworking. Dinosterane concentrations are relatively high in the upper Paleocene and lower PETM section, with lower abundance in the PETM and post-PETM sections. Organic-walled microfossils are

IODP 364, Site M0077

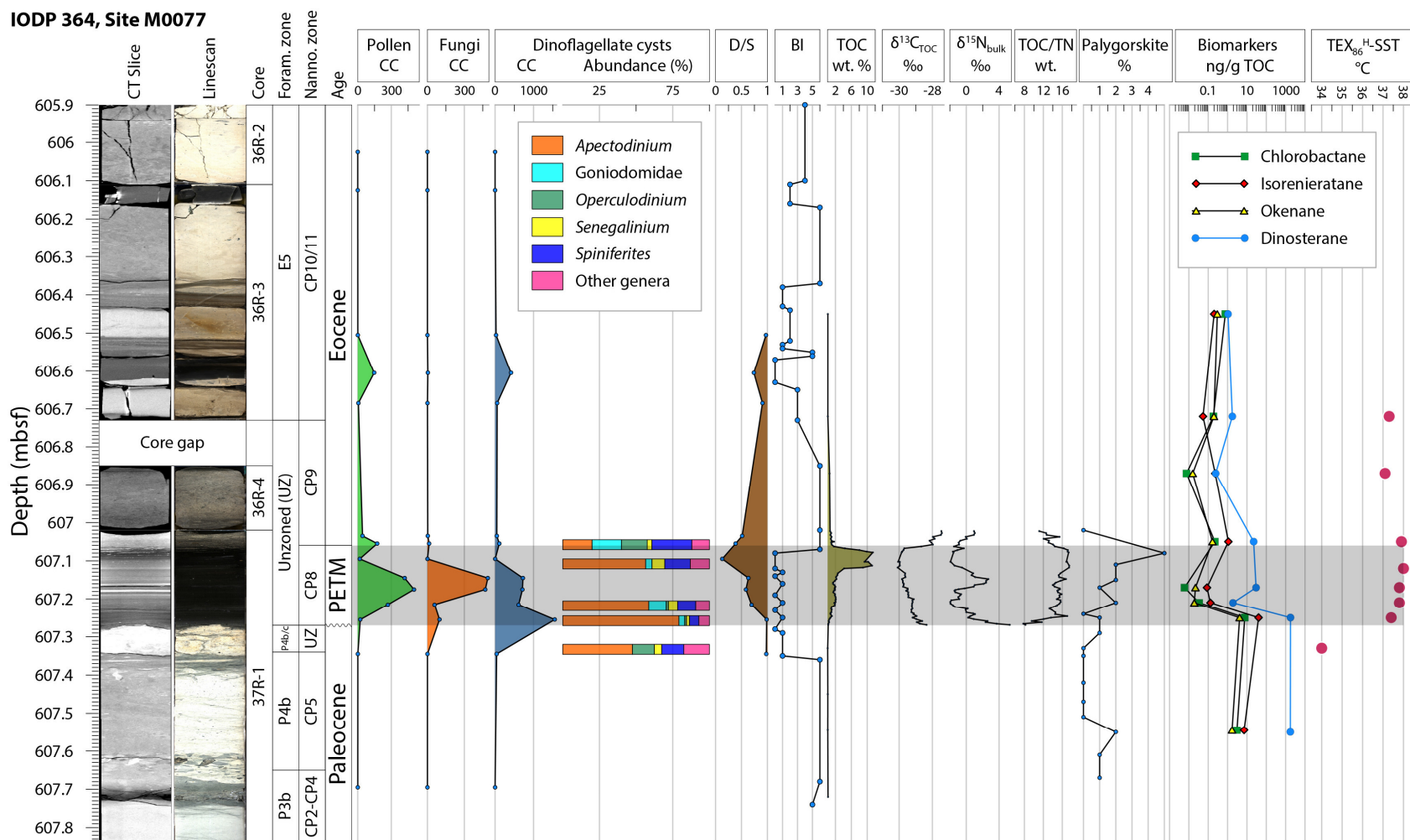


Figure 4.2. Stratigraphic column of Site M0077. Palynological concentrations (CC) are given as specimens/gram. $\delta^{15}\text{N}_{\text{bulk}}$ is reported relative to atmospheric N_2 , $\delta^{13}\text{C}_{\text{TOC}}$ is reported relative to VPDB. BI=bioturbation index (Taylor and Goldring, 1993), CT=computed tomography, D/S=dinoflagellate cyst to pollen and plant spore ratio (Warny et al., 2003), TOC=total organic carbon.

absent to rare in the Paleocene. Dinoflagellate cyst concentrations peak at 607.26 mbsf, with a decreasing trend through the rest of the PETM (Fig. 2). Relative abundances of *Apectodinium* are highest at 607.26 mbsf, and decrease through the PETM, while the highest relative abundances of Goniodomidae are found just above the event. Pollen and fungal spore concentrations peak in the middle PETM section (Fig. 2). The fungal assemblage, which reaches an acme at 607.15 mbsf, is dominated by *Nigrospora*-types, with subordinate *Lophiostoma/Lophiotrema*-types and *Strigopodia*-types. The pollen and plant spore assemblage is dominated by *Malvacipollis* (Euphorbiaceae), *Ulmipollenites* (Ulmaceae), *Bohlensipollis?* (Eleagnaceae), and angiosperm pollen of unknown lower botanical affinity, with rare gymnosperm pollen and lower plant spores.

4.4. Discussion

4.4.1 Stratigraphic significance of PETM at Site M0077

The PETM section in Site M0077 has been identified on the basis of a negative carbon isotope excursion and biostratigraphy. The earliest nannofossil PETM sample, at 607.25 mbsf, contains *Discoaster salisburgensis* var. *anartios*, a characteristic PETM excursion taxon (Bralower and Self-Trail, 2016). The global negative carbon isotope excursion (CIE) is also observed at Site M0077 (Fig. 2). In complete records of the PETM, the peak of the negative CIE and highest temperatures are observed within the first ~20 ky of the event, followed by a gradual recovery to more positive $\delta^{13}\text{C}_{\text{TOC}}$ values and lower SSTs (Hollis et al. 2019). However, at Site M0077, the most depleted $\delta^{13}\text{C}_{\text{TOC}}$ values are found in the upper PETM section. The onset and peak of the PETM CIE appear to be missing due to erosion or non-deposition; the base of the PETM section is marked by a clear unconformity (Fig. 2). The trend towards more negative $\delta^{13}\text{C}_{\text{TOC}}$ values in the PETM can be explained as the result of an increasing proportion of terrestrial organic matter. This explanation is consistent with the palynological D/S ratio, which shows the highest relative abundance of terrestrial versus marine palynomorphs at approximately the same depth as the most negative $\delta^{13}\text{C}_{\text{TOC}}$ values (Fig. 2). Increasing TOC/TN ratios are also consistent with a higher input of terrestrial organic matter through the PETM (Burdige 2006). Lithologically, the PETM section is clearly distinguished from the Paleocene section by an abrupt switch from carbonate to siliciclastic clay deposition, and an abrupt increase in detrital input, as indicated by increased magnetic parameters.

4.4.2. PETM environmental change

$\text{TEX}_{86}^{\text{H}}$ -based SSTs increased by ~4 °C between the late Paleocene and PETM (Fig. 2), with average PETM SSTs of ~38 °C, similar to values observed in the eastern equatorial Atlantic by Frieling et al. (2018), and ~3 °C higher than those observed in the Harrell Core (Sluijs et al. 2014) (Fig. 1). $\text{TEX}_{86}^{\text{H}}$ -based SSTs decreased slightly to ~38 °C following the PETM. The temperature increase from the late Paleocene to PETM section is consistent with estimates of a 4-5 °C global mean surface temperature anomaly for the PETM (Dunkley Jones et al. 2013). Frieling et al. (2017), investigating a tropical marine PETM record from Nigeria, estimated latest Paleocene SSTs of 32-34 °C, with average PETM SSTs of ~36 °C.

Several lines of evidence indicate increased terrestrial input during the PETM, including increased concentrations of terrestrial palynomorphs, increased TOC, increased D/S and

TOC/TN ratios, and an increase in detrital ferromagnetic minerals. Theoretically, this increase in terrestrial input could be the result of a relative sea level fall, but this would not be consistent with an interpreted PETM sea level rise in the Gulf of Mexico and globally (Sluijs et al. 2014). Instead, the increase in terrestrial input is interpreted to result from an intensified hydrological cycle during the PETM, as noted in other studies (e.g., Crouch et al. 2003; Bowen et al. 2004; Schmitz and Pujalte 2007; Handley et al. 2012). The exceptionally high abundance of fungal spores in the PETM section suggests that increased humidity and terrestrial weathering resulted in greater detrital and nutrient input to Site M0077A.

The relative abundance of the clay mineral palygorskite increases through the PETM section. Increases in palygorskite abundance in other PETM sections have been interpreted as evidence for increased aridity (Carmichael et al. 2017), as palygorskite commonly forms in coastal marine environments where continental alkaline waters are concentrated by evaporation (Bolle and Adatte 2001). At Site M0077, the palygorskite may have originally formed in hypersaline back-reef lagoon environments similar to other Eocene-Oligocene palygorskite deposits in the Yucatán Peninsula (de Pablo Galán 1996). The increase in relative abundance of palygorskite through the PETM section may therefore be the result of increased fluvial transport of sediments to Site M0077 from lagoonal environments to the south, rather than the result of increased aridity.

The near absence of bioturbation in the PETM section, with preserved sedimentary laminations and high TOC, is consistent with bottom water anoxia throughout the PETM, and sulfur bacteria biomarkers are indicative of photic zone euxinia (e.g., Summons and Powell 1987; Grice et al. 2005; Sluijs et al. 2014) in the earlier PETM record. Highly depleted $\delta^{15}\text{N}_{\text{bulk}}$ values, similar to those observed during ocean anoxic events (e.g., Jenkyns 2010) can be explained by upwelling of ammonium from anoxic deep waters during periods of high nutrient availability (e.g., Higgins et al. 2012), or increased cyanobacterial N_2 fixation (e.g., Bauersachs et al. 2009). The observed transient positive nitrogen isotope excursion could be due to terrigenous nitrogen, as indicated by a parallel increase in pollen and fungal abundance (Fig. 2).

4.4.3 Implications for life and climate

In the Paleocene interval of Site M0077, carbonate deposition dominates, and palynomorphs are nearly absent, probably due to poor preservation of organic material (Lowery et al. 2018). The late Paleocene palynological samples in the carbonate hardground represent the oldest dinoflagellate assemblages observed in abundances sufficient for paleoecological interpretation. Dinoflagellate cyst and dinosterane concentrations peak in the early PETM interval, then decrease through the rest of the PETM, suggesting that the extreme warmth during the PETM resulted in heat-stressed plankton within the Chicxulub impact crater, similar to the eastern equatorial Atlantic (Frieling et al. 2018). Dinoflagellate assemblages record a peak in *Apectodinium* relative abundance in the bottom PETM section, with a decreasing trend through the PETM. Increases in the relative abundance of Goniodomidae through the PETM indicate an increase in salinity stratification (e.g., Frieling and Sluijs 2018). The PETM nannoplankton assemblage contains malformed *Discoaster* specimens, which may represent ecophenotypes which migrated to a deep photic zone refuge to escape inhospitable sea surface temperatures and became malformed due to increased organic matter remineralization and calcite undersaturation (Bralower and Self-Trail 2016).

A notable acme of fungal spores occurs in the middle part of the PETM and suggests humid forest and grassland ecosystems in the source area of the terrestrial palynomorphs. The PETM pollen and plant spore assemblage is broadly similar to later Ypresian assemblages observed higher in the core, with angiosperm pollen dominant and rare lower plant spores and gymnosperm pollen. The main pollen source area is interpreted as a lowland tropical forest and shrubland (Smith et al. 2019; Smith, Warny, Jarzen, et al. 2020). Low abundances of grass pollen (*Monoporopollenites annulatus*) in the PETM suggest a minor grasslands component of the flora. Pollen with affinity to the Pinopsida and Ulmaceae may represent a contribution from more upland pollen source areas, based on their modern distributions in México and Central America. High concentrations of pollen in two PETM samples argue for a proximal pollen source area from low elevation carbonate terrain in the Yucatán Peninsula, consistent with modeled prevailing surface currents and summer wind fields from the south (Fig. 2) (Winguth et al. 2010). Globally, plant floras indicate shifts in ranges and relative abundances with low rates of extinction (Wing and Currano 2013). These shifts are broadly indicative of warming during the PETM. Although plant assemblages in midlatitude continental interiors suggest drying during the PETM (e.g., Wing et al. 2005), PETM floral records from tropical South America (Jaramillo et al. 2010) and India (e.g., Prasad et al. 2018) suggest high levels of precipitation, while in tropical East Africa (Handley et al. 2012) evidence suggests a decrease in overall humidity but an increase in the intensity of precipitation events. The proxy evidence from Site M0077 indicates increased temperature and humidity in the Yucatán Peninsula during the PETM, resulting in increased terrestrial input.

4.5. Conclusions

The PETM in the Chicxulub impact crater was a time of extremely high SSTs (~38 °C), increased terrestrial input, high surface productivity, water column stratification, and bottom water hypoxia/anoxia, with evidence for photic zone euxinia in the bottom section. The observed increase in terrestrial input is likely the result of increased weathering and fluvial discharge due to moist, hyperthermal conditions. This explanation is consistent with global evidence of sea level rise during the PETM. Seafloor anoxia decimated the marine benthos during the PETM, while high SSTs caused heat stress in the dinoflagellate assemblages. In contrast, the pollen and spore assemblage indicates the presence of a proximal humid landmass with a diverse tropical shrubby forest, which produced relatively high abundances of Euphorbiaceae pollen. These results, in combination with previously described tropical PETM floral assemblages, demonstrate that tropical vegetation was highly resilient to hyperthermal conditions.

CHAPTER 5. PALYNOLOGY AT GROUND ZERO OF THE CHICXULUB IMPACT, SOUTHERN GULF OF MEXICO

5.1. Introduction and geologic setting

At the end of the Cretaceous Period, a large bolide struck the Yucatán carbonate shelf and formed the Chicxulub impact crater (Hildebrand et al. 1991; Gulick et al. 2013). This event is generally considered to be the main cause of one of the largest extinctions in Earth history, the K/Pg mass extinction (e.g., Schulte et al. 2010, Hull et al. 2020), although some studies have argued that Deccan volcanism had a contributing or even exclusive causal role in the extinction event (e.g., Keller et al. 2013; Burgess 2019). Regardless, the regional environmental effects of the impact were catastrophic, sterilizing an area hundreds of kilometers in diameter virtually instantaneously. Immediately after the impact, a transient excavation cavity reached ~25 km depth, followed by crustal rebound and central basement uplift (Batista-Rodríguez et al. 2013). The peak ring of the Chicxulub crater was formed from uplifted, shocked, felsic basement rocks (Morgan et al. 2016), and created a circular topographic high within the crater (Figure 1).

In the hours to days following vaporization of the shallow ocean in the crater during impact, seawater re-entered the crater, resulting in a thick sequence of well-sorted, glass-rich impact breccias formed during molten fuel-coolant interaction (Osinski et al. 2020). In the Paleogene, the impact crater is characterized by a marine depositional basin dominated by carbonate and evaporite deposition (Rebolledo-Vieyra et al. 2000). Pope et al. (1996) argued that large portions of the crater rim remained emergent in the Paleocene, with submergence of the entire northern Yucatán peninsula by the middle Eocene. A global paleogeographic reconstruction for the PETM (Paleocene-Eocene Thermal Maximum) (Scotese and Wright, 2018) shows the entire crater rim as emergent. However, it is likely that only isolated portions of the southern crater rim were emergent in the early Eocene, considering the existence of a deep embayment to the north and northwest of the epicenter (Gulick et al. 2008). The paleogeography presented in Figure 1 generally follows Scotese and Wright (2018), although only a portion of the southeastern crater rim is interpreted as subaerially emergent.

The end-Cretaceous mass extinction annihilated approximately 47% of all genera and 76% of all species on Earth (Jablonski 1994), but many questions remain regarding the recovery of life in the impact region from the first day of the Cenozoic onwards. Although a plant mass extinction event is evident in more well-studied regions such as North America and New Zealand, with approximately 30% and 15% of pollen and plant spore species disappearing across the K/Pg boundary (Vajda and Bercovici 2014), whether the plant K/Pg mass extinction was truly global is uncertain (Nichols and Johnson 2008). Some pollen assemblages outside North America show little evidence for a sudden K/Pg mass extinction, for example Seymour Island in Antarctica (Askin 1990) and El Kef in Tunisia (Méon 1990). Early palynological research on late Cretaceous and early Paleogene strata in the tropics (e.g., van der Hammen 1954a; van der Hammen and Wymstra 1964; van Hoeken-Klinkenburg 1966; Germeraad et al. 1968) did not note a mass extinction event at the K/Pg boundary, but these studies were generally more concerned with practical stratigraphic correlation related to petroleum exploration rather than the identification of a mass extinction event, with coarse sampling resolution and limited age control (Tschudy 1984). More recently, de la Parra (2009) described a K/Pg mass extinction in the pollen and plant spore assemblages of Colombia, South America, but overall, the extent of the floral K/Pg mass extinction in Central America and Mexico is mostly unknown. However,

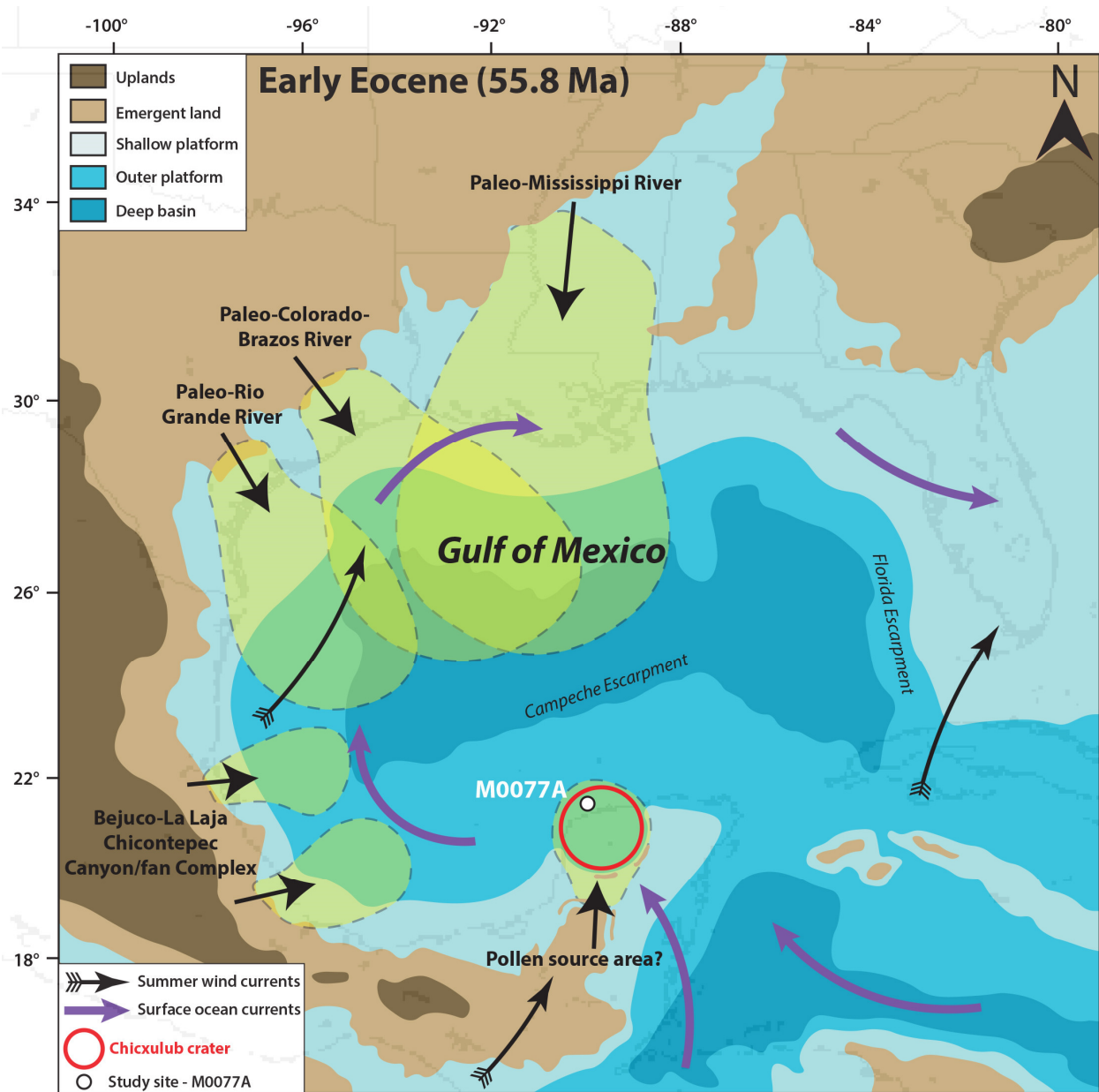


Figure 5.1. Paleogeographic map of the Gulf of Mexico and Chicxulub impact crater at the Paleocene-Eocene Thermal Maximum (55.8 Ma). Paleogeography modified from Scotese and Wright (2018). Surface ocean currents and wind fields based on PETM climate modeling in Winguth et al. (2010).

evidence for a short-term disruption in vegetation has been observed from other regions. These evidences include a spike in the relative abundance of fern and bryophyte spores immediately above the K/Pg boundary in Japan (e.g., Saito et al. 1986), Europe (e.g., Brinkhuis and Schiøler 1996; Jolley et al. 2013), North America (e.g., Sweet and Braman 2001; Nichols and Fleming 2002), South America (e.g., Renne et al. 2018), and New Zealand (e.g., Vajda et al. 2001; Vajda and Raine 2003; Ferrow et al. 2011). These are related to the initial re-establishment of herbaceous pioneer flora following massive deforestation due to global wildfires and/or an extended impact winter, with impact debris blocking solar radiation (Vajda et al. 2001).

Unlike many other groups, dinoflagellates do not appear to have undergone a mass extinction at the end-Cretaceous (Slimani et al. 2010). Smit and Brinkhuis (1996) and Brinkhuis et al. (1998) observed an invasion of high-latitude dinoflagellates into low latitudes at the K/Pg boundary, rapidly followed by an invasion of low-latitude dinoflagellates, for example *Trithyrodinium evittii*, into high latitudes, and hypothesized that these shifts were a response to initial cooling during an impact winter, followed by CO₂-driven global warming. This impact winter hypothesis, occurring over about 1-10 years after the impact, followed by global warming, is supported by TEX₈₆ sea surface temperature (SST) measurements of K/Pg outcrops along the Brazos River in Texas (Vellekoop et al. 2014).

In this study, we present the first record of post-impact palynological recovery from ground zero of the K/Pg impact, the Chicxulub impact crater. These detailed analyses were performed on sediments recovered by International Ocean Discovery Program (IODP) 364 Site M0077, drilled within the Chicxulub impact crater (Fig. 1). Site M0077 recovered Paleocene to Lower Eocene marine strata deposited on top of the impact breccia between 617.33-505.70 mbsf (meters below seafloor) (Gulick et al. 2017). Immediately above the impact breccia, between 617.33-616.58 mbsf, is a “transitional unit,” an upward-fining, fine-grained, micritic limestone, deposited within less than 30,000 years of the impact, based on foraminiferal biostratigraphy, and probably within six years of the impact, based on sediment settling times using Stoke’s Law (Lowery et al. 2018) (Fig. 2). In two previous publications (Smith et al. 2019; Smith, Warny, Jarzen, et al. 2020), the pollen and plant spore assemblages in the post-impact section of Site M0077 were fully described, including five new species of angiosperm pollen. Smith, Warny, Grice, et al. (2020) analyzed the PETM section using palynology, calcareous microfossils, ichnology, mineralogy, and geochemistry, including a TEX₈₆ record indicating PETM SSTs averaging ~38 °C. The present study focuses on the reconstruction of environmental conditions of the region surrounding the Chicxulub crater, during the post-impact phase, based on the terrestrial and marine palynological assemblages.

5.2. Methods and materials

A total of 195 palynological samples were processed independently, but processing methods are generally similar to the standard techniques described by Traverse (2007). Some samples used a *Lycopodium* spike to estimate quantitative palynomorph concentrations (specimens/gram). Slides and residues are stored in three different laboratories; at the Department of Earth and Environmental Sciences at KU Leuven, Belgium, the Department of Paleobiology at the Swedish Museum of Natural History, Sweden, and the Center for Excellence in Palynology (CENEX) at Louisiana State University, United States. All quantitative counts are provided in the supplementary materials. Pollen and plant spore taxonomy, as well as

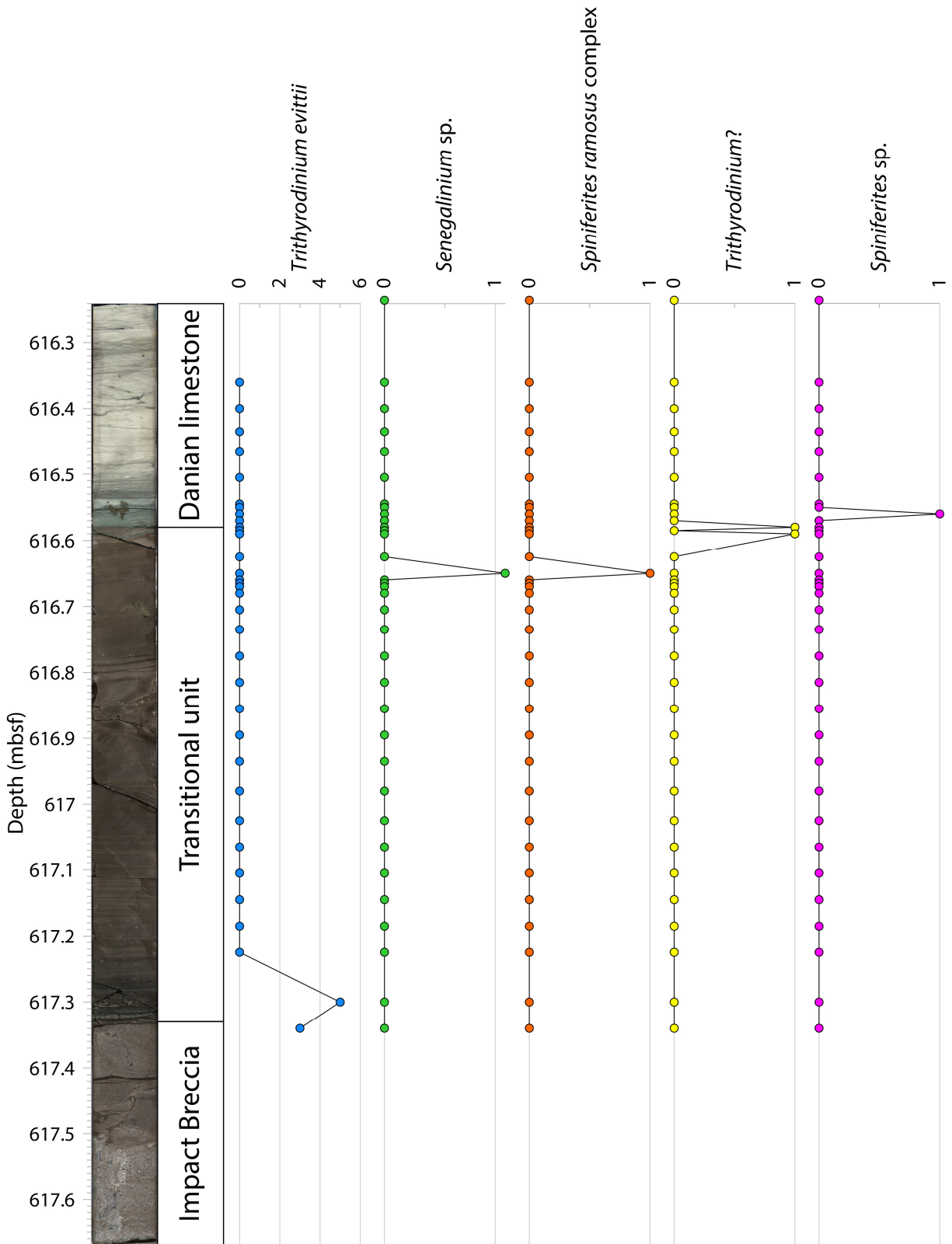


Figure 5.2. Stratigraphic section of the K/Pg section in Site M0077. Lithological boundaries are based on Gulick et al. (2017) and Lowery et al. (2018). Dinoflagellate abundances are expressed as total specimen counts in a sample.

paleoecological interpretations, are based on Smith et al. (2019) and Smith, Warny, Jarzen et al. (2020). The D/S ratio, described by Warny et al. (2003), is a proxy for the terrestrial influence in a palynological sample, defined as $D/S = nD/(nD + nS)$, where n =number of specimens counted, D =number of dinoflagellate cysts counted, and S =number of spores and pollen counted. The age model used for Site M0077 is based on Gulick et al. (2017) and can be found as a supplement in Smith, Warny, Jarzen et al. (2020). Statistical analyses were performed using PAST v. 4.1 (Hammer et al. 2001). The quantitative counts were taxonomically simplified before statistical analysis, by grouping together some taxa with similar botanical affinities, and eliminating taxa with less than ten occurrences. The stratigraphically constrained cluster analysis used an unweighted pair-group average (UPGMA) algorithm and the Brays-Curtis similarity measure, excluding the nearly barren Paleocene samples. Additional statistical results are provided in the supplementary materials.

5.3. Results

5.3.1. Palynology

Recovery varies greatly throughout the core and the interval of time recovered, with pollen and plant spore concentrations ranging from 0 to 13,561 specimens/g (average of 934 specimens/g) and dinoflagellate cyst concentrations ranging from 0 to 1,552 specimens/g (average of 169 specimens/g).

5.3.1.1. K/Pg boundary and Paleocene

The bottom two palynological samples, at 617.34 and 617.30 mbsf (Fig. 2), straddle the boundary between the K/Pg impact breccia and transitional unit at 617.33 mbsf (Fig. 2) (Gulick et al. 2017). The 617.34 mbsf sample contains three specimens of *Trithyrodinium evittii*, and the 617.30 mbsf sample contains five specimens of *T. evittii*. Isolated specimens of *Senegalinium* sp., *Spiniferites ramosus* complex, *Trithyrodinium*?, and *Spiniferites* occur near the top of the transitional unit. The Paleocene section is nearly barren, despite extensive sampling ($n=109$). Pollen and plant spore concentrations remain below 2 specimens/g through the Paleocene section, while dinoflagellate cyst concentrations are below 0.1 specimens/g on average through the Paleocene. It is only in the latest Paleocene section, a carbonate hardground below the PETM (607.35-607.27 mbsf), where concentrations rise to ~40 specimens/g. The dinoflagellate assemblage in the late Paleocene carbonate hardground is dominated by *Apectodinium* spp. (47.5% relative abundance), although the relative abundance of *Apectodinium* spp. does not peak until the early PETM section. *Areoligera*, *Cordosphaeridium*, *Operculodinium*, *Senegalinium*, and *Spiniferites* are also observed in the late Paleocene assemblage. The oldest identifiable terrestrial palynomorphs, two specimens of the trilete spore *Deltoidospora* (likely a fern), were observed at 615.50 mbsf. The total combined Paleocene terrestrial palynomorph assemblage is extremely sparse, with only 10 *Chenopodipollis* sp. A (*Amaranthaceae*), 7 *Deltoidospora* spp. (*Polypodiidae*), 2 *Alnus verus*, 2 *Scabratricolpites* sp. A (*Angiospermae*), 1 *Betula*? sp. A, 1 *Boehlensipollis* sp. A (*Eleagnaceae*), 1 *Ephedripites* (*Ephedripites*) spp. (*Ephedraceae*), 1 *Fraxinoipollenites* sp. (*Angiospermae*), 1 *Gleicheniidites senonicus* (*Gleicheniaceae*), and 1 *Trivestibulopollenites* sp. A (*Betulaceae*).

5.3.1.2. The PETM

The PETM section at Site M0077, identified biostratigraphically by Gulick et al. (2017) and on the basis of a negative CIE (carbon isotope excursion) by Smith, Warny, Grice, et al. (2020), is a black laminated shale between 607.27-607.06 mbsf. The PETM section is separated from the late Paleocene by a prominent unconformity. Dinoflagellate concentrations reach a peak of 1,552 specimens/g in the PETM section (607.21 mbsf), the highest dinoflagellate cyst concentrations in the entire post-impact section. An *Apectodinium* acme (79.2% relative abundance) is observed in the lower PETM section, at 607.25 mbsf. *Areoligera*, *Cordosphaeridium*, *Diphyes*, *Goniodomidae*, *Spiniferites*, and *Senegalinium*, and other dinoflagellate genera are also observed in the PETM section. Relative abundances of *Goniodomidae* and *Spiniferites* have an increasing trend through the PETM. Pollen, plant spore, and fungal spore concentrations increase from an average of 0.93 specimens/g in the late Paleocene hardground (607.35 mbsf) to 503 specimens/g in the middle PETM section (607.18 mbsf), then decline through the upper PETM section. The most abundant taxa in the PETM pollen and plant spore assemblage are *Malvacipollis* (Euphorbiaceae), *Ulmipollenites* (Ulmaceae), *Bohlensipollis?* (Eleagnaceae), and tricolpate/tricolporate angiosperm pollen of unknown lower botanical affinity. Fungal spore concentrations are remarkably high (>400 specimens/g) in the PETM, with the fungal spore assemblage dominated by morphologically simple, inaperturate forms similar to modern *Nigrospora* spores, which are endophytes and saprophytes on a variety of substrates (Wang et al. 2017).

5.3.1.3. Post-PETM Eocene

Immediately above the PETM section, palynomorph concentrations decline, remaining relatively low (<150 specimens/g) until a notable concentration spike (4,995 specimens/g) at 597.10 mbsf (Fig. 3). Above 597.10 mbsf, terrestrial palynomorph concentrations are variable but generally increasing, with >10,000 specimens/g in some samples. The D/S ratio generally decreases through the Eocene section. Post-PETM dinoflagellate assemblages are radically different than the PETM assemblages. *Apectodinium* is nearly absent, *Spiniferites* is the most abundant genus, *Aeroligera* is generally more abundant than in the PETM sections, and abundances of *Goniodomidae* and *Senegalinium* generally decrease upsection (Fig. 4).

The pollen and plant spore assemblage post-PETM is generally similar to the PETM assemblage, although *Bohlensipollis?* sp. A (Eleagnaceae), *Clavastephanocolpites* sp. A, *Malvacipollis* spp. (Euphorbiaceae), and *Scabratricolpites* sp. A (Fagaceae?) are generally less abundant than in the PETM. *Deltoidospora* spp. (Polypodiidae), *Echimonocolpites chichxulubensis* (Arecaceae), *Monoporopollenites annulatus* (Poaceae), *Milfordia minima* (Restionaceae), and *Psilatricolpites* sp. A (Angiospermae) are generally more abundant in the post-PETM Ypresian than the PETM. Several taxa have stratigraphically well-defined first appearances in the post-PETM section, including *Discooidites* sp. A (Tilioideae), *Milfordia hungarica* (Restionaceae), *Ilexpollenites* cf. *I. verrucatus* (Aquifoliaceae), *Echitricolporites* sp. A (Angiospermae), Polygalaceae? type A, and *Retitrescolpites* sp. C (Eleagnaceae/Sapindaceae?). Notably, no confidently observed extinction events have been identified in the pollen and plant

spore assemblage (the stratigraphic ranges of some rare taxa are uncertain). Fungal spore concentrations in the post-PETM section never approach levels observed in the middle PETM section but remain dominated by *Nigrospora*-types.

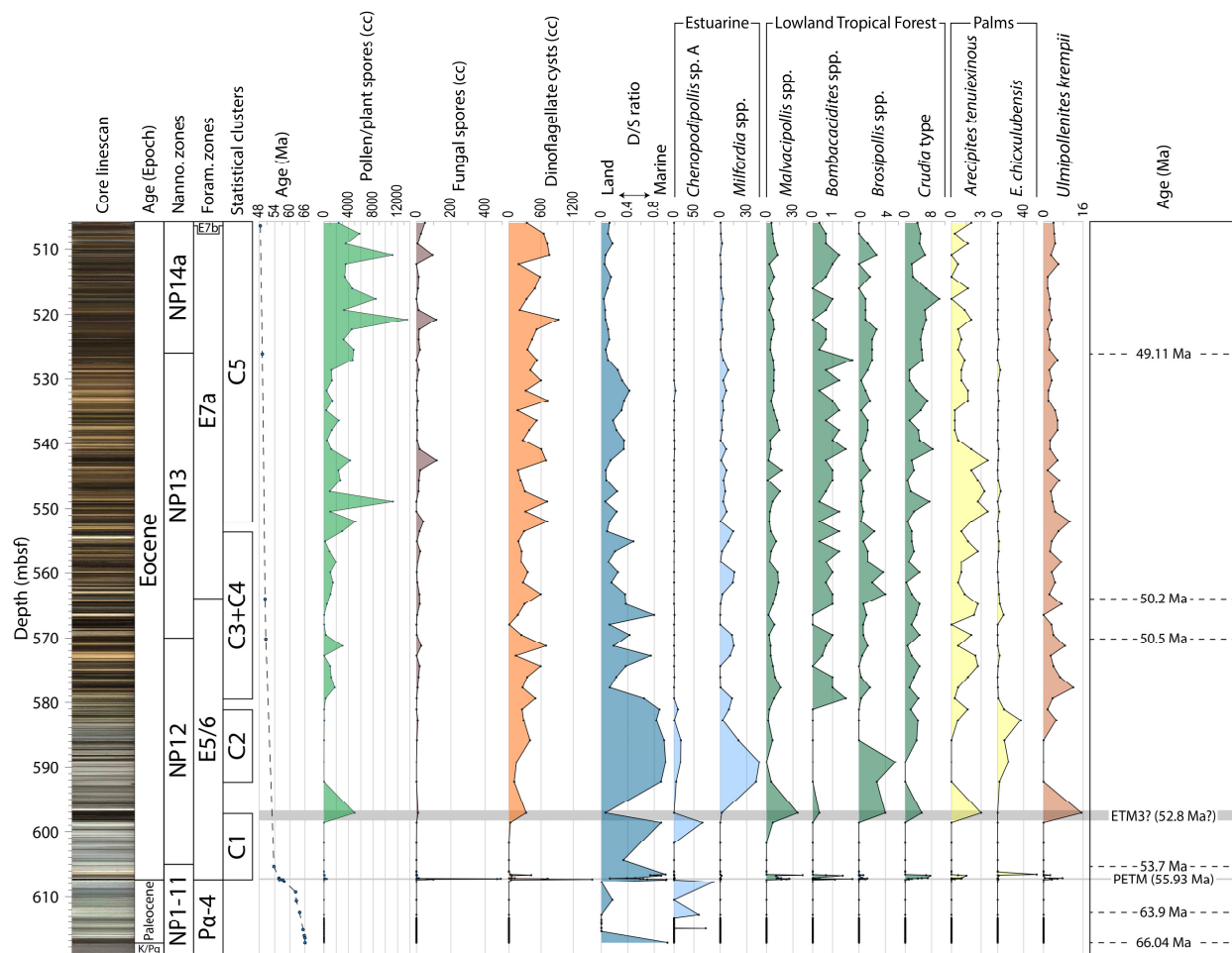


Figure 5.3. Post-impact stratigraphic section of the Site M0077 core. The foraminiferal and nannofossil biostratigraphy is modified from Gulick et al. (2017), using GTS 2012 absolute age estimates and biostratigraphic zonation (Gradstein et al. 2012). Absolute palynological concentrations (cc) are given as specimens/gram, using a Lycopodium spike. The D/S ratio is an estimate of terrestrial influence based on the ratio of dinoflagellates to plant spores and pollen, after Warny et al. (2003). Abundances of individual taxa are given as percentages relative to the entire pollen and spore assemblage.

5.3.2. Statistical analyses

A neighbor-joining cluster analysis of the simplified dataset using the Bray-Curtis similarity measure showed little evidence of clustering based on the previously assigned four paleoecological categories (Smith et al. 2019; Smith, Warny, Jarzen, et al. 2020). Stratigraphically constrained cluster analysis (Fig. 5) identified either three or five recognizable clusters, depending on the choice of similarity values cutoffs, ~0.25 or ~0.33, respectively. Merging two clusters (C3 and C4) results in a statistically supported 4-group clustering. Table 1 shows the taxa which contributed the most to the dissimilarity between the four clusters. Cluster C1 contains PETM and post PETM samples from 607.26-597.10 mbsf. Cluster C2 contains samples with low pollen abundance from 592.23-581.08 mbsf. Cluster C3-C4 contains samples from 579.39-553.54 mbsf, and cluster C5 contains samples from 551.98-505.88 mbsf. Pairwise SIMPER analyses between these four clusters (Table 1) show similar taxa dominate the inter-cluster variability, in particular *Malvacipollis* spp. and *Milfordia* spp.

Table 5.1. Statistical comparison between the four clusters identified using stratigraphically-constrained cluster analysis. OAD=Overall average dissimilarity.

C1 vs. C2 (OAD=0.840)					
Taxon	Average Dissimilarity	Contribution %	Cumulative %	Mean C1	Mean C2
<i>Malvacipollis</i> spp.	40.46	48.19	48.19	55.5	1.8
<i>Milfordia</i> spp.	8.80	10.48	58.67	1.2	7.8
<i>Ulmipollenites krempii</i>	8.01	9.54	68.21	11.8	1.8
<i>Crudia</i> type	6.46	7.69	75.9	8.2	1.6
<i>Chenopodipollis</i> sp. A	3.88	4.62	80.52	0.7	3.4
<i>Cupuliferoidaepollenites</i> spp.	3.50	4.16	84.68	3.6	1.4
C2 vs. C3+C4 (OAD=0.783)					
Taxon	Average Dissimilarity	Contribution %	Cumulative %	Mean C2	Mean C3+C4
<i>Malvacipollis</i> spp.	14.85	18.96	18.96	1.8	22.5
<i>Milfordia</i> spp.	12.91	16.48	35.44	7.8	19.2
<i>Ulmipollenites krempii</i>	9.28	11.85	47.28	1.8	14.1
<i>Cupuliferoidaepollenites</i> spp.	7.11	9.08	56.36	1.4	9.88
<i>Eucommia</i> ? sp. A	6.21	7.92	64.28	0.2	7.76
<i>Crudia</i> type	4.50	5.75	70.03	1.6	6.94
C3+C4 vs. C5 (OAD=0.445)					
Taxon	Average Dissimilarity	Contribution %	Cumulative %	Mean C3+C4	Mean C5
<i>Milfordia</i> spp.	8.18	18.39	18.39	19.2	8.27
<i>Malvacipollis</i> spp.	6.51	14.65	33.03	22.5	21.9
<i>Eucommia</i> ? sp. A	5.20	11.7	44.73	7.76	14.8
<i>Ulmipollenites krempii</i>	4.00	8.99	53.72	14.1	11.3
<i>Crudia</i> type	3.86	8.68	62.4	6.94	12.5
<i>Cupuliferoidaepollenites</i> spp.	2.09	4.71	67.11	9.88	10.8
<i>Psilastephanocolporites hammen</i>	1.95	4.4	71.51	5.12	1.4

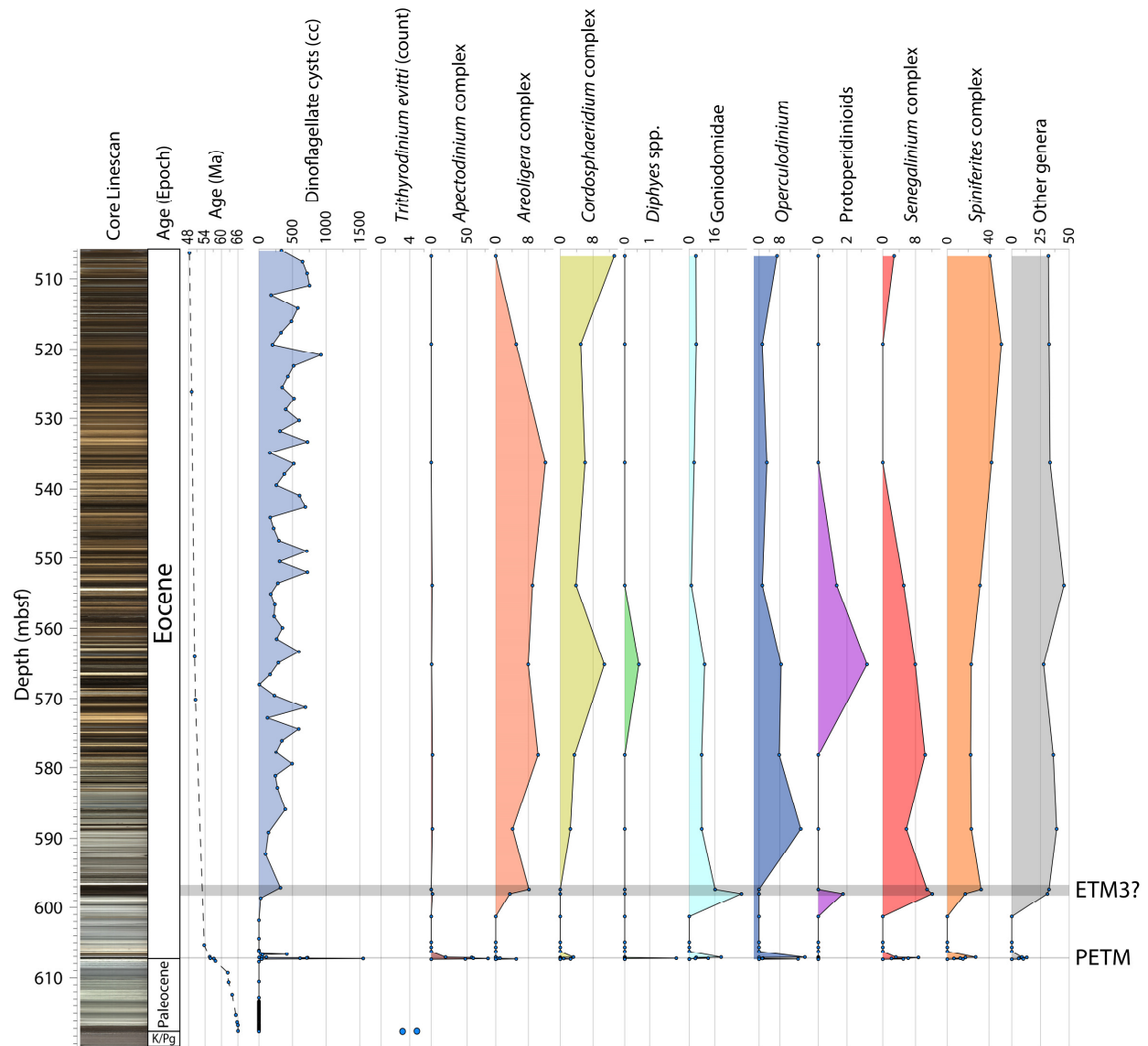


Figure 5.4. Stratigraphically-constrained cluster analysis using a simplified pollen and spore taxonomy. Low-abundance samples were excluded, taxa with less than ten occurrences were excluded, and some taxa were grouped together by genus or botanical affinity. Cluster analysis and statistical testing was performed using PAST v. 4.1. (Hammer et al. 2001). Sample depths are listed for sample numbers in the supplementary materials.

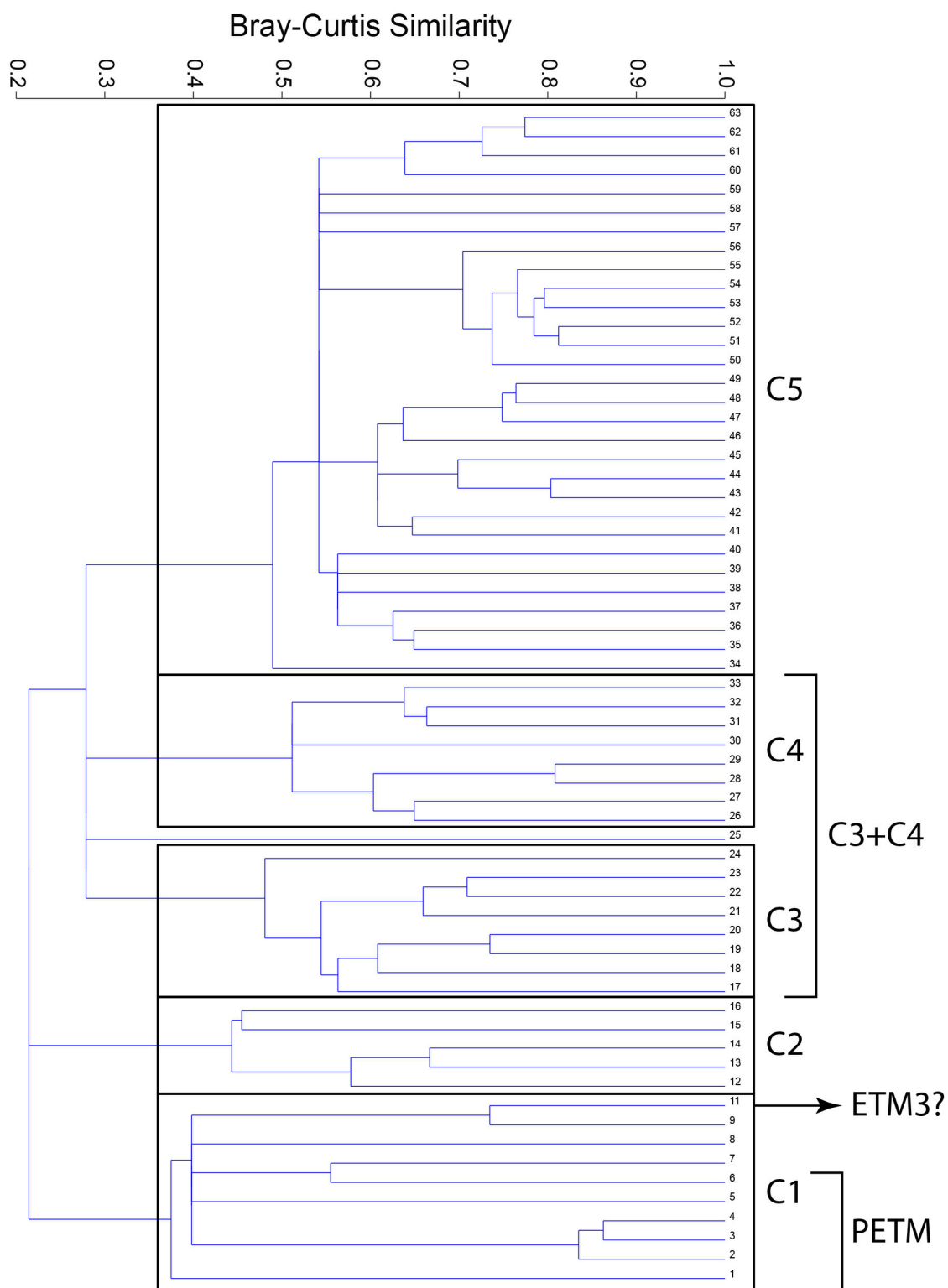


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5.4. Discussion

5.4.1. What do the statistical analyses indicate about the terrestrial palynology?

Paleoecological assignments of pollen and spore taxa were originally proposed in Smith et al. (2019) and Smith, Warny, Jarzen et al. (2020) based on the modern ecological preferences of plants producing morphologically similar pollen and spores (e.g., Correa-Metrio et al. 2011), and previous paleoecological assignments in the literature (e.g., Ramírez-Arriaga, Prámparo, et al. 2014). Cluster analysis failed to demonstrate clear clustering based on these paleoecological assignments. Based on the paleogeography and interpreted pollen source area (Fig. 1), the palynological assemblage throughout the impact section is likely dominated by coastal tropical vegetation, with only a minor contribution from more high-elevation areas of the Mexican interior. Some taxa interpreted as montane forest, for example Pinopsida and Juglandaceae pollen, may represent pollen from Mexican highlands, but if the influx of montane forest taxa was relatively constant, they might not cluster with each other, particularly considering the rarity of these pollen types in the Site M0077 assemblages.

The only taxon assigned as montane forest with high relative abundance (4.3% of the total pollen and spore count) is *Ulmipollenites krempii* (Ulmaceae). Ulmaceae pollen is associated with mountain mesophyllous forest in modern northern Central America (Correa-Metrio et al. 2011), and the paleoecology for Mexican Paleogene specimens of *Ulmipollenites* sp. (Ulmaceae) was given by Ramírez-Arriaga, Prámparo, et al. (2014) as cloud forest. However, Elsik (1968) noted that *Ulmipollenites krempii* is similar to pollen of *Planera aquatica*, a tree restricted to the southeastern United States which is generally found in lowland swamps, river and stream margins, and alluvial flood plains (Elias 1970). The high relative abundance of *Ulmipollenites krempii* in the Site M0077 post-impact section suggests that it is probably a component of the lowland tropical forest flora, not montane forest.

More statistical support is found for some of the taxa assigned an estuarine paleoecology. *Chenopodipollis* sp. A (Amaranthaceae) and *Milfordia* spp. (Restionaceae), and to a lesser extent *Deltoidospora* spp. (Polypodiidae) and *Discooidites* sp. A (Tilioideae), do cluster in correspondence analysis when the dataset is restricted to the 23 ecologically assigned taxa, with more negative first axis values (see supplementary materials). This likely confirms that the majority of the pollen is sourced from the coastal region. *Milfordia* spp. contribute heavily to the dissimilarity between the stratigraphically constrained clusters (Table 1).

5.4.2. What happened to plants and organic-walled algae right after the impact?

Answering this important question is hindered by the extremely low abundances of palynomorphs for all but the latest Paleocene. No terrestrial palynomorphs were observed until ~200,000 years after the impact, although the presence of the polyaromatic hydrocarbon perylene and charcoal in the transitional unit indicate the presence of combusted terrestrial organic matter resulting from impact-related forest fires (Gulick et al. 2019). Dinoflagellate cysts are observed in two clusters, the first cluster near the base of the transitional unit composed exclusively of eight specimens of *Trithyrodinium evittii*, and the second cluster near the top of the transitional unit composed of extremely rare *Senegalinium* sp., *Spiniferites ramosus* complex, *Trithyrodinium*?, and *Spiniferites* sp. (Fig. 2). Lowery et al. (2018) estimated the time period during which the transitional unit (617.34-616.58 mbsf) was deposited as less than six years.

Both the impact breccia and transitional unit contain clearly reworked Maastrichtian foraminifera and nannofossils, so it is probable that some or all of the dinoflagellate cysts in the transitional unit are reworked.

The lowest palynological sample containing *T. evittii*, at 607.34 mbsf, is below the top of the impact breccia, and these specimens are almost certainly reworked Maastrichtian dinoflagellate cysts. The graded laminations in the lower transitional unit, with sub-mm scale cross bedding, indicate bottom currents due to wave energy, likely from tsunamis and seiches occurring within days of the impact event (Lowery et al. 2018). With this chronostratigraphic interpretation, the occurrences of *T. evittii* just above the base of the transitional unit (617.30 mbsf) are either reworked Maastrichtian, or dinoflagellates living at the time of impact which were transported into the crater during the initial resurge of ocean water following impact. The second cluster of dinoflagellate cysts includes specimens in the upper section of the transitional unit, as well as a single occurrence of *Spiniferites* at 616.56 mbsf, 2 cm above the boundary between the transitional unit and the Danian limestone (Fig. 2). Some of these specimens may be Paleocene survivors of the impact event, as the relative abundance of foraminiferal species known to range across the K/Pg boundary increase upsection in the transitional unit; the *Spiniferites* occurrence at the base of the Danian limestone in particular is likely not reworked, as no reworked Cretaceous foraminifera were found in this section of the Danian limestone (Lowery et al. 2018).

5.4.3. What is the character of the Paleocene palynological assemblages?

The near total absence of dinoflagellate cysts in the Paleocene is curious, because foraminifera and nannofossils recolonized the impact crater quickly, and are common throughout the Paleocene section (Gulick et al. 2017, Lowery et al. 2018, Jones et al. 2019). Fragments of the calcareous-walled dinoflagellate genus *Cervisiella* were common in several Paleocene nannofossil samples. This indicates that the absence of palynomorphs in most of the Paleocene is more likely due to poor preservation of organic material, rather than inhospitable conditions for dinoflagellates. Similarly, the near absence of terrestrial palynomorphs should not be taken as any indication of distance to land or lack of vegetation on the adjacent land. The most notable feature of the depauperate Paleocene terrestrial palynomorph assemblage is the high relative abundance of *Chenopodipollis* sp. A (Amaranthaceae), a thick-walled pollen. Possibly, the wall thickness protected this type of pollen to some extent from degradation. The paleoecological interpretation of this Amaranthaceae pollen is somewhat vague, but in Smith, Warny, Jarzen et al. (2020) it was noted as possibly estuarine. This family is often abundant in recent coastal assemblages in the Gulf of Mexico (e.g., Ferguson et al. 2018a, 2018b). Nichols and Traverse (1971), studying assemblages from the Late Paleocene-Early Eocene Wilcox Group, also considered that the parent plant of the similar pollen species *Chenopodipollis multiplex* lived in a coastal environment. The higher relative abundance of Amaranthaceae pollen in the Paleocene may therefore also be the result of a more exclusively coastal influence than the high-abundance Eocene assemblages.

5.4.4. How did algae and vegetation respond to hyperthermal conditions during the PETM?

The PETM section of Site M0077 is a dark, laminated shale between 607.27-607.06 mbsf, separated from the underlying Paleocene limestone by a prominent unconformity (Gulick et al. 2017); the onset of the PETM is absent due to a depositional hiatus. Proxy evidence indicates an increase in terrestrial input, ocean anoxia, and TEX₈₆-based SSTs averaging ~38 °C (Smith, Warny, Jarzen, et al. 2020). Extremely high concentrations of fungal spores (mainly *Nigrospora*-type) in the PETM section, higher than any other sample in the Site M0077 core, indicate humid terrestrial conditions. The PETM section is distinguished by high relative abundances of *Malvacipollis* spp. (Euphorbiaceae), *Boehlensipollis* sp. A (Elaeagnaceae), and *Scabratricolpites* sp. A (Fagaceae?). Dinoflagellate assemblages record an acme of the thermophilic, probably heterotrophic genus *Apectodinium* in the lower PETM section, as observed quasi-globally (Frieling et al. 2018). An increase in salinity stratification through the PETM is indicated by an increasing trend in the relative abundance of Goniodomidae (Frieling and Sluijs 2018). Despite extremely high SSTs during the PETM, dinoflagellate assemblages persisted through the event, and the terrestrial flora was diverse, with no evidence of adverse effects.

5.4.5. What is the character of the post-PETM palynological assemblages?

Stratigraphically-constrained cluster analysis (Fig. 5) identified a statistically supported 4-group clustering for the Eocene terrestrial assemblages. A cluster containing the PETM (cluster C1) also contains some post-PETM samples. The highest sample in cluster C1, at 597.10 mbsf, is situated within a thick, dark marlstone/claystone with laminations (Gulick et al. 2017), similar to the dark, laminated shale of the PETM section, suggesting anoxic seafloor conditions. Dinoflagellate cysts and terrestrial palynomorph concentrations spike at 597.10 mbsf (Fig. 3), with a similar pollen and plant spore assemblage as that found in the PETM section. A notable increase of Goniodomidae in the dinoflagellate assemblage is also observed around 597-598 mbsf in the marlstone/claystone section (Fig. 4), indicating an increase in salinity stratification, as observed in the PETM section.

This marlstone/claystone may represent one of the early Eocene hyperthermals. Hollis et al. (2019) placed ETM2 spanning the NP11/NP10 nannofossil zone boundary, and ETM3 in early NP12. The observation of the nannofossil biostratigraphic event B *Discoaster lodoensis* at 605.33 mbsf (Gulick et al. 2017), which marks the NP12/NP11 boundary in Gradstein et al. (2012), is more consistent with the marlstone/claystone section representing ETM3. The clustering of the sample at 597.10 mbsf with the PETM samples, separated by a low-abundance section, suggests that cluster C1 may be grouping taxa which thrive during geologically rapid hyperthermal events, in particular *Malvacipollis* spp. (Table 1). Cluster C2, with a high abundance of *Milfordia* spp. (Restionaceae) pollen, may indicate a more estuarine pollen source area.

The clustering and trends seen through time in Site M0077A may represent responses to ecological shifts at one location but could also be the result of changing pollen source areas due to shifting wind and ocean currents or changing sea levels. The nearest landmasses were probably low-elevation carbonate terrain to the south in the Yucatán Peninsula throughout the post-impact section, and the tropical paleoenvironment would have remained similar throughout

the Early Eocene. Broadly, much of the upper section of the core was deposited during the Early Eocene Climatic Optimum (EECO), which begins in nannofossil zone NP11 and ends in zone NP14. The foraminiferal biostratigraphy directly above the PETM section is hampered by poor preservation and the possible environmental exclusion of marker taxa (Gulick et al. 2017), but the presence of the foraminiferal biozone E7b at the top of the core indicates that the end of the EECO occurred somewhere in the E7a biozone, using the stratigraphy given in Hollis et al. (2019). Generally, pollen and total organic carbon (TOC) abundance (IODP Expedition 364 Scientists, 2017) increases upsection, consistent with a gradual filling in and shallowing of the Chicxulub depositional basin. This trend can also be seen visually in Figure 2, as the stratigraphic section becomes darker upsection, with an increasing proportion of dark-colored marlstones and claystones. A notable increase in pollen concentrations occurs in the upper 15 m of the core, and this may be a result of sea level fall following the end of the EECO.

5.4.6. How does the Site M0077 palynological assemblage compare with other early Paleogene assemblages?

Observed stratigraphic ranges of Site M0077 taxa which may be biostratigraphically useful are illustrated in Figure 6. Paleogene ranges for terrestrial palynomorphs in the Cuayuca Formation of south-central Mexico (Ramírez-Arriaga et al. 2008) are quite different than the observed ranges in Site M0077, indicating that Paleogene vegetation in Mexico was highly endemic. For example, the pollen taxa *Bombacacidites*, *Corsinipollenites*, *Intratripoporipollenites*, and *Margocolporites vanwijhei* have first occurrences in the Middle Eocene or later in the Cuayuca Formation but are observed in the Ypresian at Site M0077. The dinoflagellate assemblage at Site M0077 contains several *Apectodinium* species which are only observed in the PETM section as well as abundant range-through taxa like the *Spiniferites ramosus* complex. *Florentinia reichartii* was originally described by Sluijs and Brinkhuis (2009) as occurring in the latest Paleocene and earliest Eocene on the New Jersey shelf, northern Gulf of Mexico coastal plain, and East Tasman Plateau. This species extends well into the Ypresian at Site M0077 and may be biostratigraphically useful in future regional studies.

Comparisons of the overall pollen and plant spore assemblage at Site M0077 with other early Paleogene assemblages reveals major compositional differences. Some botanical groups which are common in early Paleogene sections from the northern Gulf Coastal Plain (e.g., Gregory and Hart 1995; Harrington 2003, 2008; Harrington et al. 2004; Jardine and Harrington 2008; Jardine et al. 2011), for example Cupressaceae, Betulaceae/Myricaceae, bisaccate gymnosperm pollen, Juglandaceae, and the Normapolles group, are either absent or present in low abundances at Site M0077. Cupressaceae pollen are entirely absent in Site M0077A, and Normapolles pollen are represented only by several specimens of *Basopollis* sp. A. Considering that the Cretaceous Normapolles faunal province covered Europe, northern Africa, and the eastern United States, the presence of *Basopollis* sp. A indicates faunal exchange between the eastern United States and the Yucatán Peninsula by the early Paleogene. Some groups of mainly sub-tropical to tropical affinity, particularly *Bombacacidites* (Bombacoideae) and *Brosipollis* (Burseraceae), are found in both the northern Gulf Coastal Plain (e.g., Harrington 2008) and Site M0077 in the early Paleogene. In the Bighorn Basin, Wyoming, plant macrofossil assemblages during the PETM show a decline of taxa which prefer cooler and/or more mesic conditions, specifically Betulaceae, Juglandaceae, and Cupressaceae, and an increase of taxa preferring warmer, drier conditions (Wing and Currano 2013).

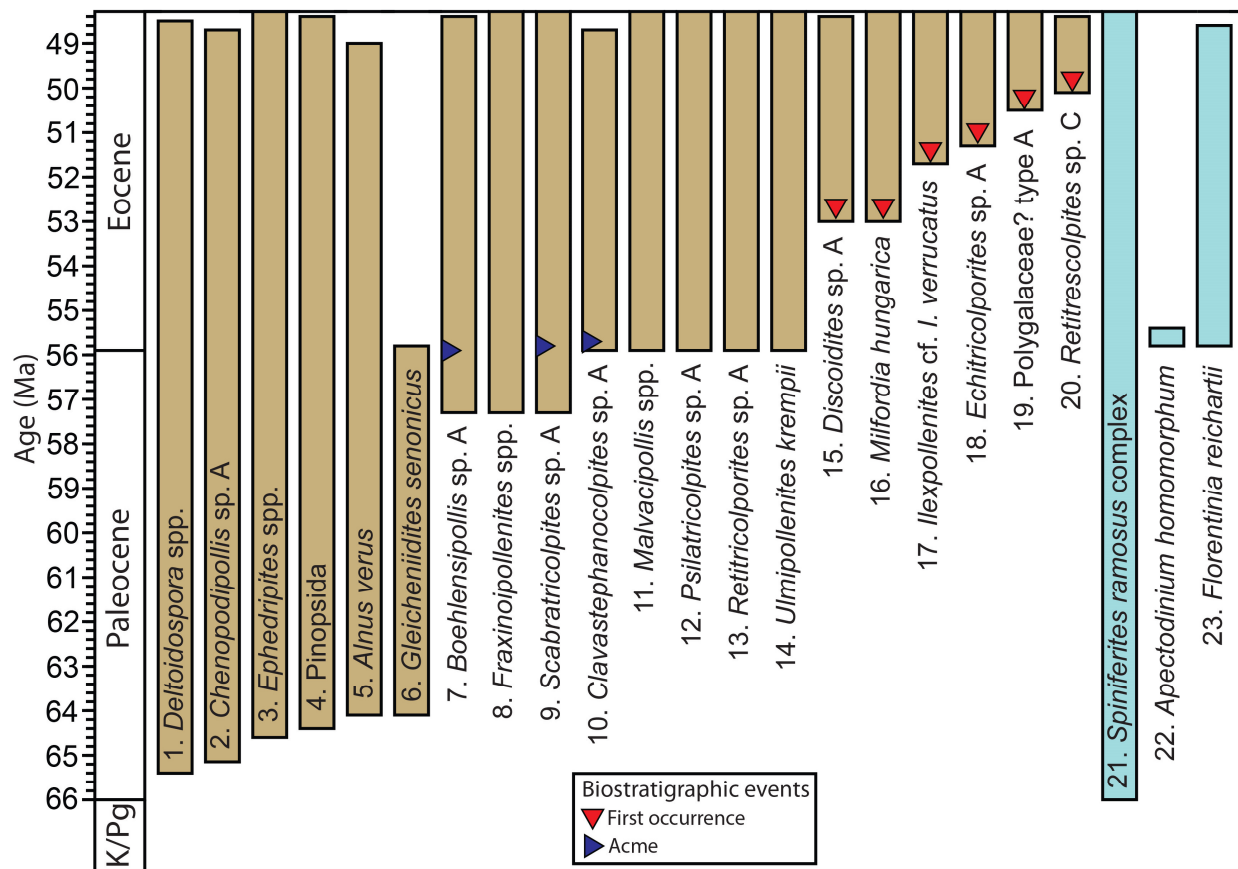


Figure 5.6. Observed stratigraphic ranges and events for selected pollen/spore (brown) and dinoflagellate (blue) taxa at Site M0077. Pollen/spore ranges are illustrated for biostratigraphically important taxa (ranges 7, 9-10, 15-20, 22-23), particularly abundant taxa (ranges 8, 11-14, 21), and taxa with observed ranges in the Paleocene (ranges 1-9, 21). The true ranges of many taxa may be longer than the observed ranges. Figure modified from Smith, Warny, Jarzen, et al. (2020).

A lower-latitude study of lower Eocene pollen from southeastern Florida (Jarzen and Klug 2010) has some similarities with Site M0077, particularly in the high relative abundances of reticulate tricolpate to tricolporate angiosperm pollen, and the presence of *Bombacacidites* and *Tiliaepollenites* (here considered a junior synonym of *Intratricolporopollenites*). Only a single specimen of *Malvacipollis* sp. was observed, however. Also, palm pollen (*Arecipites*) was more common (10% of total assemblage) than most samples in Site M0077. In PETM studies from tropical South America (Jaramillo et al. 2010) and India (Prasad et al. 2018), the assemblages contained abundant Arecaceae, including pollen from the mangrove palm *Nypa* (*Spinizonocolpites*), while at Site M0077A Arecaceae are generally only a minor component of the assemblages, represented by *Arecipites tenuixinous*, *Echimonocolpites chicxulubensis*, and possibly some other rare monocolpate genera (*Monocolpopollenites* and *Rugumonocolpites*) of uncertain lower botanical affinity. Palm pollen was also abundant in the Harrell Core in the northern Gulf of Mexico paleo-shelf during the PETM, as well as Betulaceae/Myricaceae types and other groups (Sluijs et al. 2014), but no *Malvacipollis* specimens were identified.

Paleocene and Eocene palynological studies from Mexico, Central America, and the northern Caribbean are limited (Smith, Warny, Jarzen et al. 2020). Ypresian-Lutetian palynological assemblages from the Mequitongo Formation in the south-central continental interior of Mexico (Ramírez-Arriaga et al. 2017) contain abundant pollen with affinity to *Alnus*, *Bursera*, Cupressaceae, Juglandaceae, and Pinaceae. No *Malvacipollis* pollen were observed, although other Paleogene sections from Mexico do contain this pollen genus (e.g., Ramírez-Arriaga, Prámparo, et al. 2014). A Late Eocene palynological assemblage from Panama (Graham 1985) contains high relative abundances of tricolpate to tricolporate angiosperm pollen of unknown lower botanical affinity, as well as some taxa of assigned lower botanical affinity in common with Site M0077, including Selaginellaceae spores, Arecaceae, Burseraceae, *Crudia*, Juglandaceae, and Tiliaceae. Although quantitative counts were not provided, the palynological assemblage from the Middle Eocene of Cuba described by Graham et al. (2000) is perhaps the closest analogue to the Site M0077 assemblage, containing a morphologically diverse variety of tricolpate to tricolporate, reticulate angiosperm pollen, *Arecipites*, *Liliacidites*, *Crudia* type (there identified as *Striatricolpites catatumbus*), *Bombacacidites* spp, *Basopollis*/cf. *Choanopollenites* sp. (synonymous with *Basopollis* sp. A), *Brosipollis* cf. *B. striata*, and *Malvacipollis tschudyi*. Overall, perhaps the most unusual characteristic of the Site M0077 pollen and plant spore assemblage is the consistently high relative abundances of *Malvacipollis* spp., which reach acmes in the PETM and at 597.10 mbsf, possibly during another early Eocene hyperthermal event.

5.5. Conclusions

The palynological record at Site M0077 has provided a first glimpse into a previously unknown ecosystem in and surrounding the Chicxulub impact crater. Eight specimens of *Trithyrodinium evittii* observed near the base of the transitional unit were probably deposited within days of the K/Pg impact (Lowery et al. 2018), and are likely reworked from Maastrichtian sediments mobilized during the impact event, although it is possible that these cysts were present in the water column outside of the crater at the time of impact and transported into the crater. Rare dinoflagellates in the upper section of the transitional unit may be survivor taxa, and a single specimen of *Spiniferites* observed just above the transitional unit is probably *in situ*. The near absence of palynomorphs in the Paleocene section is likely the result of poor preservation of organic matter, and not representative of an extended recovery period for either the terrestrial or marine biota. Preservation of organic matter and palynomorph abundances spike in the PETM, during which time a nearby lowland tropical forest ecosystem was thriving, and dinoflagellate assemblages responded to hyperthermal conditions. Lithostratigraphic and palynological evidence suggest the presence of another early Eocene hyperthermal event, possibly ETM3, around 597 mbsf in the Site M0077 core. The early Eocene pollen and plant spore assemblages in the Chicxulub impact crater are quite different from early Paleogene assemblages in Mexico and the southeastern United States, as well as tropical assemblages from other regions, particularly in the high relative abundance of the Euphorbiaceae *Malvacipollis* spp. Additional palynological research, particularly examining *in situ* early Paleogene terrestrial assemblages from further south in the Yucatán Peninsula, will help to clarify the pattern of floral recovery following the K/Pg mass extinction near ground zero of the Chicxulub impact.

CHAPTER 6. CONCLUSIONS

Taxonomic analysis of Site M0077 resulted in the identification of 136 pollen and plant spore taxa. Plant spores are relatively rare, with *Deltoidospora* spp. (Polypodiidae) the most common spore genus. Gymnosperm pollen are represented by rare but morphologically diverse Ephedraceae pollen, as well as rare bisaccate pollen with affinity to the Pinopsida, and a single specimen of *Cycadopites follicularis* (Cycadaceae). Angiosperm pollen dominate the assemblage, and include a variety of cosmopolitan taxa, as well as taxa with more restricted paleogeographic ranges. The paleobotanical assemblage has more taxa in common with Paleogene North America than South America (Smith, Warny, Jarzen et al. 2020), as expected given paleogeographic reconstructions for the Paleocene and Early Eocene (Scotese and Wright 2018). Two species, *Foveotrilites crater* and *Undulatisporites mineri*, have previously only been identified from Australasia and India, respectively (Smith et al. 2019). Numerous species have been named informally and may represent species endemic to the early Paleogene Yucatán Peninsula. Five new species of angiosperm pollen (*Brosipollis reticulatus*, *Echimonocolpites chicxulubensis*, *Psilastephanocolporites hammenii*, *Scabrastephanoporites variabilis*, and *Striatopollis grahamii*) have been formally described during the course of this dissertation and are now published (Smith, Warny, Jarzen, et al. 2020).

Palynological interpretation of the early recovery of life following the K/Pg impact is hindered by extremely low abundances of palynomorphs in most of the Paleocene section. Eight specimens of the dinoflagellate *Trithyrodinium evittii* at the top of the impact breccia and bottom of the K/Pg transitional unit are likely reworked from Maastrichtian sediments mobilized during the impact event. A few dinoflagellate specimens observed near the top of the transitional unit are more likely *in situ*, and a single specimen of *Spiniferites* in the basal Danian limestone above the transitional unit is most probably *in situ*. If these higher dinoflagellate occurrences in the transitional unit are not reworked, this indicates that surface ocean conditions were hospitable to marine life within years of the impact event, as corroborated by the presence of survivor nannofossils and foraminifera in the transitional unit (Lowery et al. 2018). The immediate response of terrestrial vegetation to the K/Pg impact at Site M0077 is unknown, as the oldest terrestrial palynomorphs were observed in sediments deposited at least 200,000 years after the impact.

The Site M0077 core contains a rare low-latitude record of the Paleocene-Eocene Thermal Maximum (PETM) (Smith, Warny, Grice, et al. 2020), a period of rapid global warming which has been used as an analogue for modern climate change (e.g., Alley et al. 2016). The identification of the PETM section in the core was confirmed by a negative carbon isotope excursion. Negative nitrogen isotope values in the PETM are similar to isotope ratios observed during Mesozoic oceanic anoxic events (OAEs) (e.g., Jenkyns 2010), and may result from upwelling of ammonium from anoxic deep waters during periods of high nutrient input (e.g., Higgins et al. 2012). An increase in terrestrial input during the PETM is indicated by increased concentrations of pollen and detrital ferromagnetic minerals, increased total organic carbon, and increased TOC/TN ratios. High concentrations of fungal spores indicate humid conditions during the PETM, suggesting that the increased terrestrial input is the result of increased weathering rates due to higher humidity and temperature. Although benthic communities were adversely affected by anoxic seafloor conditions, as indicated by a near absence of bioturbation and negative nitrogen isotope values in the PETM section, a nearby diverse shrubby tropical forest flora was thriving. The resilience of Paleogene tropical vegetation to hyperthermal conditions

observed at Site M0077 supports earlier research in India (e.g., Prasad et al. 2018) and South America (Jaramillo et al. 2010) which found no evidence of a loss of plant diversity across the PETM.

Statistical analysis of the pollen and plant spore assemblages in the post-PETM section of the core identified four stratigraphically constrained clusters, with cluster C1 containing the PETM section, several low abundance samples above the PETM, and a high abundance sample at 597.10 mbsf, in a dark, laminated shale lithologically similar to the PETM section. This shale section may represent one of the early Eocene hyperthermal events, possibly ETM3, based on the foraminiferal and nannofossil biostratigraphy (Gulick et al. 2017; Hollis et al. 2019). The high relative abundance of *Malvacipollis* spp. (Euphorbiaceae) pollen in cluster C1 suggests the parent plant may have been thermophilic. Cluster C2 has a high relative abundance of *Milfordia* spp. (Restionaceae), which prefer wet, brackish and coastal-plain environments (Frederiksen 1985); Cluster C2 samples may therefore represent a more estuarine pollen source area. Much of the upper section of the Site M0077 was deposited during the Early Eocene Climatic Optimum (EECO). An increase in pollen concentrations in the top 15 m of the core, with often excellent preservation, may be due to sea level fall following the end of the EECO. Site M0077 has provided a window into previously unknown terrestrial and marine communities which recolonized the Yucatán Peninsula following the end-Cretaceous impact event and responded to early Eocene hyperthermal events. Large gaps remain in our understanding of the evolution of ecosystems in the Yucatán Peninsula through the Mesozoic and Cenozoic, which can be filled in with future palynological research.

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6. This agreement (and any dispute, proceeding, claim or controversy in relation to it) is subject to English law and the parties hereby submit to the exclusive jurisdiction of the Courts of England and Wales.

APPENDIX B. SUPPLEMENTARY MATERIAL

Due to the nature of the supplementary material, in particular the large table size of the terrestrial palynological counts (150 samples and 135 taxa) and the quantity of supplementary data related to Chapter 4, it is provided as a ZIP file hosted on the document repository Zenodo, under the title “Complete supplementary data related to palynological research of International Ocean Discovery Program (IODP) Expedition 364” (Smith 2020). At the time of writing, an embargo has been placed on the supplemental material, set to expire at the same time as the embargo on the dissertation itself. A digital object identifier (DOI) has been reserved for the supplemental material (<https://doi.org/10.5281/zenodo.3756968>). The following is a complete description of the online supplemental material.

1. Supplementary methods for Chapter 4 (“Smith et al. 2020. Supplementary methods.pdf”)
2. Supplementary Excel data, organized by tabs (Smith et al. 2020. Complete supplementary data IODP 364 0418.xlsx.”)
 - 2a. Pollen and spore counts: Complete quantitative counts of the terrestrial palynology, with Lycopodium counts and concentrations.
 - 2b. Pollen and spore taxonomy: A list of all pollen and plant spore taxa, with their aperture type, botanical affinity, paleoecology, and their presence or absence in Paleogene South America and the United States.
 - 2c. Dinoflagellate taxa list: A list of all dinoflagellate taxa.
 - 2d. Dinoflagellate counts: Complete quantitative counts of the dinoflagellate cysts.
 - 2e. Taxa cluster analysis: A cluster analysis of the simplified pollen and plant spore counts.
 - 2f. Correspondence analysis 1: A correspondence analysis of the simplified pollen and plant spore counts in taxon space.
 - 2g. Correspondence analysis 2: A correspondence analysis of the simplified pollen and plant spore counts in taxon space, restricted to ecologically assigned taxa.
 - 2h. Core log integration: Integration of core and borehole data for Chapter 4.
 - 2i. High resolution CN isotope data. Stable isotope data for Chapter 4.
 - 2j. Magnetic data. Magnetic data for Chapter 4.
 - 2k. Biomarker and TEX₈₆. Biomarker and TEX₈₆ data for Chapter 4.
 - 2l. Clay mineralogy. Relative abundance of clay minerals for Chapter 4.

2m. Nannofossil data. Quantitative counts of nannofossils from Site M0077.

2n. Foraminiferal data. Quantitative counts of foraminifera from Site M0077.

2o. Ichnology: Ichnological data for Chapter 4.

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