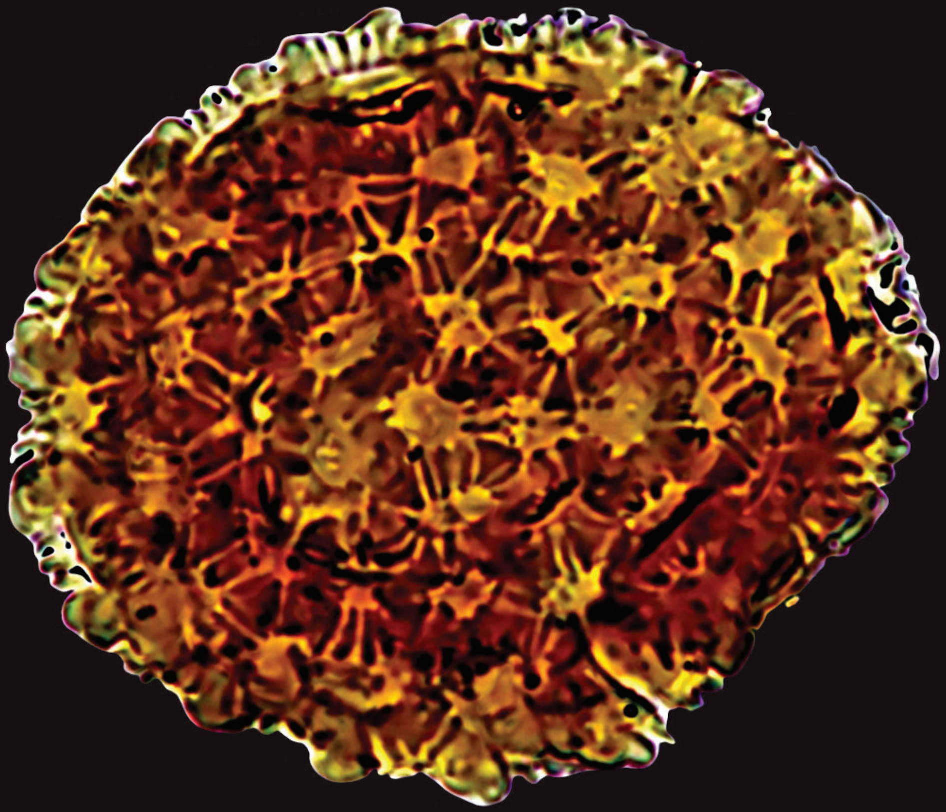
Report of Investigations No. 291

Quantitative Palynology of the Paleocene Lower Wilcox Group of Texas: Taxonomy, Biostratigraphy, and Paleoecology

Vann Smith, Lorena G. Moscardelli, Maria Antonieta Lorente, David Bord, and Iulia Olariu



Bureau of Economic Geology
Lorena G. Moscardelli, Director
Jackson School of Geosciences
The University of Texas at Austin
2025

COVER

Focus stacked photomicrograph of an *Erdtmanipollis pachysandroides* pollen grain from the Lower Wilcox Group of Texas, Jerome Olinick No. 16 well, 5951.00 ft (1813.86 m) depth. The grain is approximately 36 µm in diameter. Many thanks to José L. Pérez-Sánchez for his help with photo editing.

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Contents

ERRATA

The following corrections were made after publication:

Figures 6 and 7: The label of the rightmost column in *Paleoecological group abundances (%)* was corrected from *Coastal scrub* to *Marine*.

Abstract

Palynological analysis of four onshore wells (Edmond Olinick No. 1, Jerome Olinick No. 16, Lawrence Keseling No. 1, Moczygemba VT No. 11) in the Paleocene Lower Wilcox Group of Texas in the United States has yielded abundant and diverse palynomorph taxa from Paleocene shallow marine deltaic paleoenvironments. Information about the morphologies, biological affinities, paleoecologies, and stratigraphic ranges of the observed palynomorphs is presented here with the goal of serving as a practical reference guide for the palynology of the Lower Wilcox Group. The consistent presence of dinoflagellate cysts in the samples indicates a marine depositional environment, but the low abundance and species composition of the dinoflagellate cyst assemblages suggest a shallow or restricted marine depositional setting, possibly intermittently hypersaline. These palynological observations confirm lithological interpretations of a deltaic paleoenvironment for the studied well sections. The terrestrial pollen and plant spore assemblages are allochthonous but appear to mainly reflect a regionally proximal pollen and plant spore source area, with several common taxa indicating nearby coastal, salt marsh, and freshwater marsh or bog paleoenvironments. The palynological biostratigraphy in the onshore Lower Wilcox of Texas is generally in good agreement with previously published palynological biostratigraphy for the deepwater Gulf of America (Gulf of Mexico) Wilcox Group.

Keywords: Cretaceous–Tertiary palynology, Eocene spores,
Mesozoic biostratigraphy, Texas paleoenvironment, Wilcox Group

Chapter 1. Introduction

The Bureau of Economic Geology (Bureau) core facilities have combined holdings of nearly 2 million boxes of geologic material from wells drilled throughout Texas, the United States, and other parts of the world. From these holdings, a multitude of cores have been used by Bureau researchers and others to study the Wilcox Group stratigraphy along the Gulf Coast of the United States (e.g., Stenzel, 1951; Bebout and others, 1982; Fogg and Kreitler, 1982; Fogg and others, 1983; Hamlin, 1988; Tewalt and Jackson, 1991; Seni and Walter, 1993; Fiduk and Hamilton, 1995; Dutton, 1999; Olariu and Ambrose, 2016; Zhang and others, 2016, 2017, 2018, 2019, 2022; Hessler and others, 2017; Ambrose and others, 2018; Olariu and Zeng, 2018; Smith and others, 2024). The Wilcox Group has important economic significance for Texas given its relevance for oil and gas exploration (Fiduk and Hamilton, 1995; Olariu and Ambrose, 2016; Ambrose and others, 2018; Olariu and Zeng, 2018), coal resources (Tewalt and Jackson, 1991), freshwater aquifers (Fogg and Kreitler, 1982; Fogg and others, 1983; Hamlin, 1988; Dutton, 1999), and geothermal energy (Bebout and others, 1982; Seni and Walter, 1993). There are also a multitude of studies that have attempted to unravel the paleoclimatic and paleogeographic configuration of the Wilcox Group through time across the Gulf Coast region (e.g., Zhang and others, 2016, 2017, 2018, 2019, 2022; Hessler and others, 2017; Smith and others, 2024).

The onshore Wilcox Group is a ~10,000 ft (3,000 m) thick unit composed of fluvial, deltaic, and shallow marine clastic sediments that were deposited along the Gulf Coast region during the early Paleogene (Olariu and Ambrose, 2016). A volumetrically important portion of these sediments was bypassed toward deep-water environments of the Gulf of America (Gulf of Mexico) Basin via the action of gravity-driven flows (Zhang and others, 2016; Zarra and others, 2019). Research investigating the onshore Wilcox Group uses data sets covering different time frames in the Paleocene and Eocene; these data sets are geographically constrained within specific core or outcrop localities. However, without chronostratigraphic control using biostratigraphy or other age dating methods, attempts to correlate sections across different study areas become difficult as distance and structural compartmentalization increase between the different study areas (fig. 1). As a result, correlations made using well-log patterns and low quality onshore seismic data can have a high degree of uncertainty. This becomes particularly difficult when transects cross growth faults and transition from proximal to distal sections (e.g., onshore to offshore) (fig. 2).

In the Gulf Coast region, where growth faults and structural compartmentalization are abundant, the use of biostratigraphy, in combination with well-log and seismic data, can help bypass pitfalls associated with the use of low-resolution data sets that lack chronostratigraphic control. Biostratigraphy relies on the identification of fossils in stratigraphic sections to determine the relative age of strata and correlate sections; with calibration to an absolute time scale, biostratigraphy can provide numerical age estimates of strata. In the deep-water Gulf of America, the use of biostratigraphy for age determination is common practice in the oil and gas industry. The Zarra and others (2019) deep-water Wilcox biostratigraphic zonation uses biozones and events that are defined based on the occurrence of nannofossils, foraminifera, and palynomorphs. An earlier version of that zonation was given as a conference presentation

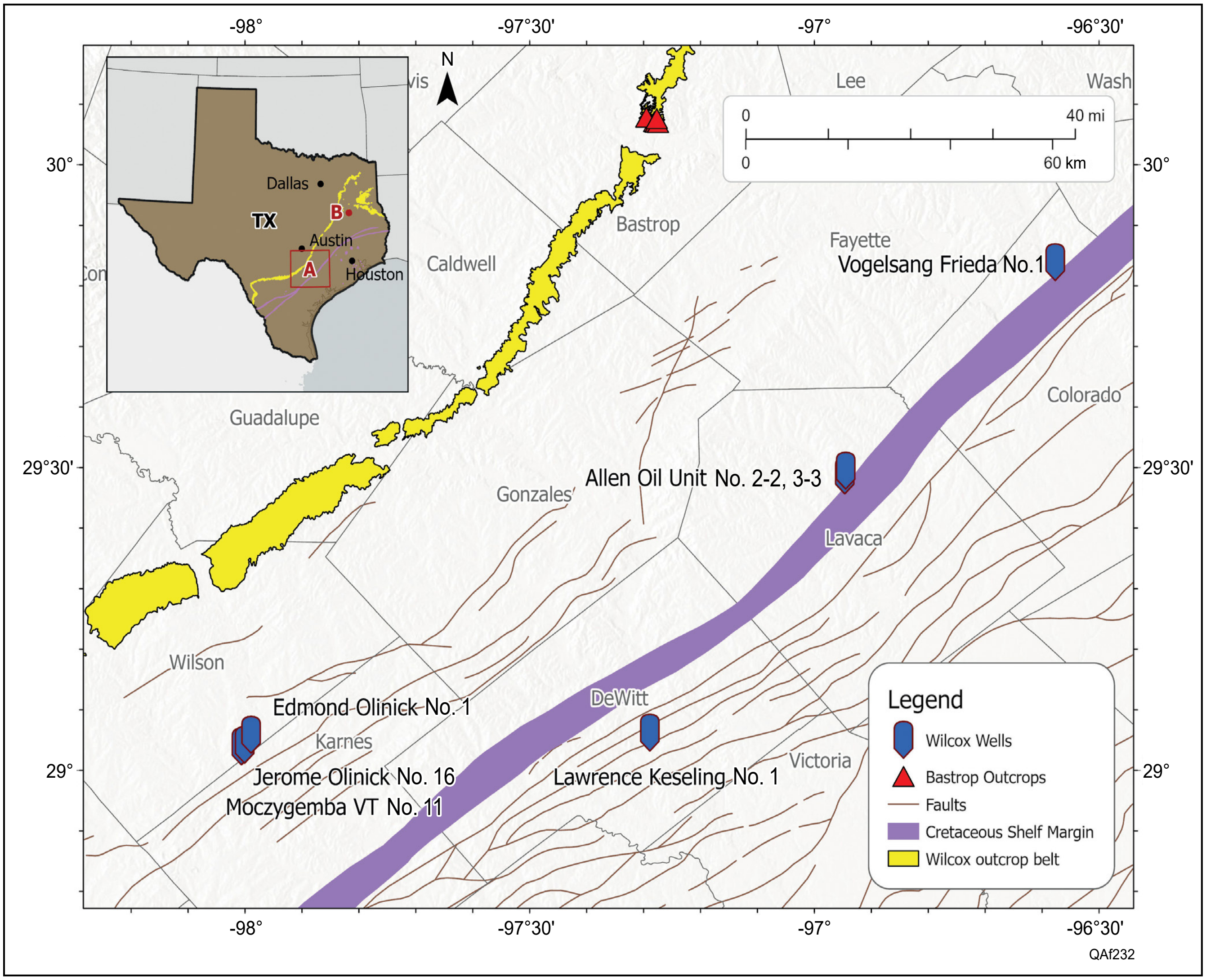

Figure 1. Wilcox Group research locations in north-central Texas. This report of investigation presents results for four subsurface well cores in Karnes and DeWitt counties (Edmond Olinick No. 1, Jerome Olinick No. 16, Moczygemba VT No. 11, and Lawrence Keseling No. 1) (A on inset map). B in the inset map denotes the location of subsurface data used in Garcia (2023). Growth faults were modified from the work of Olariu and Ambrose (2016). Using well-log signatures or seismic data alone is insufficient to perform accurate stratigraphic correlations among wells located in different structural blocks within the study area. This highlights the need to use biostratigraphy as a tool to generate robust chronostratigraphic frameworks that can be used to bracket stratigraphic correlations in areas affected by structural deformation.

(Hackworth and others, 2018). However, this biostratigraphic zonation may not be completely applicable to the onshore Wilcox Group, given that depositional paleoenvironments are significantly different between these two regions.

The deepwater Wilcox zonation (Zarra and others, 2019) used nannofossil and foraminiferal events which have global absolute age calibrations (Gradstein and others, 2012; Ogg and others, 2016) to provide numerical age estimates for palynological zones and events in the offshore Wilcox Group. While nannofossils, foraminifera, and marine palynomorph groups such as dinoflagellates may settle from the marine water column during sedimentary deposition as essentially in situ specimens, contemporaneous terrestrial palynomorphs were transported to the marine environment via sedimentary processes such as suspended sedimentary load and gravity-driven processes, in particular turbidity currents. Brackish and nearshore marine palynomorphs may also be transported to more distal marine environments via similar depositional processes. The term "contemporaneous terrestrial palynomorphs" includes organic remains, like pollen and plant spores, that originated onshore at approximately the same time as marine microfossils but that were transported and deposited offshore. Although the contemporaneous terrestrial palynomorphs are not in situ in the same sense as marine microfossils, they should not be confused with reworked fossils from older time periods which may also be deposited in Wilcox Group sediments.

We identified the lack of an updated onshore Wilcox biostratigraphic zonation as an important knowledge gap that needed to be addressed as part of current and future research efforts. A vital component of biostratigraphy is the description and illustration of fossil taxa (i.e., taxonomic description), which ensures that different researchers use consistent definitions of biostratigraphically important species. For that reason, all identifiable palynomorphs aside from dinoflagellate cysts have been discussed and included in photographic plates. Dinoflagellate cysts have not been included in the taxonomic discussion because of the low abundance and generally poor preservation of dinoflagellate cysts in the studied well sections, and because the taxonomy of the dinoflagellate cysts in the Wilcox Group is generally more firmly established than the terrestrial palynomorph taxonomy. The taxonomy of the dinoflagellate cysts in the onshore Wilcox Group may be evaluated in a future publication. Developing onshore biostratigraphic zonations for the Wilcox Group, in combination with the use of other techniques such as geochemistry, will allow us to refine our correlations in the highly compartmentalized subsurface of the Gulf Coast region. The capacity to reduce uncertainty when performing subsurface correlations along the Gulf Coast is particularly important nowadays given that current decarbonization efforts seek to identify target zones in the subsurface for purposes of carbon storage and sequestration.

An additional outstanding issue regarding Wilcox correlations pertains to the source to sink configuration of the system. Gross correlations between source terrains and depocenters have been successfully pursued in the past using detrital zircon U-Pb age spectra and other correlation methods (e.g., Mackey and others, 2012; Blum and others, 2017; Snedden and others, 2018); however, these studies do not provide enough chronostratigraphic resolution to confidently tie well data with regional horizons. The approach presented here will help facilitate data integration, comparisons, and correlations for the Wilcox Group across the greater Gulf of America Basin (e.g., Garcia, 2023; Vimpere and others, 2023; Smith and others, 2024).

In this report, we present results from an in-depth palynological study with a focus on the Lower Wilcox Group using core samples and cuttings from the Edmond Olinick No. 1, Jerome Olinick No. 16, and Moczygemba VT No. 11 wells in Karnes County, and the Lawrence Keseling No. 1 well in DeWitt County (fig. 1 and table 1). It is important to notice that structural compartmentalization, controlled by growth faults, is less likely to impact the stratigraphic correlations between wells Edmond Olinick No. 1, Jerome Olinick No. 16, and Moczygemba VT No. 11 since these wells are in close proximity to each other, and within the same structural block (fig. 1). The following analysis and discussion includes palynological taxonomy and paleoecology, the observed biostratigraphy in the four wells, and a comparison of the observed biostratigraphy with previously published biostratigraphic studies of the Wilcox Group and age-equivalent strata.

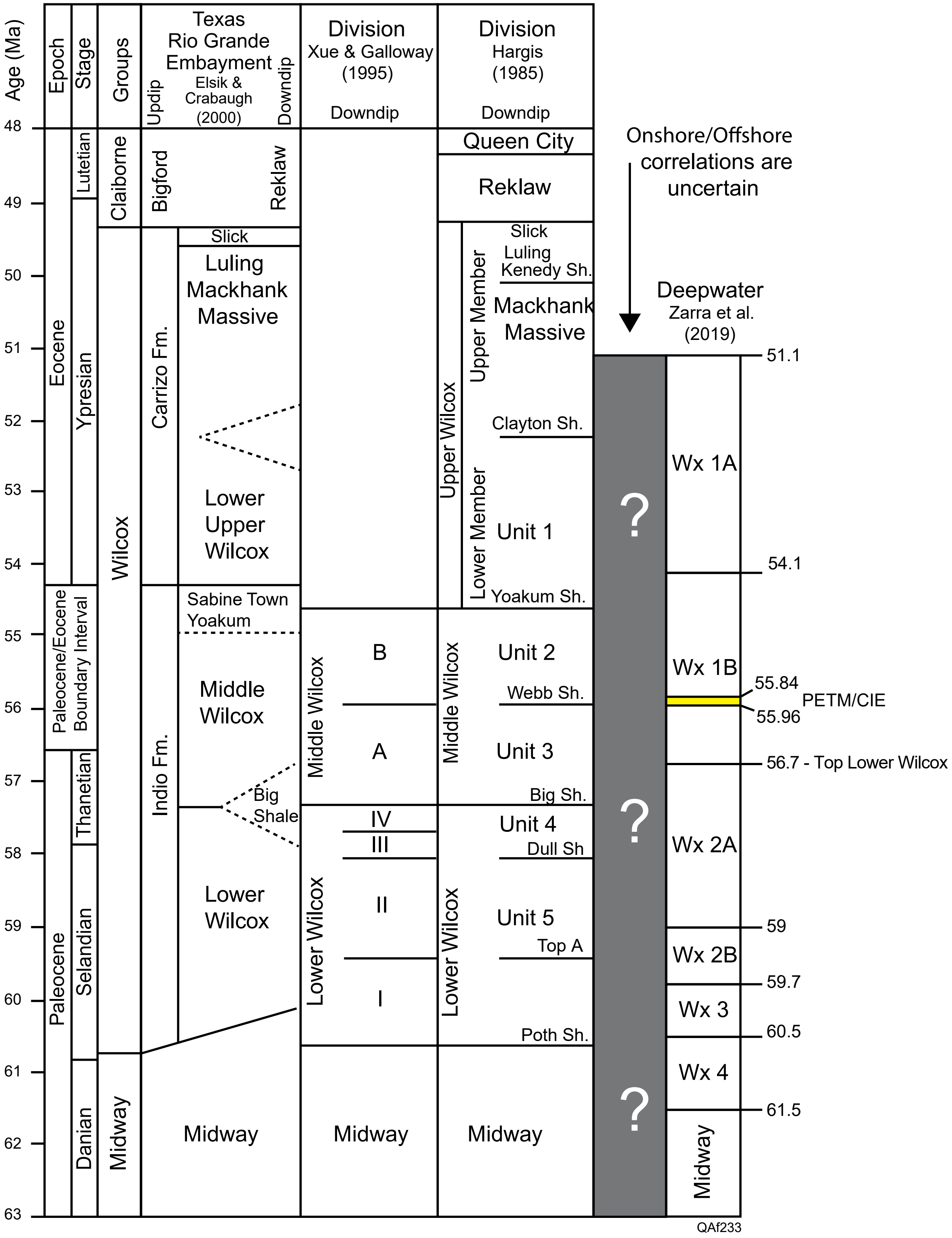
Age (Ma)
Epoch
Stage
Groups
Texas
Rio Grande
Embayment
Elsik &
Crabaugh
(2000)
Updip
Downdip
Division
Xue & Galloway
(1995)
Downdip
Division
Hargis
(1985)
Downdip
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
Eocene
Paleocene/Eocene
Paleocene
Lutetian
Ypresian
Boundary Interval
Thanetian
Selandian
Danian
Claiborne
Wilcox
Midway
Bigford
Reklaw
Carrizo Fm.
Indio Fm.
Slick
Luling
Mackhank
Massive
Lower
Upper
Wilcox
Sabine Town
Yoakum
Middle
Wilcox
Big
Shale
Lower
Wilcox
Midway
Middle Wilcox
B
A
Lower Wilcox
IV
III
II
I
Midway
Queen City
Reklaw
Upper Wilcox
Upper Member
Slick
Luling
Kenedy Sh.
Mackhank
Massive
Clayton Sh.
Lower Member
Unit 1
Yoakum Sh.
Middle Wilcox
Unit 2
Webb Sh.
Unit 3
Big Sh.
Lower Wilcox
Unit 4
Dull Sh
Unit 5
Top A
Poth Sh.
Midway
Onshore/Offshore
correlations are
uncertain
?
?
?
Deepwater
Zarra et al.
(2019)
51.1
Wx 1A
54.1
Wx 1B
55.84
PETM/CIE
55.96
56.7 - Top Lower Wilcox
Wx 2A
59
Wx 2B
59.7
Wx 3
60.5
Wx 4
61.5
Midway
QAf233

Table 1. Wells and depth ranges of core samples and cuttings[1]

Well Name and API	County	Depth Range (ft)	Core	Cuttings
Jerome Olinick No. 16	Karnes	5096.17–5991.42	X	
Lawrence Keseling No. 1	DeWitt	8994.17–11,070.42	X	
Moczygemba VT No. 11	Karnes	4610.00–6072.83	X	
Edmond Olinick No. 1	Karnes	4979.00–6191.00		X

[1] For sedimentological descriptions see Olariu (2023).

◀ **Figure 2.** Comparison of onshore Texas and deepwater Gulf of America stratigraphy. Onshore stratigraphic and lithostratigraphic nomenclature is richer given access to outcrops and more subsurface data; however, age control might be limited or outdated with a tendency to attempt correlations of lithological units. Chronostratigraphic control in the deepwater (Zarra and others, 2019) is more robust given the abundance of marine microfossils and contemporaneous transported palynomorphs that can be calibrated with absolute ages. Onshore lithostratigraphic subdivisions and offshore seismic sequences have been roughly correlated using numerical age estimates given in Crabaugh and Elsik (2000) and Zarra and others (2019; question marks have been added to the correlation to indicate uncertainty in these correlations based on limited chronostratigraphic control in the onshore Wilcox Group. Image modified from Crabaugh and Elsik (2000), Crabaugh (2001), and Olariu and Ambrose (2016) for the onshore lithostratigraphy, and Zarra and others (2019) for the offshore seismic sequences. Onshore lithostratigraphic subdivisions are based on Hargis (1985), Hamlin (1998), Xue and Galloway (1995), and Crabaugh and Elsik (2000). "Wx"=Wilcox, "Fm."=formation, "Sh."=shale, "PETM"=Paleocene–Eocene Thermal Maximum, "CIE"=carbon isotope excursion.

Chapter 2. Methods

Core and drill cutting samples were processed using mineral acid techniques as summarized by Riding (2021). Drill cutting samples from the Edmond Olinick No. 1 well generally represent circa 30 ft (10 m) stratigraphic intervals; in other words, the palynological assemblages represent a mix of palynomorphs from a circa 30 ft (10 m) stratigraphic interval. Core samples represent a much smaller sampling interval and their depths are given as point samples from the midpoint of the sampled stratigraphic interval. Due to core gaps in the well and the lack of suitable fine-grained rock layers in some sections, large sample gaps are present in Jerome Olinick No. 16, Lawrence Keseling No. 1, and Moczygemba VT No. 11. The Lawrence Keseling No. 1 and Moczygemba VT No. 11 wells were also sampled and processed for nannofossil analysis at the same depths as the palynological analysis for additional biostratigraphic control. Full nannofossil counts are provided in the Supplementary Materials. Nannofossil slides, palynological slides, and palynological sample residues used in this study are stored at the Bureau of Economic Geology in Austin, Texas, at the same location as the analyzed core sections, in order to facilitate potential future micropaleontological analysis of the samples by other researchers.

The palynological assemblages were analyzed using quantitative counts. A commonly used method for estimating the relative abundance of palynomorphs in a slide is to count specimens until a predetermined number of palynomorphs has been counted, or if the abundance is low, until the slide has been fully scanned. Commonly 300 palynomorphs are counted, although different researchers vary in the cutoff number to stop counting, and the number of palynomorphs counted may vary within an individual research project (e.g., Jaramillo and Dilcher, 2001; Slimani and others, 2010; Warny and others, 2018; Crouch and others, 2020). This practice allows for quantitative statistics to be performed on the counts but may ignore rare palynomorph species which are present in the slide but not observed; for the purposes of biostratigraphy this is undesirable. This study will use a modified version of the cascading count technique described by Styzen (1997). Although originally intended for nannofossil paleontology, it can be applied to any microfossil group. The modified cascading count technique used in this study involves estimation of the relative abundances of the most abundant taxa based on the number of slide traverses after a minimum of 300 identifiable pollen and plant spores have been counted. The remainder of the slide is then scanned to add rare taxa to the counts. For example, if over 300 identifiable pollen and plant spores have been counted at the end of 15 traverses, and 30 traverses are required to observe the entire slide, the counts of more common taxa (in this study four or more specimens) are multiplied by two. The remainder of the slide is scanned and taxa are only counted if they were not observed or observed as a single specimen. This practice indicates whether rare taxa were observed as isolated or multiple occurrences without overly distorting the relative abundance data.

Full quantitative counts of palynomorphs and nannofossils are provided in the Supplementary Materials (Supplement 1) in the form of Excel spreadsheets. Stratigraphic charts created using StrataBugs software have been used to visualize relative abundance changes in the overall assemblages (Supplement 2.1–2.4), observed stratigraphic ranges of biostratigraphically important taxa (Supplement 2.5–2.8), and complete palynomorph counts (Supplement 2.9–2.12). Plates created in Adobe InDesign provide photomicrographs of all identified palynomorphs in the study (Appendix 1). Biostratigraphic abbreviations will follow the terminology used in Gradstein and others (2012); specifically, the abbreviation "B" before a taxon name indicates the base or first appearance datum of the taxon, and the abbreviation "T" before a taxon name indicates the top or last appearance datum of the taxon. The word "common" following the abbreviation indicates the top or bottom common occurrence of the taxon.

Chapter 3. Biostratigraphy

3.1. Wilcox Group biostratigraphic framework

The earliest palynological study of the Wilcox Group that we are aware of is a master's thesis by R. E. McLaughlin (1952). Pioneering palynological research on the Wilcox Group and preliminary attempts at biostratigraphic zonation were published by Eugene L. Jones (1960, 1961a, 1961b, 1962). William C. Elsik substantially enhanced the palynological knowledge of the Wilcox Group across several decades with detailed descriptions of new species and biostratigraphic range charts (e.g., Elsik, 1965, 1968a, 1968b, 1969, 1974, 1978; Stover and others, 1966; Fairchild and Elsik, 1969; Crabaugh and Elsik, 2000; Elsik and Crabaugh, 2001). Other important early figures in the development of the Paleogene palynology of the northern Gulf of America coastal plain include Norman O. Frederiksen (e.g., Frederiksen, 1973, 1978, 1980a, 1980b, 1985, 1988, 1991, 1998, 2001), Douglas J. Nichols (e.g., Nichols, 1970, 1973; Nichols and Traverse, 1971), and Robert H. Tschudy (e.g., Tschudy, 1973a, 1973b, 1975). William A. Gregory and George F. Hart investigated a subsurface marine Wilcox well section in southwestern Louisiana (Gregory, 1991; Gregory and Hart, 1992, 1995a, 1995b) and provided observed ranges of biostratigraphically important taxa, as well as a summary range chart of Wilcox palynomorphs based on previous publications.

Several other more recent publications deal with Wilcox Group palynology but are not primarily focused on biostratigraphy (e.g., Harrington and Kemp, 2001; Harrington, 2003, 2008; Harrington and others, 2004; O'Keefe and others, 2005; Harrington and Jaramillo, 2007; Jardine and Harrington, 2008; Yancey and others, 2010; Jardine, 2011; Jardine and others, 2012; Denison and others, 2017; Garcia, 2023). Regina L. Dickey analyzed samples from Paleocene–Eocene outcrop sections near Bastrop, Texas, and found some palynological evidence (notably the presence of *Bagelopollis verrucatus*) that the Calvert Bluff Formation of the Wilcox Group is earliest Eocene in age (Dickey and Yancey, 2010; Dickey, 2017). Demchuk and others (2019) also provided age estimates for Wilcox Group outcrops near Bastrop, Texas, based on palynological biostratigraphy, but concluded that the Calvert Bluff Formation exposed in the outcrops are Thanetian rather than Ypresian in age. Harrington (2017) presented a detailed discussion of the palynological taxonomy and biostratigraphy of the Wilcox Group, including rough chronostratigraphic ages for numerous palynological events in the Paleocene. The palynological biostratigraphy of the continental interior of the United States has limited applicability to the Gulf Coast Wilcox Group but is useful as a comparison, particularly for taxa in the *Carypollenites–Momipites* lineage (e.g., Nichols and Ott, 1978, 2006; Pocknall, 1987; Nichols, 1998, 2003).

The palynological biostratigraphic zonation primarily used for this study was published in Zarra and others (2019) for the deepwater Wilcox Group. This zonation was preferred because it is the most recently published palynological zonation specific to the Wilcox Group and because it integrates the palynological biostratigraphy with nannofossil and foraminiferal biostratigraphy and calibrated ages from Gradstein and others (2012). Zarra and others (2019) created palynological zones and subzones labeled "CVX Paly," or simply "Paly." Sharman and others (2023) also listed several additional palynological events in a deepwater Wilcox Group well. For the onshore Lower Wilcox wells in this study, we created an alternative event-driven palynological zonation (fig. 3).

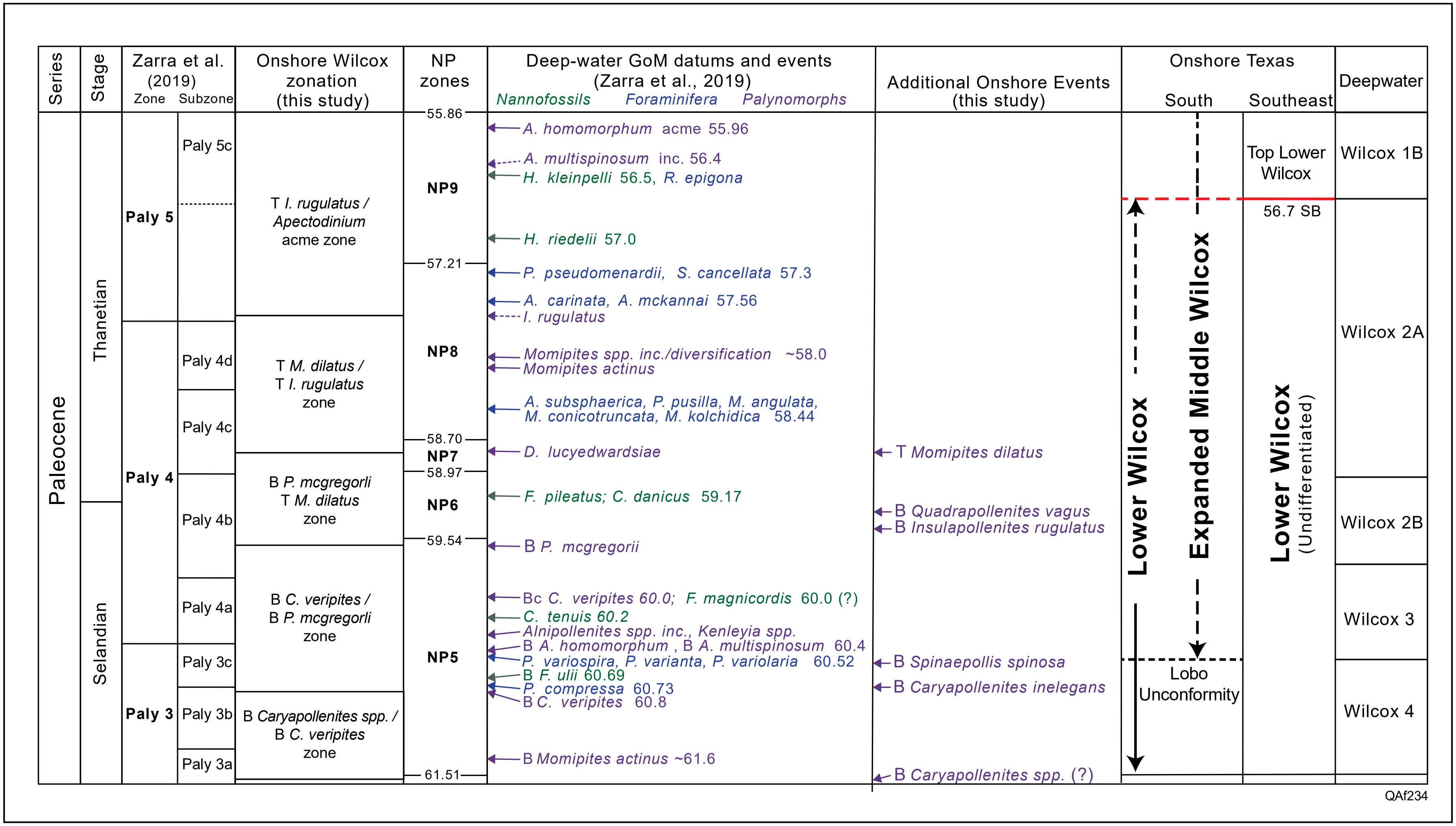

Figure 3. Biostratigraphic comparison of events and zones in the offshore Lower Wilcox Group (Zarra and others, 2019) and the onshore Lower Wilcox Group in central Texas (this work). The order and particularly the scaling of additional onshore palynological bioevents not listed in Zarra and others (2019) are considered tentative and subject to revision. B *Pistillipollenites mcgregorii*, Bc *Caryapollenites veripites*, and B *Caryapollenites veripites* were clearly observed in our sections. Other palynological events listed in Zarra and others (2019) were not clearly observed; further discussion of events is provided in Chapter 3.3. “inc.”=increase, “T”=top, “B”=base, “Bc”=base common. Events with taxon names in Zarra and others (2019) lacking prefixes or suffixes (B, Bc, acme, increase, etc.) are top occurrences. NP: nannofossil zonation of Martini (1971).

Nannofossil biostratigraphy provides additional age control for the Lawrence Keseling No. 1 and Moczygemba VT No. 11 wells, although many samples had nannofossil recovery which was too poor for biostratigraphic age determination. The nannofossil zonation uses the NP zones of Martini (1971). Stratigraphic charts with detailed palynological and nannofossil biostratigraphic information are provided for all wells in Supplement 2. Biostratigraphic events in the charts indicate the sample where the event was observed; the uncertainty regarding the actual depth of events varies depending on sample gaps. For example, in the Moczygemba VT No. 11 well there is a circa 1080 ft (330 m) sample gap between 4976.33–6047.00 ft (1516.79–1843.13 m) due to missing core section. The observed base of multiple species (*Caryapollenites inelegans*, *Caryapollenites veripites*, *Lanagiopollis lihoka*, and *Spinaepollis spinosa*) at the same sample depth 4976.33 ft (1516.79 m) in Moczygemba VT No. 11 is therefore likely an artifact of this large sample gap; the true strati-graphic bases of these taxa may be anywhere in the circa 1080 ft (330 m) sample gap. The true stratigraphic base of these taxa can only be roughly estimated as the midpoint depth of the sample gap (e.g., Shamrock and others, 2012), with the caveat that the events are almost certainly not simultaneously occurring at the midpoint of the sample gap.

3.2. Observed biostratigraphy in the onshore Lower Wilcox

Full stratigraphic charts with biostratigraphic comments are provided in Supplement 2. A comparison of the biostratigraphic zonation used in Zarra and others (2019) and additional events observed in the onshore Lower Wilcox is provided in figure 3. The exact chronostratigraphic position of additional events in the onshore Lower Wilcox is considered tentative; more precise quantitative numerical estimates of event ages are considered a subject of future research after additional sections have been analyzed. The reliability of observed palynological bioevents is dependent on the total abundance of palynomorphs in a sample, with lower total abundances increasing the uncertainty regarding the true depth of the event. The lower the total abundance, the less likely taxa used as biostratigrapher markers are observed. In Lawrence Keseling No. 1, for example, total palynomorph abundances were generally lower than the other three wells, possibly as a result of taphonomic effects resulting from greater burial depth and thermal maturity (Traverse, 2007). Qualitatively, the palynomorphs in Lawrence Keseling No. 1 were generally darker brown in color than palynomorphs in the other three wells, consistent with a higher thermal maturity (e.g., Goodhue and Clayton, 2010). There is therefore generally more uncertainty regarding the tops and bases of taxa in Lawrence Keseling No. 1 compared to the other three shallower well sections.

The biostratigraphic events in the zonation of Zarra and others (2019) most reliably observed in these onshore Lower Wilcox wells are B *Pistillipollenites mcgregorii* and B *Caryapollenites veripites*. Where nannofossil biostratigraphy was available in these onshore wells, event ages in our wells are broadly consistent with the ages given by those authors. For example, B *P. mcgregorii* was observed in lower NP6 in Moczygemba VT No. 11, while Zarra and others (2019) give B *P. mcgregorii* as uppermost NP5 in age. Higher abundances of *Apectodinium homomorphum* at the top of Lawrence Keseling No. 1, interpreted as NP8 to NP9 in age, are consistent with zone Paly 5 in the zonation of Zarra and others (2019). Several other taxa not listed in their zonation have observed tops and bases in the analyzed sections. There is increased uncertainty whether the observed ranges of particularly rare taxa in the wells represent their true stratigraphic position; many taxa have been excluded as potential markers because only a few specimens were observed in the section. Palynological bioevents involving abundance changes described by Zarra and others (2019) were not clearly observed in these onshore samples, likely because these assemblages represent a more local signal, while the offshore assemblages represent a more mixed signal from a larger terrestrial palynomorph source area. The following two sections discuss individual events with biostratigraphic significance. These events have been divided into primary biostratigraphic events, which are used to construct an alternative bioevent-driven zonation for the onshore Lower Wilcox, and secondary events, for which we have some evidence regarding the relative sequence but lower confidence than primary events. Primary and secondary events are given in order from youngest to oldest, subject to revision after analysis of additional well sections.

Numerous other potential biostratigraphic events in the Paleocene of the United States were not included as primary or secondary events here. The *Caryapollenites–Momipites* lineage experienced an evolutionary radiation in the Paleocene with numerous species used as markers in the continental interior of the United States (e.g., Nichols and Ott, 1978, 2006). Three, or possibly four, events in this group were observed in our sections: T *Momipites dilatus*, B common *Caryapollenites veripites*, B *Caryapollenites veripites*, and B *Caryapollenites* spp. Nichols and Ott (2006) provide a Paleocene range chart for the lineage which includes numerous other events. Several of these may occur in our analyzed sections, but the sequence of events is clearly different in the Wilcox Group. For example, in the range chart of Nichols and Ott (2006) the ranges of *Caryapollenites imparalis* and *Momipites leffingwellii* do not overlap, while in our sections the ranges of the taxa do substantially overlap. Because of issues with the rarity of some of these species and the stratigraphic coverage of our sections, we have not included other potential events in this lineage here, but we anticipate that analysis of additional sections will clarify the sequence of events.

Several other taxa outside of the *Caryapollenites–Momipites* lineage are not included in our list of primary and secondary events but may have true range tops or bases in our stratigraphic sections. Some of these taxa were described as having biostratigraphic utility in the Paleocene of the northern Gulf of America region (e.g., Tschudy, 1973b; Frederiksen, 1991, 1998; Gregory and Hart, 1995a; Elsik and Crabaugh, 2001) but were either not observed or observed too rarely to have confidence in their true stratigraphic ranges.

Biostratigraphic work by Crabaugh and Elsik (2000) and Elsik and Crabaugh (2001) on the Wilcox Group is particularly relevant here as it represents the most recent attempt to develop a chronostratigraphically calibrated palynological biostratigraphy based on stratigraphic sections from onshore Texas. Comparing the biostratigraphy described for the onshore Wilcox Group by Elsik and Crabaugh (2001) with the biostratigraphy in Zarra and others (2019), there is surprisingly little overlap between the events used, and we found the biostratigraphy in Zarra and others (2019) more applicable to our sections. The most useful events for our purposes in Elsik and Crabaugh (2001) are "*Carya* spp. <30 µm Base" (considered synonymous with our B *Caryapollenites* spp.) and T *Momipites dilatus*. For two taxa described by Elsik and Crabaugh (2001) as having tops in the Lower Wilcox, we are uncertain about the taxonomic concepts used; their "*Maceopolipollenites* sp." is an undescribed species and there is some ambiguity about the taxonomic concept used for *Maceopolipollenites* *granulatus*, which is possibly synonymous with pollen identified here as *Momipites rotundus* (see discussion of *M. rotundus* in the taxonomic section for more information). Scalariform sieve plates were not observed in our sections and we did not observe any *Choanopollenites eximius* specimens as strictly defined (we did rarely observe morphologically similar but smaller types identified as *Choanopollenites* aff. *eximius*). In summary, although there are some limitations to the applicability of the zonation of Zarra and others (2019) regarding our onshore Lower Wilcox samples, particularly zonal boundaries based on assemblage changes and dinoflagellate cyst events, the general sequence of terrestrial pollen events is similar. The addition in this study of events not listed in the zonation of Zarra and others (2019) will improve the biostratigraphic resolution of the Lower Wilcox Group, and the analysis of additional sections will likely lead to the identification of additional secondary events with biostratigraphic utility.

The following section provides discussion of all Paleocene palynological events provided in the zonation of Zarra and others (2019). Selected Paleocene nannofossil events used as zonal boundaries in the NP zonation of Martini (1971) are listed for chronostratigraphic reference. Additional palynological events which may have biostratigraphic use in the onshore Lower Wilcox Group are also listed and discussed. Palynological events in Zarra and others (2019) are given numerical age estimates based on the stated age for the event in Appendix 1 when possible; where age estimates are not explicitly stated (e.g., B *Pistillipollenites mcgregorii*) the age is estimated based on the height of the event relative to the chronostratigraphic column. Palynological events not listed in the zonation of Zarra and others (2019) are provided as an estimated age range. Events are listed in their interpreted chronological order, from youngest to oldest. The proposed onshore biozones for the Lower Wilcox Group illustrated in figure 3 are listed in bold font.

3.3. Sequence of biostratigraphic events

T *Insulapollenites rugulatus–Apectodinium* acme zone (Paly 5 equivalent)

Discussion: This zone is defined at the top by an acme of the dinoflagellate genus *Apectodinium* and at the bottom by T *Insulapollenites rugulatus*. The top of this zone is identical with the top of zone Paly 5 in the zonation of Zarra and others (2019) and the bottom of the zone is defined by one of the marker events used in the zonation to define the base of zone Paly 5, namely T *Insulapollenites rugulatus*.

Apectodinium homomorphum acme (55.96 Ma)

Discussion: The Paleocene–Eocene boundary is globally associated with an acme in the dinoflagellate genus *Apectodinium* (Denison, 2021). Most Lower Wilcox samples in this study are clearly older than this event. The youngest samples in this study are the top three samples in Lawrence Keseling No. 1, interpreted as nannofossil zone NP9 and zone Paly 5 based on the overall palynomorph assemblage and high relative abundances of *Apectodinium* spp. Nannofossil zone NP9 is mainly in the Paleocene, ranging slightly into the earliest Eocene in Gradstein and others (2012). Although relative abundances of *Apectodinium* are high in the top Lawrence Keseling No. 1 samples, fewer than ten *Apectodinium* spp. were observed in each sample and these occurrences do not clearly represent an acme. We consider it likely that the top samples in Lawrence Keseling No. 1 are late Thanetian in age and older than the Paleocene–Eocene boundary. If a section is fully terrestrial and dinoflagellate cysts are absent, the base of *Platycarya* spp. and *Bagelopollis verrucatus* were described by Elsik and Crabaugh (2001) as earliest Eocene markers in the Wilcox Group. The age of 55.96 Ma for this event is given in Zarra and others (2019). This numeric age coincides with the estmated age of the base of the Eocene in GTS 2012 (Gradstein and others, 2012).

Adnatosphaeridium multispinosum increase (56.4 Ma)

Discussion: This event was listed in the Paly 5c zone but not discussed in the text of Zarra and others (2019). We assume this event is a downhole (rather than uphole) increase in the relative abundance of *Adnatospheridium multispinosum*. This event was not clearly observed in our Lower Wilcox wells. Only the top three samples of Lawrence Keseling No. 1 are in Paly 5 and these samples are not well suited for identifying changes in relative abundance of *A. multispinosum* because of low sample resolution and low dinoflagellate cyst abundances. The age of 56.4 Ma for this event is given in Zarra and others (2019).

B common *Discoaster multiradiatus* (57.21 Ma)

Discussion: This nannofossil bioevent defines the NP8–NP9 boundary. The age of 57.21 Ma for this event is given in Gradstein and others (2012).

T *Momipites dilatus*–T *Insulapollenites rugulatus* zone (Paly 4c–4d equivalent)

Discussion: This zone is defined at the top by T *Insulapollenites rugulatus* and at the bottom by T *Momipites dilatus*. The top of this zone is defined by one of the marker events used by Zarra and others (2019) to define the Paly 4–5 boundary. The bottom of this zone is defined by T *Momipites dilatus*, an event not listed in Zarra and others (2019) but probably occurring in Paly 4c, nannofossil zone NP7.

T *Insulapollenites rugulatus* (~57.7 Ma)

Discussion: Zarra and others (2019) place T *Insulapollenites rugulatus* at approximately the top of the Paly 4d zone. Although Zarra and others (2019) describe the lowest occurrence of *I. rugulatus* as a marker at the top of Paly 4d, this is a typographical error, and the authors intended to indicate that the highest occurrence (i.e., top) of *I. rugulatus* is at the top of Paly 4d (Rebecca Hackworth, personal communication). *Insulapollenites rugulatus* appears to have a highly restricted stratigraphic range in the onshore Lower Wilcox with a tentative base in zone Paly 4b, lower NP6 equivalent. T *I. rugulatus* was not clearly observed in our sections. It is likely that this event and possibly other assemblage changes described by Zarra and others (2019) were not observed because stratigraphic sections of the appropriate age (nannofossil zone NP8 equivalent) were not well sampled. The age of 57.7 Ma for this event is estimated based on its height relative to the chronostratigraphic column in Zarra and others (2019).

Momipites spp. inc. (and diversification) (~58 Ma)

Discussion: This event was not clearly observed in our well sections, possibly because of the sample coverage, or possibly because assemblage changes in the deepwater Wilcox Group do not always correlate with assemblage changes in these onshore Wilcox Group wells. The age of 58 Ma for this event is given in Zarra and others (2019).

T Momipites actinus (58.1 Ma)

Discussion: No specimens of *Momipites actinus* were observed in our four onshore wells, although the species has been observed as a rare component of pollen assemblages in other onshore Lower Wilcox stratigraphic sections in Texas (personal observation). It appears that *M. actinus* may be more abundant in the deepwater than in the likely more regionally restricted pollen source area for our onshore Wilcox Group wells. *Momipites actinus* has a restricted range in the Paleocene zones P3 and P4 in the Rocky Mountains and Great Plains region of the United States (Nichols and Ott, 2006). The age of 58.1 Ma for this event is given in Zarra and others (2019).

B *Heliolithus riedelii* (58.70 Ma)

Discussion: This nannofossil bioevent defines the NP7–NP8 boundary. The age of 58.70 Ma for this event is given in Gradstein and others (2012).

T *Deflandrea lucyedwardsiae* (~58.8 Ma)

Discussion: *Deflandrea lucyedwardsiae* was originally described from Paleocene strata in South Carolina by Lucas-Clark (2006), who observed the species to range from nannofossil zone NP1–NP9 (Danian-Thanetian). In the zonation of Zarra and others (2019) *D. lucyedwardsiae* has an earlier stratigraphic top in the Gulf of America in nannofossil zone NP7. Only one specimen of *D. lucyedwardsiae* was observed in our sections, well below its true stratigraphic top. This event is likely more useful in more open marine paleodepositional environments. The age of 58.8 Ma for this event is estimated based on its height relative to the chronostratigraphic column in Zarra and others (2019).

B *Pistillipollenites mcgregorii*–T *Momipites dilatus* zone (Paly 4b–4c equivalent)

Discussion: This zone is defined at the top by T *Momipites dilatus* and at the bottom by B *Pistillipollenites mcgregorii*. T *Momipites dilatus* was not listed in the zonation of Zarra and others (2019) but is estimated to lie within their zone Paly 4c. B *Pistillipollenites mcgregorii* is placed within zone Paly 4b in Zarra and others (2019).

T *Momipites dilatus* (58.97–58.7 Ma?)

Discussion: Although this event was not listed in Zarra and others (2019), Elsik and Crabaugh (2001) used T *Momipites dilatus* as a marker for the top of the onshore Lower Wilcox in the lower Calvert Bluff Formation onshore. Harrington (2017) estimated the age of T *M. dilatus* in the Wilcox Group as at the Selandian-Thanetian boundary or in the lower Thanetian. Crabaugh and Elsik (2000, fig. 2) illustrated T *M. dilatus* as occurring in the upper portion of nannofossil zone NP6. The top of *M. dilatus* in South Carolina is apparently younger, at approximately the Paleocene–Eocene boundary in the Clubhouse Crossroads core (Frederiksen and Christopher 1978). Fairchild and Elsik (1969) gave an even younger top for *M. dilatus* in the Ypresian of the northern Gulf of America coastal plain; it is unclear to us whether this discrepancy is due to outdated chronostratigraphic concepts, or whether *M. dilatus* ranges younger in the eastern Gulf of America region than our sampling area in Texas. The most clearly observed top of *M. dilatus* in our four wells is in Moczygemba VT No. 11 in NP7, lower Thanetian. The short-ranging NP7 zone falls entirely within the lower part of Paly 4c. The sample immediately below the observed top of *M. dilatus* in Moczygemba VT No. 11 is in upper NP6, so the difference in interpreted age between T *M. dilatus* in this study and in Crabaugh and Elsik (2000) is fairly minor and possibly due to either temporal diachroneity in the event itself, the observation of T *M. dilatus* below its true stratigraphic top in Crabaugh and Elsik (2000), or reworking of the two *M. dilatus* specimens observed in NP7 in Moczygemba VT No. 11. The latter possibility we consider unlikely as reworking does not appear to be common in Moczygemba VT No. 11. Analysis of additional wells with nannofossil or foraminiferal control will help to confirm an NP7 age for T *M. dilatus*. The age range of 58.97–58.7 Ma for this event is roughly estimated using GTS 2012 ages for the base and top of nannofossil zone NP7 (Gradstein and others, 2012).

B *Discoaster mohleri*
(58.97 Ma)

Discussion: This nannofossil bioevent defines the NP6–NP7 boundary. The age of 58.97 Ma for this event is given in Gradstein and others (2012).

B *Quadrapollenites vagus*
(59.54–58.97 Ma?)

Discussion: Although this event is not listed in Zarra and others (2019), Frederiksen (1998) placed the base of *Quadrapollenites vagus* in NP6 on the eastern Gulf Coast. Harrington (2017) also listed B *Q. vagus* as an event in the Lower Wilcox. Our confidence in the range of *Q. vagus* in our sections is somewhat limited by the rarity of the species. That said, the observed base of *Q. vagus* in NP6 in Moczygemba VT No. 11 is consistent with the age given by Frederiksen (1998). In Edmond Olinick No. 1, B *Q. vagus* was observed at 5935–5965 ft (1808.99–1818.33 m), in the sample above B *C. veripites*, zone Paly 4a–3c (NP5 equivalent). These occurrences may be caved from upsection as the Edmond Olinick No. 1 samples are well cutting samples. B *Q. vagus* was observed at 5308 ft (1617.88 m) in Jerome Olinick No. 16 in zone Paly 4b–4a (NP5–NP6 equivalent) but is probably above its true stratigraphic bottom due to a large sample gap downsection. *Quadrapollenites vagus* was not observed in Lawrence Keseling No. 1, probably because of poor pollen preservation and low pollen abundances; B *Q. vagus* is probably not reliable in lower abundance sections because of the rarity of the species in the Lower Wilcox. An age range of 59.54–58.97 Ma for B *Q. vagus* is tentatively estimated using GTS 2012 ages for the base and top of nannofossil zone NP6 in Gradstein and others (2012) based on its occurrence in Moczygemba VT No. 11.

B *Insulapollenites rugulatus*
(59.54–58.97 Ma?)

Discussion: This event is not listed in Zarra and others (2019), but Pocknall (1987) placed B *Insulapollenites rugulatus* slightly above B *Pistillipollenites mcgregorii* in the Paleocene Fort Union Formation in Wyoming and Montana. *Insulapollenites rugulatus* is a rare species in our sections, limiting its biostratigraphic reliability, but if its range in the Wilcox Group is similar to the range given by Pocknall (1987) in the continental interior, the event should be present. In Edmond Olinick No. 1, four specimens of *I. rugulatus* were observed; B *I. rugulatus* was observed at the same depth as B *C. veripites*, but there is some uncertainty about the validity of these events due to the possibility of caving from upsection in the cutting samples. In Jerome Olinick No. 16, two specimens of *I. rugulatus* were observed, with B *I. rugulatus* at the same depth as B common *C. veripites* and B *Caryapollenites inelegans*. In Lawrence Keseling No. 1, the top section is NP8–NP9 in age and probably above the range of *I. rugulatus*; the bottom section is zone Paly 3c–3b in age and *I. rugulatus* was not observed, either because the section is below the range of *I. rugulatus* or because of low abundances in the section. In Moczygemba VT No. 11, B *I. rugulatus* was observed at 4945.83 ft (1507.49 m), one sample below B *Q. vagus* and one sample above B *P. mcgregorii* in lower NP6. Because of the slightly higher abundances of *I. rugulatus* in Moczygemba VT No. 11 compared to the other well sections, we considered the observed base of B *Q. vagus* most reliable in Moczygemba VT No. 11. The tentative age range of 59.54–58.97 Ma for B *I. rugulatus* in the Lower Wilcox of Texas is based on GTS 2012 ages for the base and top of nannofossil zone NP6 in Gradstein and others (2012).

B *Heliolithus kleinpellii*
(59.54 Ma)

Discussion: This nannofossil bioevent defines the NP5–NP6 boundary. The age of 59.54 Ma for this event is given in Gradstein and others (2012).

B *Caryapollenites veripites*–B *Pistillipollenites mcgregorii* zone (Paly 3b–4b equivalent)

Discussion: This zone is defined at the top by B *Caryapollenites veripites* and at the bottom by B *Pistillipollenites mcgregorii*. Both events are listed in Zarra and others (2019); B *C. veripites* lies near the top of Paly 3b and B *P. mcgregorii* lies within Paly 4b.

B *Pistillipollenites mcgregorii*
(~59.6 Ma)

Discussion: B *Pistillipollenites mcgregorii* is one of the most reliable biostratigraphic datums in these onshore Lower Wilcox sections. As well as being a marker in Zarra and others (2019), B *P. mcgregorii* is used as a biostratigraphic marker in the Paleocene Powder River Basin of Montana and Wyoming (Pocknall, 1987; Nichols, 2003). Gregory and Hart (1995a) gave a range chart for selected taxa in a Wilcox Group study with a base of *P. mcgregorii* in the Thanetian, while the zonation of Zarra and others (2019) places the base of *P. mcgregorii* in the late Selandian. Fortunately, in Moczygemba VT No. 11, B *P. mcgregorii* was observed in a section with sufficient nannofossil recovery to determine a lower NP6 age for the observed event, slightly younger than the uppermost NP5 age given for B *P. mcgregorii* in Zarra and others (2019). This discrepancy may be due to the observation of B *P. mcgregorii* above its true stratigraphic bottom in Moczygemba VT No. 11, or it may be due to regional diachroneity in the event. We will use the approximate age of 59.6 Ma for B *P. mcgregorii* in Zarra and others (2019), estimated based on its height relative to the chronostratigraphic column, pending analysis of additional sections and further calibration with nannofossil and foraminiferal biostratigraphy.

B common
Caryapollenites veripites
(60.0 Ma)

Discussion: B common *Caryapollenites veripites* is synonymous with *C. veripites* LDCO (lowest downhole common occurrence) in Zarra and others (2019). Events involving abundance changes, in this case a downhole decrease in abundance of *C. veripites*, are inherently more subjective than tops and bases of taxa but are still commonly used and useful in biostratigraphy, particularly in well cutting samples. B common *C. veripites* appears to be most clearly observed in Edmond Olinick No. 1, with approximately 20 specimens of *C. veripites* and ~1.3% relative abundance in the identified pollen and plant spore assemblage at 5515–5545 ft (1680.97–1690.12 m); below this depth range only zero, one, or two specimens of *C. veripites* were observed in samples with similar or greater total pollen and plant spore abundances. In the other three wells B common *C. veripites* was not clearly observed, probably because the event occurs within large sample gaps. The age of 60.0 Ma for this event is given in Zarra and others (2019).

Alnus spp. inc. (~60.3 Ma)

Discussion: Abundances of *Alnus* spp. (syn. *Alnipollenites* spp.) were too low and variable in our sections to have confidence in a consistent downhole increase in the Selandian. More generally, changes in the relative abundance of *Alnus* spp. and other taxa which were used as criteria to distinguish zones Paly 3 and Paly 4 in the zonation of Zarra and others (2019) were not clearly observed in our sections. Again, this may result from an issue with stratigraphic sampling, or relative abundance changes in the deepwater Wilcox Group may not be applicable to these onshore sections. The age of 60.3 Ma for this event is estimated based on its height relative to the chronostratigraphic column in Zarra and others (2019).

T *Kenleyia* spp.
(~60.3 Ma)

Discussion: No specimens of *Kenleyia* spp. were observed in our sections. T *Kenleyia* spp. is likely a more useful event in the deepwater Wilcox Group than the onshore Wilcox Group. The age of 60.3 Ma for this event is estimated based on its height relative to the chronostratigraphic column in Zarra and others (2019).

B *Adnatosphaeridium vittatum*
(60.4 Ma)

Discussion: We found it difficult to consistently separate *Adnatosphaeridium multispinosum* and *Adnatosphaeridium vittatum* and follow Fensome and others (2009) in considering *A. multispinosum* a junior synonym of *A. vittatum*. Depending on the species definition used by Zarra and others (2019), B *A. vittatum* may be equivalent to B *A. multispinosum*. In Edmond Olinick No. 1, the observed base of *A. vittatum* at 5935–5965 ft (1808.99–1818.33 m) may represent the true stratigraphic base of the species, but confidence is limited because only two samples were analyzed downsection of the observed base of *A. vittatum*. The biostratigraphic utility of this event is limited in these onshore wells. The age of 60.4 Ma for this event is given in Zarra and others (2019), assuming B *A. vittatum* is equivalent to B *A. multispinosum*.

B *Apectodinium homomorphum*
(60.4 Ma)

Discussion: Zarra and others (2019) give the base of *A. homomorphum* in the Selandian, nannofossil zone NP5. Speijer and others (2020) give the base of *A. homomorphum* in the Thanetian in northwestern Europe, but the base of *Apectodinium* spp. is significantly earlier in lower latitudes. Brinkhuis and others (1994) gave the base of the genus *Apectodinium* (specifically *A. hyperacanthum*) near the Danian-Selandian boundary at El Kef, Tunisia. *Apectodinium homomorphum* and *Apectodinium* spp. in general are rare in our Lower Wilcox samples and their bases are therefore not possible to determine with accuracy from our sections, but *A. homomorphum* certainly ranges well below the Selandian-Thanetian boundary in the Lower Wilcox. The age of 60.4 Ma for this event is given in Zarra and others (2019).

B *Spinaepollis spinosa*
(61.51–59.54 Ma?)

Discussion: B *Spinaepollis spinosa* appears to be a useful marker even if its stratigraphic position in these wells is somewhat ambiguous. Elsik and Crabaugh (2001) placed B *S. spinosa* "…in the upper Hooper at about the middle of the Lower Wilcox." Harrington (2017) also listed B *S. spinosa* as an event in the Lower Wilcox. In Jerome Olinick No. 16 and Moczygemba VT No. 11 B *S. spinosa* was identified at the same depth as B *Caryapollenites veripites* (possibly due to a large sample gap downsection and an unconformity downsection, respectively). In Edmond Olinick No. 1 *S. spinosa* was present in the bottom sample below B *C. veripites*, but there is greater uncertainty due to the possibility of caving. In Lawrence Keseling No. 1 B *S. spinosa* appears to be above B *C. veripites*, but the low overall abundances reduce our confidence in the sequence of events. The age range of 61.51–59.54 Ma for B *Q. vagus* is tentatively estimated using GTS 2012 ages for the base and top of nannofossil zone NP5 in Gradstein and others (2012) based on its occurrence in Moczygemba VT No. 11.

B *Caryapollenites inelegans*
(61.51–59.54 Ma?)

Discussion: Harrington (2017) considered that *Caryapollenites veripites* and *Caryapollenites inelegans* share a synchronous base in the middle Selandian, nannofossil zone NP5. Pocknall (1987) gave a slightly lower base for *C. inelegans* relative to *C. veripites* in the Paleocene Powder River Basin of Montana and Wyoming. In Edmond Olinick No. 1 B *C. inelegans* was observed one sample above B *C. veripites* at the same depth as B *Quadrapollenites vagus*, but the observed bases are treated with more skepticism due to the possibility of caving. In Jerome Olinick No. 16 B *C. inelegans* was observed above B *C. veripites* and at the same depth as B *Insulapollenites rugulatus*. In Lawrence Keseling No. 1 both species were observed in the bottom analyzed sample and the order of events is indeterminate. In Moczybegma VT No. 11 B *C. veripites* and B *C. inelegans* were observed at the same sample depth above a large sample gap and the order of events is indeterminate. The age range of 61.51–59.54 Ma for B *C. inelegans* is tentatively estimated using GTS 2012 ages for the base and top of nannofossil zone NP5 in Gradstein and others (2012) based on its occurrence in Moczygemba VT No. 11.

B *Caryapollenites* spp.–B *Caryapollenites veripites* zone (Paly 3a–3b equivalent)

Discussion: This zone is defined at the top by B *Caryapollenites veripites* and at the bottom by B *Caryapollenites* spp. Zarra and others (2019) list B *C. veripites* near the top of zone Paly 3b but does not list B *Caryapollenites* spp. The oldest event listed in the zonation of Zarra and others (2019) near the base of the Wilcox Group and the Danian-Selandian boundary is B *Momipites actinus*, a species which was not observed in our onshore sections due to regional rarity or absence. The event B *Caryapollenites* spp. is somewhat questionable; more information is given below in the discussion for B *Caryapollenites* spp.

B *Caryapollenites veripites*
(60.8 Ma)

Discussion: In addition to being listed in Zarra and others (2019) as an event near the top of zone Paly 3b (lower NN5), B *Caryapollenites veripites* is widely used as a Paleocene marker in the continental interior of the United States (e.g., Nichols and Ott, 1978, 2006; Pocknall, 1987; Nichols, 2003). Oddly, Elsik and Crabaugh (2001) do not describe B *C. veripites* as an event in the Wilcox Group, unless their "*Carya* spp. <30 µm" consists only of *C. veripites* or *Caryapollenites inelegans*. The age of 60.8 Ma for this event is given in Zarra and others (2019).

B *Momipites actinus*
(~61.6 Ma)

Discussion: No specimens of *Momipites actinus* were observed in our samples, although *M. actinus* has been rarely observed in other Texas Lower Wilcox onshore sections (personal observation). The age of 61.6 Ma for this event is given in Zarra and others (2019).

B *Fasciculithus tympaniformis*
(61.51 Ma)

Discussion: This nannofossil bioevent defines the NP4–NP5 boundary. The age of 61.51 Ma for this event is given in Gradstein and others (2012).

B *Caryapollenites* spp.
(63.25–61.51 Ma?)

Discussion: With the stratigraphic coverage in our wells, it was not possible to be certain about the range of some *Caryapollenites* spp., particularly the species which appear earliest in the Paleocene of the U.S. continental interior (*Caryapollenites imparalis*, *Caryapollenites prodromus*, and *Caryapollenites wodehousei*). B *Caryapollenites* spp. was only observed in Jerome Olinick No. 16 at 5966 ft (1818.44 m), but this event is somewhat questionable as only two samples were analyzed downsection of 5966 ft (1818.44 m). "*Carya* spp.

<30 µm Base" was used as a marker for the base of the Lower Wilcox by Elsik and Crabaugh (2001). Other authors (e.g., Frederiksen, 1991; Gregory and Hart, 1995a; Jardine, 2011) do not use the modern genus *Carya* in Paleocene strata and instead use the form genus *Caryapollenites*. We will therefore consider the base of *Caryapollenites* spp. (<29 µm) in Gregory and Hart (1995a) as approximately synonymous with *Carya* spp. <30 µm Base in Elsik and Crabaugh (2001); this is supported by the similar ranges given in both publications near the base of the Wilcox Group. Frederiksen (1980a) confusingly lists two taxa with slightly overlapping sizes, "*Carya* spp. <29 µm" and "*Carya* spp. >28 µm."

The division of this type into size classes has utility in the Eocene as larger forms become more common (Tschudy, 1973b) but becomes problematic when the genus is speciated using the taxonomy of Nichols and Ott (2006); several Paleocene species of *Caryapollenites* are described as sometimes being larger than 30 µm, consistent with our observation of occasional specimens of *Caryapollenites* spp. >30 µm in the onshore Paleocene Lower Wilcox. Frederiksen (1991) established three palynological zones for the eastern Gulf Coast; a *Pseudoplicapollis serena* Interval Zone from the base of the Paleocene to the top of *P. serena*, a *Tricolpites asper* Interval Zone from the top of *P. serena* to the base of the *Caryapollenites prodromus* group with consistently occurring *T. asper*, and a *Caryapollenites prodromus* Interval Zone from the base of the *C. prodromus* group to the top of consistently occurring *Carya* >29 µm. The *Caryapollenites prodromus* group includes both *C. prodromus* and *Caryapollenites imparalis* (Frederiksen and others, 2002); these species have been identified separately in this study. Frederiksen (1991, p. 116) stated that the base of *C. prodromus* and *C. imparalis* appears to "…coincide approximately with the regional boundary between calcareous nannofossil zones NP4 and NP5." Zarra and others (2019) place the NP4–NP5 boundary at approximately the base of zone Paly 3a, which is also approximately the Danian-Selandian boundary and the boundary between the Midway Group and Wilcox Group in the deepwater Gulf of America.

In summary, we consider the base of *Carya* sp. 22–28 µm in Tschudy (1973b), the base of *Carya* spp. (<29 µm) in Frederiksen (1980a), the base of the *Caryapollenites prodromus* group in Frederiksen (1991), the base of *Caryapollenites* spp. (<29 µm) in Gregory and Hart (1995a), and the base of *Carya* spp. (<30 µm) in Elsik and Crabaugh (2001) synonymous with our B *Caryapollenites* spp. No limitation on maximum size is necessary for this event as the smaller forms of *Caryapollenites* spp. appear first in the stratigraphic record in the southeastern United States (Tschudy, 1973b; Frederiksen, 1980a). The age range of 63.25–61.5 Ma for this event is tentatively estimated using GTS 2012 ages for the base and top of nannofossil zone NP4 in Gradstein and others (2012) based on the chronostratigraphic placement of the Midway-Wilcox boundary in Crabaugh and Elsik (2000).

B *Ellipsolithus macellus*
(63.25 Ma)

Discussion: This nannofossil bioevent defines the NP3–NP4 boundary. The age of 63.25 Ma for this event is given in Gradstein and others (2012).

Chapter 4. Paleoecology

4.1. Review of concepts

Paleoecology, a subdiscipline of ecology, studies the relationships between ancient organisms and their past environments across geologic timescales. It helps us better understand the life cycles, interactions, environments, and preservation of ancient life. In this chapter, we delve into the subsurface applicability of paleoecological concepts, using palynological data from the Lower Wilcox Group in the subsurface of central Texas.

Sporomorphs (i.e., pollen and other spores) can be categorized into groups of different taxa representing specific vegetation belts, such as upland forests or coastal scrubs, much like in modern environments. By rigorously identifying and counting sporomorphs in a stratigraphic succession, we can uncover changes in the composition of the fossil record over time. These changes are influenced by ecological factors. This approach illustrates how the fossil record can be used to extract information that goes beyond the determination of geologic age or plain depositional environments to also reveal ecosystem changes through geologic time.

Ecostratigraphy merges concepts related to the development of fossil communities over time with traditional stratigraphic concepts (Martinsson, 1973; Margalef, 1986). The central premise of ecostratigraphy is that evolution occurs not only within isolated taxa but also within ecosystems and ecological successions (Margalef, 1986; Rull, 2002). While ecostratigraphic concepts have been successfully applied to reconstruct ancient paleoenvironments in more academic pursuits (van der Hammen, 1957; Poumot, 1989), they have also seen sporadic use in the oil and gas industry for exploration purposes. A few published case studies associated with the oil and gas industry include the Oligo-Pliocene and Eocene sections of the Maracaibo Basin in Venezuela (Rull and Poumot, 1997; Rull and Lorente, 1999; Rull, 2002), and a case study in the Eastern Venezuelan Basin (Salazar and others, 2011). These applied studies demonstrate that ecostratigraphy has a wide range of applications in the subsurface.

A significant application of ecostratigraphy in palynology is the detection of changes in vegetation belts, revealed by quantitative variations captured when analyzing palynological assemblages. These changes in vegetation belts are driven by various factors, including eustasy, basin-level changes (e.g., tectonism), and global climatic change (Rull, 2002). The main challenge in applying ecostratigraphic concepts in the subsurface is the lack of access to robust datasets with sufficient specimen counts for quantitative paleoecological analysis.

Palynoecological groups, defined as associations of palynomorphs linked to different vegetation belts, were first established by Poumot (1989). He used well cuttings from Neogene sections from West Africa and Southeast Asia to identify five sporomorph groups: (1) spores, (2) Palmae-*Pandanus*, (3) mangrove, (4) Rubiaceae-Euphorbiaceae, and (5) *Casuarina* or Gramineae. These five groups, each containing quantitative counts for each identified species, were arranged into a palynoecological diagram. In this diagram, abundance peaks for individual sporomorph groups were termed "ecological phases" (fig. 4). An ascending succession of ecological phases defines a "palynocycle." According to Poumot (1989), the co-occurrence of different ecological phases at the same stratigraphic level, and missing ecological phases in a palynocycle, can be attributed to a variety of factors, including low-density sampling and missing stratigraphic sections. As we will see later in this chapter, some

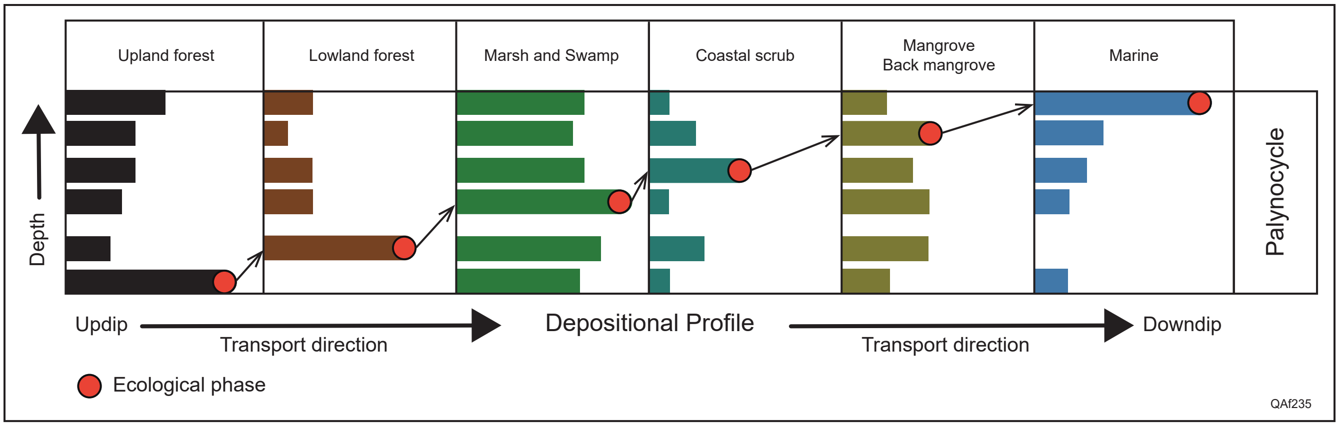

Figure 4. This hypothetical palynoecological diagram features a complete palynocycle. Palynological diagrams using observed data, as seen in Figures 5 and 6 of this chapter, are composed by the vertical stacking of multiple palynocycles. The vertical axis on the plot is depth. Each column corresponds to a palynoecological group, representing a hypothetical paleoecological succession in the Lower Wilcox of central Texas. Each colored bar denotes the percent relative abundance of each group relative to the total palynomorphs counted. In the plot, palynoecological groups (each column) are arranged such that inland paleoenvironments are on the left, while marine paleoenvironments are on the right. Ecological phases for each palynological group are highlighted with red circles (peaks). The ascending trajectory of ecological phases (arrows), from upland forest to marine palynoecological groups, serves as a criterion to define the base and top of palynocycles. Marine ecological phases, which typically define flooding events, are usually the first to be identified during the interpretation of palynoecological diagrams. Not all palynocycles display an ascending trajectory for the different ecological phases for various reasons.

of these interpretations by Poumot (1989) can be attributed to other causes in addition to low-density sampling or missing record.

4.2. Interpretation of Lower Wilcox palynomorph paleoecology

Although it is difficult to be certain of the paleoecological preferences of palynomorph taxa in the Paleocene Lower Wilcox, comparisons with the modern ecological preferences of extant relatives of these taxa, as well as comparisons between palynomorph assemblages in different depositional environments in the Paleogene, can guide paleoecological interpretations. A list of all identified palynomorphs (aside from dinoflagellate cyst taxa), along with interpretations of their biological affinities and interpreted terrestrial paleoecologies where known, is provided in Supplement 1. More detailed discussion of the interpreted paleo-ecologies for particular taxa is provided in Chapter 5. The discussion here will focus on the more common components of the palynomorph assemblages.

Harrington (2008) compared palynological assemblages from Paleocene swamp and marginal marine environments in Mississippi and Alabama. They noted that Taxodiaceae pollen (identified as *Inaperturopollenites hiatipites* in this study) is dominant in marginal marine samples and Betulaceae–Myricaceae pollen is dominant in swamp samples. Harrington (2008) suggested that the ecology of Betulaceae–Myricaceae pollen during this time period may be similar to extant coastal stands of *Myrica* shrubs along the Atlantic coast of the United States (Crawford and Young, 1998). Frederiksen (1985) discussed some evidence that Betulaceae–Myricaceae pollen in the Paleogene Gulf of America may represent brackish-water marshes and coastal sand dunes. Frederiksen (1985) also noted several pollen types which appear to represent more temperate, upland vegetation, notably including *Abies*, *Alnus*, *Picea*, *Pinus*, and *Tsuga*, although he cautioned that some genera, particularly *Pinus*, may have been present to some extent in warm temperate to tropical lowland forests as well. The distinctive pollen of *Alnus* is confidently assignable to the modern genus even in these Paleocene samples, and *Alnus* has been interpreted as mainly being restricted to montane forests in low-latitude pollen assemblages (e.g., Ramírez-Arriaga and others, 2014; Smith and others, 2020c). The low abundance of *Alnus* pollen and bisaccate pollen referable to Class Pinopsida are here interpreted as the pollen of higher elevation, more temperate plants which have been transported long distances from the continental interior.

Comparisons with modern swamp vegetation of the northern Gulf Coast provide another potential source of evidence for the paleoecological affinities of the terrestrial palynomorph assemblage. Prominent extant trees in the swamps of the northern Gulf of America coast include bald cypress (*Taxodium*) and tupelo (*Nyssa*). Two common pollen types in our samples are *Inaperturopollenites hiatipites* and *Nyssapollenites* spp. Although *I. hiatipites* pollen may represent vegetation from Taxaceae, Taxodiaceae, or Cupressaceae , the morphology of the species is consistent with a botanical affinity to *Taxodium*. *Nyssapollenites* is a form genus and the name does not necessarily indicate affinity with the extant genus *Nyssa*; the specimens in this study identified as *Nyssapollenites* spp. are generally similar to *Nyssa kruschii* sensu Frederiksen (1980a, 1980b), but due to the uncertainty in whether this pollen is congeneric with modern *Nyssa*, they have been identified using the form genus name. The botanical affinity of *Nyssapollenites* spp. in our samples may be with the Nyssaceae (Jardine, 2011). It is tempting to interpret the paleoecology for *I. hiatipites* and *Nyssapollenites* spp. as pollen from swamp vegetation, but Frederiksen (1985) discusses some of the uncertainties regarding these paleoecological interpretations. Nichols and Traverse (1971) noted that taxodiaceous pollen was more common in their clay than their lignite samples, possibly indicating *I. hiatipites* is allochthonous and does not represent marsh vegetation adjacent to the nearshore sites of deposition. Harrington (2008) also observed higher abundances of *I. hiatipites* (identified as *Cupressacites hiatipites*) in marginal marine samples than swamp samples from the Paleocene and Eocene Gulf of America coastal plain.

The paleoecological affinities of some other common pollen and plant spores in these samples are less clear, often because they are not easily assignable to a modern botanical group. *Thomsonipollis magnificus* is a common pollen type in the Wilcox Group but begins to disappear near the top of the Wilcox (Zarra and others, 2019); the botanical affinity of the pollen is uncertain, possibly with the Balanopsidaceae or Rubiaceae (Elsik, 1968b; Srivastava, 1972a). *Thomsonipollis magnificus* has a wide distribution in the Paleocene of North America and Europe (e.g., Willumsen, 2004). Despite the uncertainty about the botanical affinity, Lenz and others (2021) associated *T. magnificus* with mangrove ecosystems in Eocene assemblages from Germany.

Classopollis classoides pollen is fairly common and consistently present in these Lower Wilcox samples. Although mainly a Mesozoic group, we consider occurrences of *Classopollis* in the Lower Wilcox as derived from contemporaneous Paleocene vegetation rather than reworked from Mesozoic strata; arguments for this position are provided in Smith and others (2024). *Classopollis* is commonly associated with arid environments in the Paleogene and is often restricted to evaporite deposits, possibly as a result of the genus becoming more ecologically limited in its distribution after the K/Pg mass extinction

(Srivastava, 1976; Sun and Wang, 2005; Berry, 2022). The high abundances of *Classopollis* pollen in these Lower Wilcox wells suggest that *Classopollis* survived locally as a relict population in brackish or even hypersaline coastal marshes. *Chenopodipollis* spp., another relatively common pollen type in these samples, has a probable botanical affinity with the Amaranthaceae, many members of which are xerophytes and halophytes; the presence of *Chenopodipollis* pollen may also indicate coastal salt marsh environments (Nichols and Traverse, 1971; Smith and others, 2020c).

Broadly speaking, relative abundances of lower plant spores from ferns and mosses, as well as abundances of terrestrial fungal spores, may indicate moister paleoenvironments. In particular, the spore genus *Stereisporites* (Sphagnaceae), which is common in these samples, is generally associated with swamps and bogs (Frederiksen, 1985). These plant spores may be mainly derived from a more inland, less xeric source area than *Classopollis* and *Chenopodipollis*. The fern spore *Deltoidospora microadriennis* is common in our samples; several modern genera produce similar spores, including *Acrostichum*, *Antrophyum*, and *Lygodium*. These genera are associated with back-mangrove, wetland or moist tropical forest, and tropical cloud forest environments, respectively (Graham, 1989; Jarzen and Dilcher, 2006; Smith and others, 2020b). The deltaic depositional paleoenvironment indicated by lithostratigraphic associations suggests a back-mangrove or wetland source for *D. microadriennis* in the Lower Wilcox of Texas.

These Lower Wilcox assemblages also contain pollen and plant spores with close morphological similarity to extant tropical groups, suggesting a warm temperate to tropical paleoenvironment. Several species of *Bombacacidites* are present, probably representing tropical Bombacoideae (Smith and others 2020c); the pollen is particularly close in morphology to modern *Ceiba* pollen, a genus native to Mexico, Central America, the Caribbean, and tropical West Africa. *Kuylisporites* spp. are rarely present in the assemblages; the form genus has a botanical affinity with the modern tree fern genus *Cnemidaria* (Smith and others, 2020b), which grows in montane tropical forests in Mexico and the Caribbean. Rare *Spinizonocolpites* spp. have an affinity with the mangrove palm *Nypa*, currently restricted to mainly tropical areas in Australasia and China (Gee, 2001).

A shallow water marine environment is indicated for all samples in these Lower Wilcox wells. Dinoflagellates are present in low relative abundances compared to pollen in all samples, with less than ten observed cysts in many samples. A relatively abundant dinoflagellate cyst type is *Operculodinium*-group spp. This morphological group is essentially synonymous with the dominant dinoflagellate cyst type observed in a subsurface Wilcox Group section from southwestern Louisiana, named "*Cleistosphaeridium-Operculodinium* spp." (Gregory and Hart, 1995a). The later emendation of *Cleistosphaeridium* by Eaton and others (2001) restricted *Cleistosphaeridium* to cysts with process terminations which are at least in part dolabrate; cysts clearly identifiable as *Cleistosphaeridium* were very rare in these samples. Brinkhuis (1994) and Pross and Brinkhuis (2005) described the *Operculodinium*-group as a coastal taxon. The generally low diversity of dinoflagellate cysts and the absence of more deepwater oceanic taxa such as *Cannosphaeropsis*, *Impagidinium*, and *Nematosphaeropsis* support this interpretation (Pross and Brinkhuis, 2005; Sluijs and others, 2005). This is consistent with the interpretation derived from lithological associations indicating neritic paleoenvironments.

Although deposited in shallow water, the dinoflagellate assemblages do not show evidence of reduced salinity; in fact, there is some indication of a hypersaline restricted marine environment in the dinoflagellate assemblages. The ratio of peridiniacean dinoflagellates to gonyaulacacean dinoflagellates has been used as a proxy for salinity, with peridiniacean dinoflagellates having a higher relative abundance in low salinity environments (Harland, 1973). In particular, *Cerodinium*, *Deflandrea*, *Phthanoperidinium*, and *Senegalinium* are considered tolerant of low salinity (Frieling and Sluijs, 2018). The samples in this study generally contain high relative abundances of the gonyaulacacean *Operculodinium*-group, and peridiniacean dinoflagellate cysts are rare. *Homotryblium* and *Polysphaeridium* are both present in these samples, with *Polysphaeridium* more common; these genera have been associated with hypersaline lagoons (Dybkjær, 2004; Pross and Brinkhuis, 2005). *Spiniferites ramosus* group dinoflagellate cysts are relatively common in the samples; *Spiniferites* is a cosmopolitan, generalist taxon, but has been associated with open marine outer neritic paleoenvironments (Frieling and Sluijs, 2018; Mahboub and Slimani, 2020). A potential explanation for the low dinoflagellate cyst abundance or diversity and the dominance of gonyaulacacean cysts is that these Wilcox Group sediments were deposited in restricted shallow marine to outer neritic paleoenvironments which were intermittently hypersaline. The presence of xeric pollen taxa such as *Classopollis* and *Chenopodipollis* are also consistent with local hypersaline paleoenvironments in the form of coastal salt marshes or lagoons.

4.3. Ecostratigraphy and palynocycles

This study utilized partial stratigraphic sections from the Jerome Olinick No. 16 well from 5096.17–5308.00 ft (1553.31–1617.88 m) and from the Moczygemba VT No. 11 well from 4865.25–4976.33 ft (1482.93–1516.79 m) to examine the applicability of ecostratigraphic concepts within the Lower Wilcox of central Texas. The selection of these wells and depth ranges was based on their sampling density, the completeness of their stratigraphic record, and their excellent sporomorph preservation. Palynomorph taxa have been grouped into simplified paleoecological types. All in situ dinoflagellate cysts have been grouped into a marine paleoecological group. Supplement 1 contains a list of all other palynomorphs and their paleoecological interpretation. A simplified subset of the more common terrestrial palynomorph taxa (table 2) have been grouped into five different paleoecologies; rare taxa (defined as taxa with less than 20 occurrences in the four analyzed wells) have been excluded from these groups. The counts of taxa listed for each paleoecological group in table 2 have been summed and the total abundances of each group were calculated as percent relative abundance compared to the total sum of all palynomorph taxa listed in table 2.

The six simplified paleoecological groups are, moving from hinterland to marine paleoenvironments: upland forest, lowland forest, marsh and swamp, coastal scrub, mangrove and back-mangrove, and marine. In the nearshore deltaic paleodepositional environment of these Lower Wilcox cores, the marine group can be considered the in situ portion of the assemblage and the terrestrial groups can be considered the allochthonous fraction which has been transported from the terrestrial environment by wind and water to the nearshore deltaic site of deposition (fig. 5). We modified Poumot's (1989) approach by incorporating dinoflagellate cysts into the marine palynoecological group; we also included different taxa within each group based on their abundance and affinity to vegetation belts.

Figure 6 and figure 7 illustrate the palynoecological diagrams for partial stratigraphic sections from the Jerome Olinick No. 16 and Moczygemba VT No. 11 cores. In these plots, palynocycles were defined by qualitatively fitting observed relative abundance changes of major

Table 2. Summary of taxa included in each palynoecological group for the Lower Wilcox[1]

Palynoecological Group	Taxon
1. Upland forest	*Gleicheniidites senonicus* *Eucommia?* spp. *Alnus* spp. Class Pinopsida
2. Lowland forest	*Echinatisporis* spp. *Bombacacidites* spp. *Hamulatisporis* spp. *Malvacipollis* spp. (Euphorbiaceae type) *Cycadopites* spp. *Inaperturopollenites hiatipites* *Ulmipollenites krempii*
3. Swamp and marsh	*Cyathidites minor* *Cicatricosisporites* spp. *Classopollis classoides* *Nyssapollenites* spp. *Betulaceae/Myricaceae* type *Laevigatosporites* spp. *Stereisporites* spp. *Stereisporites buchenauensis*
4. Coastal scrubs	*Gnetaceaepollenites jansonii* *Arecipites tenuiexinous* *Arecipites* spp. (punctate/scabrate) *Chenopodipollis* spp.
5. Mangrove–Back mangrove	*Proxapertites magnus* *Thomsonipollis magnificus* *Deltoidospora microadriennis*
6. Marine	Dinoflagellate cysts

[1] Main vegetation belts are shown in figure 5.

paleoecologic groups to the theoretical sequence of relative abundance peaks illustrated in figure 4. In both wells, major marine ecological phases determined from relative abundance peaks in marine palynomorphs are interpreted as marine flooding events. Relative abundance peaks in dinoflagellate cysts mark the top of the palynocycles, while relative abundance peaks in upland forest taxa define the base. It is important to note that changes in the abundance of palynomorphs associated with more inland terrestrial palynoecological groups (upland and lowland forests,

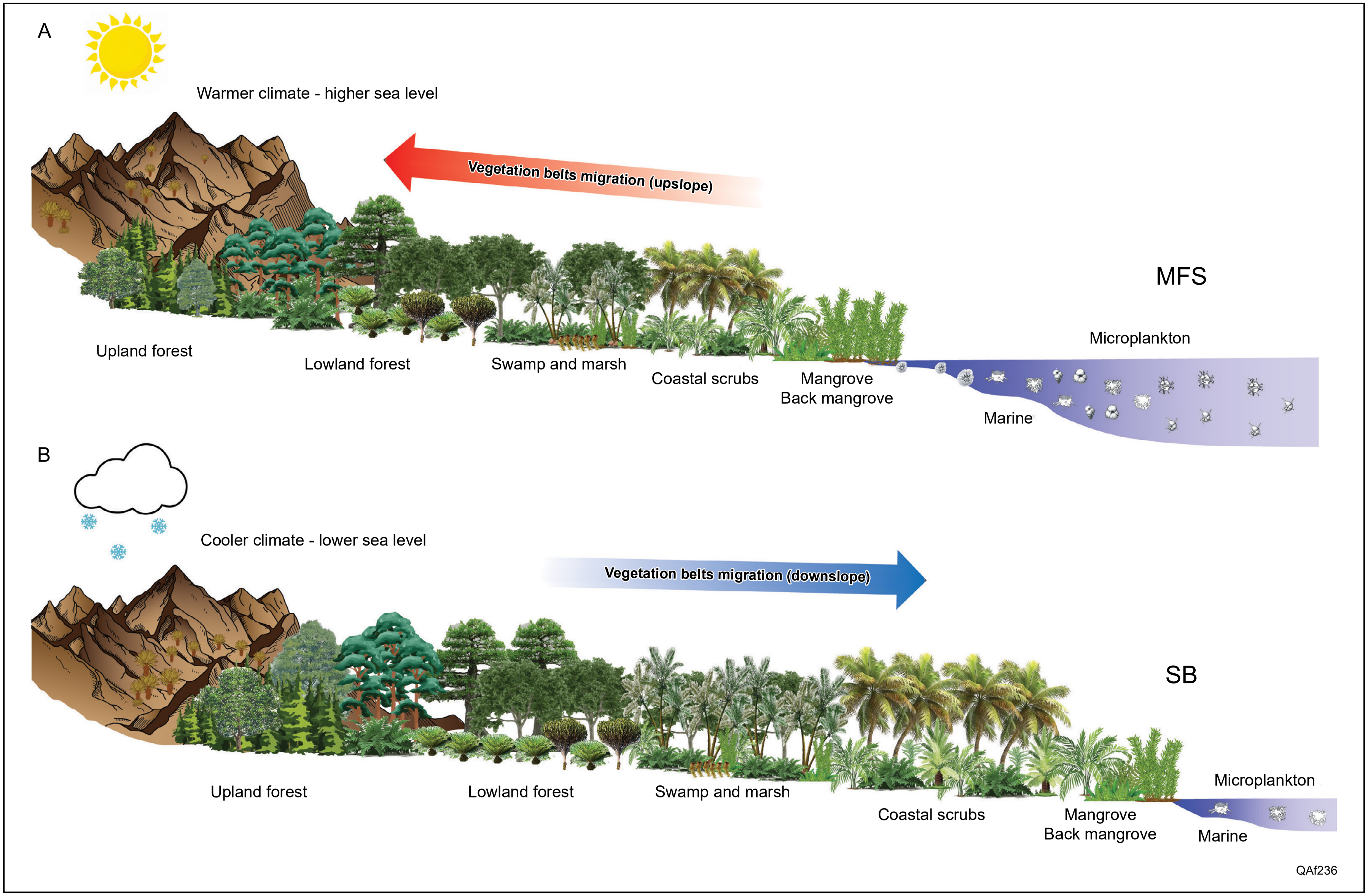

Figure 5. Hypothetical model of vegetation belts across the Lower Wilcox source area during the Paleogene. A) Configuration of vegetation belts during higher sea level (warmer climate). B) Configuration of vegetation belts during lower sea level (cooler climate). Modified from previous models by Poumot (1989), Rull and Lorente (1999), and Rull (2002).

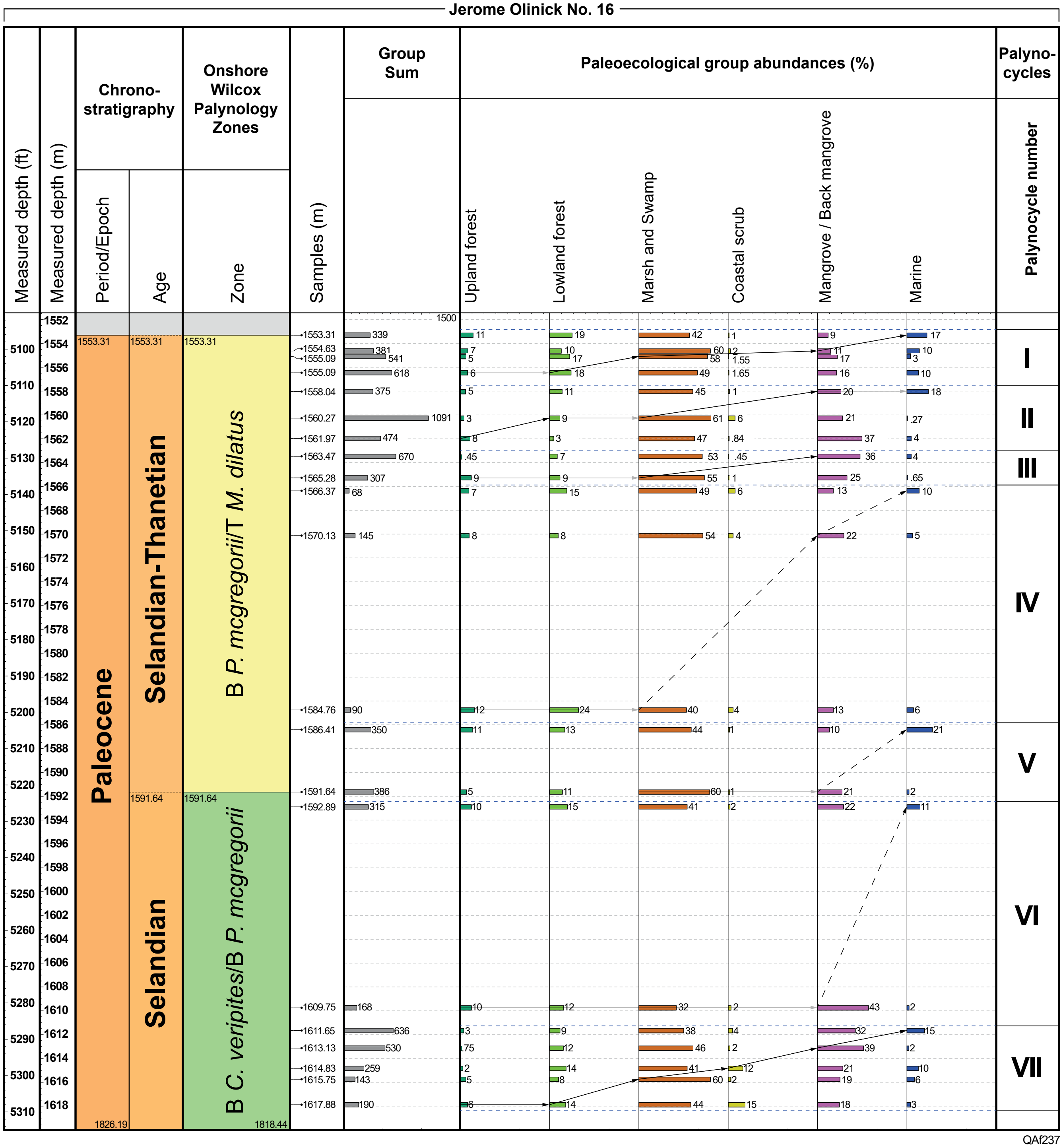

Figure 6. Palynocycles in the upper section of the Jerome Olinick No. 16 core. The top and base of palynocycles 1 to 6 are defined by marine and upland forest ecological phases (abundance peaks) respectively. In terms of abundance, all palynocycles showcase a strong influence of the marsh/swamp and mangrove palynoecological groups. Clear dinoflagellate cyst peaks are identifiable on the marine palynological group defining the top of palynocycles. Coastal scrubs are more dominant toward the base of the section (palynocycle 6).

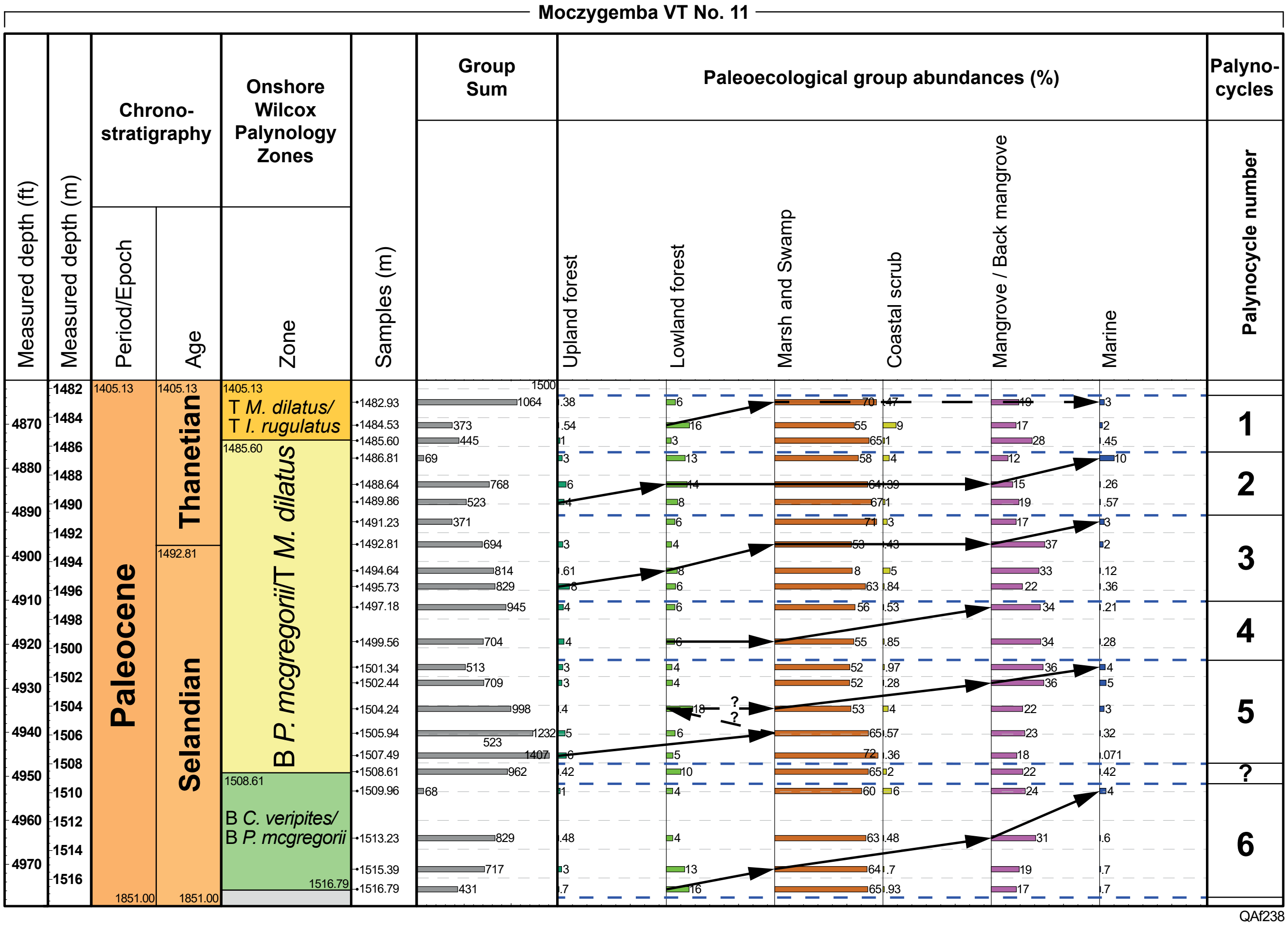

Figure 7. Palynocycles in the middle section of the Moczygemba VT No. 11 core. The magnitude of the flooding events seems lower in this section than in the Olinick No. 16 section.

and swamps and marshes) are typically interpreted as a response to climatic variations affecting inland vegetation belts. Conversely, variations in the abundance of palynomorphs associated with coastal palynoecological groups (coastal scrubs, mangrove and back-mangrove, and marine) are interpreted as an immediate response to relative sea-level changes (Poumot, 1989).

In the examined sections of the Jerome Olinick No. 16 and Moczygemba VT No. 11 cores, not all palynocycles are complete or exhibit a perfect ascending trajectory of ecological phases from upland forest to marine palynoecological groups. In the Jerome Olinick No. 16 well (fig. 6) seven palynocycles were identified (using Roman numerals). Palynocycles I, II, and VII are complete, demonstrating ascending trajectories of ecological phases. Palynocycles III, IV, V, and VI appear incomplete, but this may be an artifact of two larger sample gaps within that section. Conventional palynological biostratigraphic identified two biozones in the upper section of the Jerome Olinick No. 16 core. However, the identification of these seven palynocycles enhances the resolution of the interpretation, as each palynocycle likely represents a higher frequency stratigraphic cycle (fourth order cycles or higher cycles).

In the Moczygemba VT No. 11 partial stratigraphic section (fig. 7), six palynocycles were also identified (using Arabic numerals). Palynocycle 1 seems incomplete, with a strong marsh or swamp signal. Palynocycle 2 seems complete, also with a strong marsh or swamp signal. Palynocycle 3 seems complete with an increase in the relative abundance of mangrove or back-mangrove elements relative to palynocycles 1 and 2. Palynocycle 4 seems incomplete with very little marine influence. Palynocycle 5 has an interruption in the cycle with an out of phase peak in the lowland forest group. The meaning of this backwards step in the expected sequence of relative abundance peaks is not clear. The sample at 4949.50 ft (1508.61 m) depth does not easily fit into either palynocycle 5 or 6 and it may represent a small interruption in the stratigraphic record. Palynocycle 6 is almost complete, missing only the expected peak in upland forest taxa; this may be because the bottom of palynocycle 6 was not sampled.

This middle section of Moczygemba VT No. 11 generally exhibits a weaker signal from the hinterland and a stronger signal from marshes and swamps compared to the Jerome Olinick No. 16 partial stratigraphic section. The average relative abundance of the marine ecological group compared to the other five terrestrial ecological groups is lower in the Moczygemba VT No. 11 partial section than the Jerome Olinick No. 16 partial section, indicating a more inland position with respect to the paleocoastline. The increased marine influence in the Jerome Olinick No. 16 partial section compared to the Moczygemba VT No. 11 partial section is confirmed with a calculation of the relative abundance of dinoflagellate cysts compared to the entire terrestrial pollen and plant spore assemblage.

The sample spacing and resolution in these wells is not high enough to establish a one-to-one correlation between palynocycles in these two wells. However, these two wells and the studied stratigraphic sections are similar enough to identify subtle variations in paleoenvironmental interpretations when the paleoecological groups are examined in detail. In addition, the increased resolution in the definition of individual palynocycles, in conjunction with other tools (e.g., biostratigraphy and chemostratigraphy), can significantly increase our ability to correlate units in the future with a higher degree of confidence.

4.4. Final remarks

According to Poumot (1989), incomplete palynocycles and flat ecological phases reflect a combination of factors, including low sampling density, high sedimentation rates, and missing stratigraphic sections. Relative taxon abundances are also subject to increased uncertainty when total abundances are lower, possibly as a result of taphonomic effects or even degradation of core material after long-term storage. However, these factors are unlikely to explain the incompleteness of some of our palynocycles since our sampling frequency is high in both sections, the stratigraphic interval under study is continuous, and palynomorph abundances are generally high. Instead, we interpret the irregularities in the succession of ecological phases as related to how sporomorphs and other palynomorphs are transported and preserved across the depositional profile.

Pollen, spores, and other palynomorphs exhibit behavior like clastic sedimentary particles during transport across the depositional profile (Traverse, 2007). As a result, palynomorphs belonging to specific paleoecological groups are sorted during their journey from proximal (inland) to distal (marine) environments (e.g., Muller, 1959). In essence, palynological assemblages in marine sections comprise an in situ fraction and an allochthonous fraction, the latter originating from inland portions of the depositional profile. This allochthonous fraction is transported downward along the sedimentary profile by wind and water. The relative abundances of palynomorphs can increase or decrease based on these sedimentary processes and environmental fluctuations, causing some ecological phases (i.e., relative abundance peaks) to coincide at the same depth or to be absent altogether due to erosion, poor preservation, or low abundance. The presence of upland forest taxa from the hinterland in the deltaic paleo-depositional environments of these core sections provides useful information about paleoclimatic conditions in the continental interior. These palynocycle techniques shown here are not new; however, they are underutilized tools for subsurface stratigraphic correlation in hydrocarbon extraction or carbon capture and storage (CCS) projects, particularly in well sections with poor recovery of marine microfossils. Based on these results, we believe it is worth incorporating and expanding the use of these techniques into modern workflows for subsurface interpretation.

Chapter 5. Systematic Palynology

5.1. Introductory comments

A detailed catalog of all identified palynomorphs from the four analyzed wells is provided as an Excel spreadsheet in Supplement 1. This catalog, the descriptions and discussion provided in the systematic taxonomy section, and plates containing photomicrographs of all identified palynomorphs in the study provide a unified framework for practical reference by specialists studying Lower Wilcox units along the Gulf Coast and within the broader Gulf of America Basin. Clearly specified definitions of palynomorph taxa are crucial for biostratigraphic and paleoenvironmental interpretations of the Lower Wilcox Group because, without consistent definitions of taxa, palynologists with different backgrounds may incorrectly identify key species. The discipline in charge of finding, describing, and naming taxa is known as alpha taxonomy. The palynological literature unfortunately contains a multitude of synonymous or overlapping taxon names compared to other micropaleontological disciplines, and numerous species described below have been reassigned to multiple different genera, resulting in a great deal of confusion, particularly with non-specialists who are unaware of potential synonymies. Even taxa which are very abundant in our Lower Wilcox samples are given different names by different authors. For example, a pollen type identified here as Betulaceae–Myricaceae type, which may be identified by other authors as *Casuarinidites* spp., *Triatriopollenites* spp., or *Triporopollenites* spp. (Jardine, 2011). This highlights the importance of building a robust alpha taxonomy to ensure consistency during the identification of species by multiple palynologists.

Four previous publications by the lead author (Smith and others, 2020a, 2020b, 2020c, 2021) dealt with the palynology of International Ocean Discovery Program (IODP) Expedition 364, Site M0077 in the Chicxulub impact crater, including the systematic taxonomy of pollen and plant spores from the core. This published taxonomy was combined with additional taxonomic descriptions originally provided as supplements in previous publications in Smith (2020). To simplify citations to this research, only Smith (2020) will be cited in the following taxonomic section. To maintain consistency with informal identifications given in Smith (2020), species will not be informally identified with the same name as a species in Smith (2020) if they are not considered synonymous. The use of open nomenclature follows recommendations given by Bengtson (1988). In particular, the species name is not abbreviated after the use of "cf." or "aff." For example, a formally undescribed taxon similar to but smaller than *Choanopollenites eximius* in this study has been identified as *Choanopollenites* aff. *eximius* (small) rather than *Choanopollenites* aff. *L. eximius*. We have taken a conservative approach towards the formal naming of new species and have not formally described any new species in this report; several rare types identified informally here may deserve formal description if additional specimens are observed in other locations.

Morphological terms for pollen and spores generally follow definitions given by Punt and others (2007) unless otherwise noted. This study will use a simplified system for describing the shape of pollen grains. If the equatorial diameter is significantly longer than the polar axis, the grains are described as oblate; if the equatorial diameter and polar axis are approximately equal in length, the grains are described as spheroidal; if the equatorial diameter is significantly shorter than the polar axis, the grains are described as prolate. Pollen types only observed in polar view are assumed to be oblate or spheroidal. Practically, it is unfeasible to differentiate species based on detailed measurements of individual specimens based on their P/E ratios while counting thousands of pollen grains. In particular, the genus *Tricolpites* technically includes some subprolate pollen grains; this study will restrict the use of *Tricolpites* to spheroidal or oblate pollen grains as we defined those terms above.

Additionally, the distinction between zona and cingulum in plant spores is qualitative and gradational. As defined by Punt and others (2007), both zona and cingulum refer to structures which project from the equatorial region of the spore but do not extend over the distal or proximal face. A cingulum is distinguished by being thicker than a zona, although no quantitative cutoff in terms of width was provided by Punt and others (2007). Similarly, Traverse (2007, pp. 105, 204) defined the zona as an equatorial exinal thickening of the spore, and the cingulum as a type of zona which is particularly thick. Elsik (1968a, p. 304) simply considered the terms cingulum and zona synonymous.

Fungal spores have been identified based on the taxonomy presented in Saxena and others (2021) and Kalgutkar and Jansonius (2000) unless otherwise noted. The term "acritarch" is used sensu Evitt (1963), including all palynomorphs of uncertain biological affinity. Smooth-walled, more or less spherical, morphologically nondescript acritarchs (i.e., leiosphaerids) have not been included in the palynomorph counts for this study or described in the taxonomic section. This is not intended to deny the usefulness of leiosphaerids in other situations (e.g., Tahoun and Mohamed, 2015; Spiridonov and others, 2017; Mishra and others, 2021), but full consideration of the morphological variation and biological affinities for the group has been set aside for later research. The taxonomic description of dinoflagellate cysts is considered outside the scope of this study and has also been set aside for later research.

5.2. Trilete spores

Genus *Aequitriradites*
Delcourt and Sprumont, 1955 emend.
Cookson and Dettmann, 1961

Aequitriradites aff. *spinulosus*
(Cookson and Dettmann, 1958a)
Cookson and Dettmann, 1961

Plate 1, figure 22

Discussion: The single observed specimen of this type has laesurae which extend into a wide, scabrate zona. The equatorial diameter of the spore including the cingulum is circa 41 µm. Widely scattered small verrucate to baculate or conate projections are present, mainly on the distal side of the spore. The surface is also finely punctate. This spore resembles *A. spinulosus* sensu stricto (Cookson and Dettmann, 1958a; Dettmann, 1963), in particular specimens observed in the Maastrichtian of Alberta, Canada (Srivastava, 1972b, Plate 2, figs. 4–7). However, this specimen is smaller than the size range given for *A. spinulosus*, and punctate sculpture is not present in *A. spinulosus* (Cookson and Dettmann, 1958a). It is unclear whether the ragged outline of the zona is a morphological feature or the result of taphonomic processes.

Botanical affinity: *Aequitriradites* has a similar morphology as some modern hepatic spores, particularly in the family Sphaerocarpaceae (Dettmann, 1963).

Stratigraphic comments: *Aequitriradites spinulosus* and related forms are mainly restricted to the Mesozoic (Srivastava, 1972b; PalynoData Inc. and White, 2008); *Aequitriradites* aff. *spinulosus* is considered probably reworked from Mesozoic strata.

Genus *Appendicisporites* Weyland and Krieger, 1953

Appendicisporites spp.

Plate 4, figure 3

Discussion: These specimens of *Appendicisporites* are essentially synonymous with specimens identified by Jardine (2011) as *Appendicisporites* spp. The ridges or muri are either smooth or have sparse rounded verrucae. An illustration of the type species *Appendicisporites tricornitatus* in Jansonius and Hills (1976) has much longer angular appendages than our specimens, although a specimen of *A. tricornitatus* imaged by Stanley (1965, Plate 33, figs. 8–9) has much shorter appendages and is more similar to the specimens in this study. *Nodosisporites crenimurus* possesses densely arranged baculate, verrucate, or warty projections on the muri, but is otherwise similar.

Botanical affinity: *Anemia* (Schizaeaceae) (Stanley, 1965; Dettmann and Clifford, 1992).

Paleoecology: Possibly freshwater swamp, given the interpreted paleoecology for *Cicatricosisporites paradorogensis*, a species with a similar botanical affinity, given by Akkiraz and others (2008).

Genus *Baculatisporites* Pflug and Thomson in Thomson and Pflug, 1953 emend. Krutzsch, 1967

Discussion: We will follow Krutzsch (1967), whose reasoning is summarized in Jansonius and Hills (1976, card 219), and consider that *Osmundacidites* and some other form genera used for spores referable to the Osmundaceae are junior synonyms of *Baculatisporites*.

Baculatisporites spp.

Plate 1, figure 19

Discussion: This pollen type has ornamentation of variable morphology, including baculae, papillae, verrucae, and rugulae, similar to spores produced by modern *Osmunda*. This broadly defined type is more or less synonymous with spores identified by Stanley (1965) as *Osmunda comaumensis* and spores identified by Couper (1953) as *Osmundacidites wellmanii*. Spores identified here as *Verrucosisporites* spp. are distinguished by being exclusively verrucate. *Clavatisporites* sp. A is somewhat similar but is distinguished by being prominently clavate.

Botanical affinity: Osmundaceae.

Genus *Camarozonosporites* Pant, 1954 from Potonié, 1956

Camarozonosporites grootii Srivastava, 1972

Plate 2, figure 8

Discussion: This species of trilete spore is easily distinguished from other trilete spores in the Wilcox Group by its extremely coarse reticulum.

Botanical affinity: Lycopodiaceae (Srivastava, 1972a).

Genus *Cicatricosisporites* Potonié and Gelletich, 1933 emend. Potonié, 1966

Cicatricosisporites dorogensis Potonié and Gelletich, 1933 emend. Potonié, 1966

Plate 4, figure 1

Discussion: Jardine (2011) provided arguments that *C. dorogensis* and *Cicatricosisporites paradorogensis* are morphologically overlapping and it is not feasible to consistently differentiate the two types. However, in this study we have retained the distinction between the two species, restricting *C. pardorogensis* to distinctly foveo-striate forms. Intermediate forms have been retained in *C. dorogensis*.

Botanical affinity: *Anemia* or *Mohria* in the Schizaeaceae family (Frederiksen, 1980a).

Paleoecology: Probably freshwater swamp, given the interpreted paleoecology for *C. paradorogensis* given by Akkiraz and others (2008).

Cicatricosisporites paradorogensis Krutzsch, 1959

Plate 4, figure 2

Discussion: *Cicatricosisporites paradorogensis* is distinguished from *C. dorogensis* by having foveo-striate, rather than simply striate, sculpture, although intermediate forms exist (Jardine 2011).

Botanical affinity: *Anemia* or *Mohria* in the Schizaeaceae family.

Paleoecology: Probably freshwater swamp (Akkiraz and others, 2008).

Genus *Cingulatisporites* Thomson in Thomson and Pflug, 1953 emend. Hiltmann, 1967

Discussion: The short original description of *Cingulatisporites* by Thomson and Pflug (1953) mentions only the presence of a zona no wider than 1/5 of the total spore diameter. Hiltmann (1967) emended *Cingulatisporites*, restricting the genus to trilete spores with a triangular amb with a narrow cingulum, and specifically excluding spores with a crassitude or zona, as well as verrucate to "corrugate" forms. The emendation by Hiltmann (1967) is somewhat problematic, as part of the emendation by Hiltmann (1967) translated by Jansonius and Hills (1976) states *Cingulatisporites* has a trilete mark which "…reaches the inner edge of the zona." However, the type species *Cingulatisporites levispeciosus* as redescribed by Pocock (1961, fig. 1) has laesurae which do not always reach the inner edge of the cingulum. A broad definition of *Cingulatisporites* will be used here which includes all trilete spores with a prominently developed cingulum no wider than 1/5 of the total spore diameter. The differentiation between *Cingulatisporites* and *Stereisporites* is examined in the discussion for *Stereisporites*.

Cingulatisporites sp. A

Plate 1, figure 5

Discussion: *Cingulatisporites* sp. A has a convex subtriangular amb, psilate sculpture, and short, faint laesurae which are not marginate. The type species *Cingulatisporites levispeciosus* was redescribed by Pocock (1961), who noted that the laesurae extend over 2/3 the radius of the central body. The laesurae in *Cingulatisporites* sp. A are significantly shorter. *Cingulatisporites dakotaensis* is somewhat similar (Stanley, 1965), but *C. dakotaensis* has a Y-shaped thickened area on the distal surface which *Cingulatisporites* sp. A lacks. Also, the laesuarae are longer in *C. dakotaensis*. Jardine (2011) identified specimens of *Cingulatisporites* without speciating them and gave their botanical affinity as *Sphagnum*.

Botanical affinity: Bryophyta or Pteridophyta sensu lato, possibly Sphagnaceae.

Genus *Clavatisporites* Kedves and Simonciscs, 1964

Discussion: *Clavatisporites* was originally described as an azonotrilete microspore with clavate sculpture. Although originally described as uniformly clavate, the type species *Clavatisporites clarus* has larger clavae on the distal face (Jansonius and Hills, 1976, card 515). A broad definition of *Clavatisporites* is used here which includes all trilete spores where clavae are the most prominent sculptural element. *Clavatriletes* Herbst, 1965 and *Clavatriletes* Regali and others, 1974 are both considered junior synonyms of *Clavatisporites* sensu lato, as well as obviously homonyms of each other.

Clavatisporites sp. A

Plate 1, figure 18

Discussion: This rarely observed type of trilete spore is distinguished from other trilete taxa in the Lower Wilcox by having prominent clavate ornamentation which is mainly restricted to the distal face of the spore. This type is somewhat similar to trilete spores identified by Pocknall and Nichols (1996) as "*Baculatisporites* sp.," except that in their species the ornamentation is mainly baculate.

Botanical affinity: Possibly Osmundaceae.

Genus *Cyathidites* Couper, 1953

Discussion: A review of the differentiation between *Cyathidites* and *Deltoidospora* is provided in the discussion for Deltoidospora.

Cyathidites minor Couper, 1953

Plate 1, figure 1

Discussion: *Cyathidites minor* is distinguished from *Deltoidospora* spp. by having significantly concave sides of the amb (see discussion for *Deltoidospora* for further detail). *Cyathidites australis* is larger (≥54 µm in diameter) (Couper, 1953).

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

Paleoecology: Wakefield and Monteil (2002) described *C. minor* specimens from the Cretaceous and Paleogene of Pakistan as back-mangrove or brackish swamp representatives.

Cyathidites sp. A

Plate 1, figure 2

Discussion: The single observed specimen of this type is distinguished from *C. minor* by having prominently marginate laesurae.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Genus *Deltoidospora* Miner, 1935

Discussion: The original description of *Deltoidospora* by Miner (1935, p. 618) is as follows: "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." Several other form genera for psilate, trilete plant spores are at least partially synonymous with *Deltoidospora*, including *Leiotriletes*, *Lygodiumsporites*, and *Psilatriletes* (Smith, 2020). Jansonius and Hills (1976, card 748) state that *Cyathidites* is distinguished from *Deltoidospora* by having "… distinctly concave sides." However, the type species of *Deltoidospora*, *Deltoidospora hallii*, was described by Miner (1935) as having straight or slightly concave sides. Jardine (2011) grouped psilate, trilete spores with concave sides together with straight-sided and convex-sided forms into an unspeciated "*Deltoidospora* spp." taxon and indicated some skepticism regarding whether the shape of the sides is a taphonomic artifact. In this study, the circumscription of *Cyathidites* is restricted to psilate, trilete spores where all three sides are significantly concave. A small, morphologically transitional specimen between the two genera is illustrated in Plate 1, figure 3; because two sides of the amb are slightly concave and the third side is approximately straight-sided, it has been identified as *Deltoidospora* sp. A detailed morphometric study of these forms would help to clarify whether there is any utility in splitting psilate, trilete plant spores in the Wilcox Group. Arguably, a more consistent differentiation between the two genera would exclude specimens where any one side of the amb is concave from *Deltoidospora*, but this would require excluding the type species *Deltoidospora hallii* from the genus.

Deltoidospora spp.

Plate 1, figures 3, 7

Discussion: Psilate, trilete spores with slightly concave, straight, or convex sides of the amb have often been assigned to *Deltoidospora microadriennis*, *Deltoidospora adriennis*, or left unspeciated as *Deltoidospora* spp. (e.g., Cookson, 1953; Anderson, 1960; Frederiksen and others, 1983; Graham and others, 2000; Jardine, 2011). *Deltoidospora adriennis* and *D. microadriennis* appear to be distinguished mainly on the basis of size in the literature; *D. adriennis* was originally described as being 63–75 µm in diameter (Jansonius and Hills, 1976, card 1651) and *D. microadriennis* was described by Frederiksen and others (1983) as being 35–65 µm in diameter. This separation based on size is not consistent in the literature; various authors have described specimens of *D. adriennis* with a size range of 30–65 µm in diameter (e.g., Cookson, 1953; Anderson, 1960; Graham and others, 2000). Although most palynologists consider *D. adriennis* as a primarily or exclusively psilate form (e.g., Cookson, 1953; Anderson, 1960; Graham and others, 2000), this is somewhat problematic as *D. adriennis* was originally described as having a finely punctate exine (Jansonius and Hills, 1976, card 1651). This study will follow Jardine (2011) in part by not speciating *Deltoidospora*, but unlike Jardine (2011), we have separately identified small to medium-sized, psilate, trilete spores which have three significantly concave sides as *Cyathidites minor*. A type of psilate, trilete spore with prominently marginate, non-undulating laesurae has been separately identified as *Deltoidospora* sp. A.

Botanical affinity: Polypodiidae, possibly *Acrostichum* (Pteridaceae), *Antrophyum* (Pteridaceae), or *Lygodium* (Schizaeaceae); all three genera produce spores similar to *D. microadriennis* (Graham, 1989; Jarzen and Dilcher, 2006; Smith, 2020).

Paleoecology: Possibly back-mangrove if the botanical affinity is with *Acrostichum*, possibly tropical cloud forest if the affinity is with *Antrophyum*, possibly wetland or moist tropical forest if the botanical affinity is with *Lygodium* (Graham, 1989; Jarzen and Dilcher, 2006; Smith, 2020).

Deltoidospora sp. A

Plate 1, figure 4

Discussion: This type is distinguished from other *Deltoidospora* spp. in this study by having prominent margines . *Undulatisporites* has marginate labra which are undulating; the marginate labra in *Deltoidospora* sp. A are relatively straight.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Genus *Echinatisporis* Krutzsch, 1959

Echinatisporis spp.

Plate 2, figures 10–13

Discussion: This morphotype includes small to medium-sized, echinate, trilete spores. There is substantial variability between specimens in the size, density, and shape of the echinae, but due to the rarity of this type, it is not clear whether these represent a morphological continuum or can be meaningfully subdivided.

Botanical affinity: Probably Selaginellaceae.

Paleoecology: Lowland temperate or tropical forest, based on the paleoecology given for Paleogene specimens identified as *Echinatisporis* sp. A with affinity to the Selaginellaceae in Smith (2020).

Genus *Gleicheniidites* Ross, 1949

Gleicheniidites senonicus Ross, 1949

Plate 1, figure 6

Discussion: Smith (2020) provides discussion on the taxonomy of the genus and species.

Botanical affinity: Gleicheniaceae (Jardine, 2011).

Paleoecology: Uncertain, possibly montane forest or freshwater marsh (Smith, 2020).

Genus *Hamulatisporis* Krutzsch, 1959 emend. Srivastava, 1972b

Hamulatisporis amplus Stanley, 1965

Plate 2, figure 9

Discussion: *Hamulatisporis amplus* is similar to *Hamulatisporis hamulatis* but is larger (>50 µm in diameter) (Stanley, 1965).

Botanical affinity: Possibly *Lycopodium* (Stanley, 1965).

Hamulatisporis hamulatis Krutzsch, 1959 sensu lato

Plate 2, figures 6, 7

Discussion: *Hamulatisporis hamulatis* was originally described as having rugulate (i.e., hamulate) sculpture that is more pronounced on the distal face (Jansonius and Hills, 1976). The implication of this description is that there is some development of rugulae on the proximal face. However, Stanley (1965), using a broad species concept, included specimens with no rugulae developed on the proximal face in *H. hamulatis*. *Hamulatisporis amplus* is larger (50–70 µm in diameter) than *H. hamulatis*; Stanley (1965) described their specimens of *H. hamulatis* as 27–34 µm in diameter. We have used a broad definition of *H. hamulatis* which includes all spores of this type less than 50 µm in diameter.

Botanical affinity: Lycopodiaceae (Smith, 2020).

Paleoecology: Possibly lowland forest or marsh (Smith, 2020).

Genus *Kuylisporites* Potonié, 1956

Kuylisporites hamulatis Krutzsch, 1965

Plate 1, figure 20

Discussion: *Kuylisporites hamulatis* is similar to *Kuylisporites waterbolkii*, the type species of the genus, differing primarily by having rugulate (i.e., hamulate) sculpture.

Botanical affinity: Cyatheaceae, possibly *Cnemidaria* (Mohr and Lazarus, 1994; Smith, 2020).

Paleoecology: Probably moist temperate to tropical montane forest (Mohr and Lazarus, 1994; Smith, 2020).

Stratigraphic comments: The only occurrences of *K. hamulatis* previously documented by Palynodata Inc. and White (2008) are from the type locality in the Upper Cretaceous of Germany. Their observation here appears to be the first published occurrence in the Paleocene of the United States. Possibly in situ specimens of *K. hamulatis* have also been observed rarely in Lower Miocene deepwater Gulf of America strata (personal observation). *Cnemidaria* currently has a relict distribution in South and Central America (Mohr and Lazarus, 1994).

Kuylisporites waterbolkii Potonié, 1956

Plate 1, figure 21

Discussion: See discussion in Smith (2020) for *K. waterbolkii*.

Botanical affinity: Cyatheaceae, possibly *Cnemidaria* (Mohr and Lazarus, 1994; Smith, 2020).

Paleoecology: Probably moist temperate to tropical montane forest (Mohr and Lazarus, 1994; Smith, 2020).

Stratigraphic comments: Possibly in situ specimens of *K. waterbolkii* have been rarely observed in Lower Miocene deepwater Gulf of America sediments (personal observation). This spore type may have gone extinct sometime in the Miocene along the northern Gulf of America coastal plain.

Genus *Microreticulatisporites* Knox, 1950

Discussion: *Microreticulatisporites* is distinguished from other reticulate, trilete spore genera by having lumina less than 6 µm in diameter, and by having an irregular reticulum with branching, verrucate, or baculate muri (Jansonius and Hills, 1976; Jardine, 2011). Elsik (1968a) noted the presence of intermediate forms between *Micro-*

reticulatisporites and *Cicatricosisporites*. Elsik (1968a) and Jardine (2011) did not identify *Microreticulatisporites* to the species level.

Microreticulatisporites spp.

Plate 3, figure 4

Discussion: Ravn (1986) discussed the ambiguity regarding the morphology of *Microreticlatisporites lacunosus* and concluded that the sculpture in *M. lacunosus* is actually microfoveolate, in conflict with the generic description using the terminology of Punt and others (2007). Palynodata Inc. and White (2008) list 151 species in *Microreticulatisporites*. This study will follow Elsik (1968a) and Jardine (2011) and not speciate *Microreticulatisporites* spores. *Microreticulatisporites* spp. can be distinguished from other reticulate, trilete taxa in the Wilcox Group by having an "imperfect" reticulum, where the muri do not completely connect with one another, sometimes branching out towards but not reaching neighboring muri.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Genus *Nodosisporites* Deák, 1964

Nodosisporites crenimurus
(Srivastava, 1972) Davies, 1985

Plate 3, figure 5

Discussion: *Nodosisporites crenimurus* is a distinctive large, trilete spore type with appendices at the angles of the triangular amb and muri with baculate to verrucate projections. *Appendicisporites dentimarginatus* is a similar type distinguished on the basis of size; *N. crenimurus* is 37–60 µm in diameter and *A. dentimarginatus* is 22–34 µm in diameter (Srivastava, 1972a).

Botanical affinity: *Anemia* (Dettman and Clifford, 1992).

Paleoecology: Probably freshwater swamp, based on the paleoecological affinity given for *Cicatricosisporites dorogensis* by Akkiraz and others (2008).

Genus *Polypodiaceoisporites* Potonié, 1956

Polypodiaceoisporites gracillimus granoverrucatus
Krutzsch and others, 1967

Plate 2, figure 5

Discussion: This distinctive trilete spore type was described and imaged by Frederiksen and others (1983). In some of the specimens found in this study the distal verrucae or ridges fuse and form a reticulate pattern, which may be poorly- or well-developed. Korasidis and others (2023, Plate 1, figs. 1–8) have excellent images of this subspecies.

Botanical affinity: This spore type has a similar morphology to the modern species *Cerosera chrysosora* (Gymnogrammaceae) (Frederiksen and others, 1983).

Genus *Punctatriletes* Pierce, 1961

Punctatriletes sp. B

Plate 2, figure 14

Discussion: The single observed specimen of this type has a mainly punctate ornamentation, although some of the lumina are slightly larger than 1 µm in diameter and are foveolate. The laesurae are marginate and extend circa 2/3 the distance to the equator. The equatorial diameter is 36 µm and the amb is rounded subtriangular. This type is similar to *Punctatriletes* sp. A described in Smith (2020), but the laesurae margines in *Punctatriletes* sp. B are more prominent. *Punctatriletes parvimundus* has laesurae which extend to the equator (Pierce, 1961).

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Genus *Retitriletes* Pierce, 1961

Retitriletes globosus Pierce, 1961 sensu lato

Plate 2, figure 15

Discussion: The specimens observed in this study closely match *R. globosus*, the type species of the genus, in their small size, coarsely reticulate ornamentation, and approximately spherical shape. Pierce (1961) gave a maximum diameter for *R. globosus* of approximately 39 µm. *Retitriletes austroclavatidites* is similar but mainly includes larger (37–48 µm) forms. Although the size of the lumina in the reticulum of *R. globosus* was not stated (beyond describing the spores as coarsely reticulate), *R. austroclavatidites* appears more coarsely reticulate than *R. globosus*, with lumina circa 8–11 µm in diameter (Cookson, 1953; Pierce, 1961). Palynodata Inc. and White (2008) list 171 species and informally named types of *Retitriletes*; a full analysis of the potential synonymies is outside the scope of this paper.

Botanical affinity: Lycopodiaceae (Pierce, 1961).

Retitriletes? sp. C

Plate 3, figure 1

Discussion: The single observed specimen of this type is fairly large (ca. 66 µm in diameter), rounded subtriangular in shape, and possesses a coarse, polygonal reticulum with relatively thin muri. The trilete mark is not clearly visible, but based on the overall morphology of the palynomorph, the specimen is presumed to be a trilete spore. The central body of *Balmeisporites glenelgensis* has a somewhat similar reticulum, but *B. glenelgenis* is significantly larger than *Retitriletes*? sp. C (107–135 µm in diameter) and possesses an outer layer which forms a tripartite acrolamella proximally (Cookson and Dettmann, 1958b; Dettmann, 1995). We consider it possible that this specimen may be a spore similar to *B. glenelgensis* but smaller, where only the central body has been preserved. Hu (2006, Plate 24, figs. 2–3) photographed a specimen of *B. glenelgensis* which appears to have partially lost its outer layer. This type has been provisionally identified as *Retitriletes*? sp. C; *Retitriletes* sp. A and *Retitriletes* sp. B in Smith (2020) are much smaller and otherwise morphologically different from *Retitriletes*? sp. C.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Stratigraphic comments: The similarity to *B. glenelgensis* as discussed above and the dark color of the spore suggest the specimen may be reworked from the Upper Cretaceous, but due to the uncertainty in the taxonomic assignment, we are not confident that it is reworked.

Genus *Selaginella* Beauvois, 1804

Selaginella perinata (Krutzsch and others, 1963) Frederiksen, 1980

Plate 1, figures 15, 16

Discussion: Although originally placed in the form genus *Lusatisporis*, Martin and Rouse (1966) noted the strong similarity of *S. perinata* with extant species of *Selaginella*, in particular *Selaginella wallacei* and *Selaginella oregona*, which are indistinguishable using light microscopy. They erected a new species, *Selaginella sinuites*, which appears morphologically indistinguishable from similar Mesozoic spores identified as *Lusatisporis perinatus*. For this reason, Frederiksen (1980b) transferred *L. perinatus* to the genus *Selaginella* and considered *S. sinuites* a junior synonym of *S. perinata*. *Lusatisporis dettmannae* is a similar species which is distinguished from *S. perinata* in possessing a wider flange and a granulate exoexine (Srivastava, 1972b). *Selaginella fusca*, originally described from the nation of Georgia, is morphologically similar to *S. perinata* (e.g., Shatilova and others, 2016, Plate 4, figs. 6–7) and may also be synonymous with *S. perinata*.

Botanical affinity: *Selaginella*.

Stratigraphic comments: *Selaginella perinata* and similar forms range from the Holocene (represented by modern spores of *Selaginella*) to the Mesozoic.

Genus *Stereisporites*
Pflug in Thomson and Pflug, 1953

Discussion: *Stereisporites* is a form genus generally used for small, trilete spores with affinity to the Sphagnaceae. Jardine (2011) stated that *Stereisporites* is distinguished from *Cingulatisporites* by lacking a well-developed cingulum, but this is not entirely clear from the original description for *Stereisporites*, which describes the spore wall simply as two-layered. Also, Jansonius and Hills (1976, card 3511) describe *Stereisporites* as cingulate, i.e., possessing a cingulum. Elsik (1968a, p. 298) stated that "…the equatorial zona or cingulum or flange of various authors is a variable feature. Specimens with especially wide zona have been placed in other form genera than *Sphagnumsporites* or *Stereisporites*. There is no doubt of their affinity to *Sphagnum*, however." The emendation of *Stereisporites* by de Jersey (1964) limited the genus to spores <50 µm in diameter, with straight, relatively simple laesurae, and a smooth to scabrate exine. The presence of a cingulum is not mentioned but the exine is described as thick (≥1.5 µm). *Cingulatisporites* is here distinguished from *Stereisporites* somewhat arbitrarily by having a more prominent, thickened cingulum.

Stereisporites spp.

Plate 1, figures 8, 9

Discussion: There appears to be a morphological continuum for the *Stereisporites* specimens observed in this study. Most specimens could be placed in a broad definition of the type species *Stereisporites stereoides*. In some specimens a distal thickening is present; these could be placed in *Stereisporites antiquasporites* using the species concept of Dettmann (1963), although this characteristic was not made clear in the original description. Without formal emendation, *S. antiquasporites* is arguably a junior synonym of *S. stereoides*. Some specimens have variably developed faint verrucae on the distal surface; these could be separated as *Stereisporites granistereoides* or *Stereisporites regium*. Only *Stereisporites* spp., with forms that depart markedly from the typical morphology have been identified separately.

Botanical affinity: *Sphagnum* (Sphagnaceae) (Jardine, 2011).

Paleoecology: Swamps and bogs (Frederiksen, 1985).

Stereisporites buchenauensis
(Krutzsch, 1963) Elsik, 1968

Plate 1, figures 13, 14

Discussion: This species of *Stereisporites* is easily distinguished by the serrated margin of the cingulum.

Botanical affinity: *Sphagnum*.

Paleoecology: Probably swamps and bogs, based on the interpreted paleoecology for other *Stereisporites* species with affinity to *Sphagnum* (Frederiksen, 1985).

Stereisporites sp. A

Plate 1, figures 10, 11

Discussion: This very rarely observed type of *Stereisporites* has a triradiate thickening and holes on the distal face of the spore which sometimes obscure the laesurae on the proximal face.

Botanical affinity: *Sphagnum*.

Paleoecology: Probably swamps and bogs, based on the interpreted paleoecology for other *Stereisporites* species with affinity to *Sphagnum* (Frederiksen, 1985).

Genus *Tripartites* Schemel, 1950

Tripartites incisotrilobus (Naumova, 1938) Potonié and Kremp, 1956 emend. Karczewska and Turnau, 1974

Plate 2, figure 3

Discussion: The single specimen of *T. incisotrilobus* observed here corresponds well with the emended description given by Karczewska and Turnau (1974), a specimen of *T. incisotrilobus* imaged by Lopes and others (2019, Plate 1, fig. 20) as well as a reworked *T. incisotrilobus* specimen from the Paleocene Naheola Formation of Alabama (McLean, 1968, Plate 187, fig. 6). The taxonomy is complicated; Jansonius and Hills (1976, cards 3041, 4560) considered *Tripartites* a junior synonym of *Platyptera*.

Botanical affinity: Bryophyta or Pteridophyta, possibly Filicineae (Schemel, 1950).

Paleoecology: Reworked from the Lower Carboniferous (Tournaisian-Visean) (Owens and others, 1978; Stempień and Turnau, 1988; Lopes and others, 2019).

Genus *Triplanosporites* Pflug in Thomson and Pflug, 1952 from Thomson and Pflug, 1953

Triplanosporites spp.

Plate 1, figure 17

Discussion: In many specimens the trilete mark is not clearly distinguishable, being mainly indicated by folding. An indistinct trilete mark appears to be somewhat characteristic of the genus (Jansonius and Hills, 1976). The type species *Triplanosporites sinuosus* was described as 35–120 µm in size (Thomson and Pflug, 1953); the smallest specimen observed in this study is circa 25 µm by 23 µm in size. Gregory and Hart (1995a, Plate 4, figs. 8, 12) imaged specimens identified as "*Triplanosporites* sp. 8" which appear similar to the specimens in our study.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Genus *Undulatisporites* Pflug in Thomson and Pflug, 1953 emend. Smith, 2020

Undulatisporites elsikii Frederiksen, 1973 sensu lato

Plate 1, figure 12

Discussion: See Smith (2020) for a detailed discussion of this species. Only a single specimen has been observed in these samples.

Botanical affinity: Probably Polypodiaceae or Ophioglossaceae (Smith, 2020).

Genus *Verrucingulatisporites* Kedves, 1961 sensu lato

Discussion: A broad genus concept is used here to include trilete spores with reduced verrucae on the proximal face.

Verrucingulatisporites sp. A

Plate 2, figure 1

Discussion: The single observed specimen of this type has a very prominent verrucate cingulum. The distal face is coarsely and completely verrucate, but the verrucae are less developed on the proximal face. The type species *Verrucingulatisporites verrucatus* is significantly larger (50–60 µm) (Jansonius and Hills, 1976, card 3178).

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Genus *Verrucosisporites*
Ibrahim, 1933

Verrucosisporites spp.

Plate 2, figures 2, 4

Discussion: A variety of verrucate, trilete spores are included in this type. Several distinct morphotypes appear to be present, but due to the rarity of this type in these samples, it is unclear whether these morphotypes represent a morphological continuum or could be coherently subdivided.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Genus *Zlivisporis* Pacltová, 1961

Zlivisporis spp.

Plate 3, figures 2, 3

Discussion: Specimens referable to both *Zlivisporis blanensis* and *Zlivisporis novamexicanum* have been observed in this study. The two species are differentiated by the size of the lumina and muri (Jardine, 2011), but these characteristics appear to be continuously variable and splitting the type into two species based on the coarseness of the reticulum was considered overly arbitrary. *Zlivisporis reticulatus* is a similar species.

Botanical affinity: Marchantiales, possibly *Riccia* L., based on the botanical affinities suggested for *Z. reticulatus* (Vallati and others, 2020).

Stratigraphic comments: *Zlivisporis novamexicanum* and related species have been identified from Cretaceous and Paleogene strata in North America (Palynodata Inc. and White, 2008).

5.3. Monolete spores

Genus *Laevigatosporites* Ibrahim,
1933 emend. Schopf and others, 1944

Laevigatosporites haardtii (Potonié and
Venitz, 1934) Thomson and Pflug, 1953

Plate 4, figure 4

Discussion: Taxonomic discussion for this species is given in Smith (2020).

Botanical affinity: Probably Polypodiales or Iosetaceae (Smith, 2020).

Paleoecology: Probably marsh or swamp (Smith, 2020).

Laevigatosporites major Cookson, 1947

Plate 4, figure 6

Discussion: *Laevigatosporites major* is distinguished from *L. haardtii* by being >50 µm long (Nichols, 1970).

Botanical affinity: Probably Polypodiales or Iosetaceae (Knox, 1950; Jardine, 2011).

Paleoecology: Probably marsh or swamp.

Genus *Microfoveolatosporis* Krutzsch, 1959
emend. Potonié, 1966

Microfoveolatosporis pseudodentatus
Krutzsch, 1959

Plate 4, figure 7

Discussion: *Reticuloidosporites pseudomurii* is irregularly and faintly reticulate rather than densely punctate as in *M. pseudodentatus*. There appears to be a wide variability in the size range of *M. pseudodentatus* (Jardine, 2011).

Botanical affinity: Bryophyta or Pteridophyta sensu lato, possibly Psilotaceae or Schizaeaceae (Frederiksen, 1980b).

Genus *Polypodiisporonites* Potonié, 1931

Polypodiisporonites alienus (Potonié, 1931)
Frederiksen, 1980

Plate 4, figure 11

Discussion: *Polypodiisporonites alienus* is distinguished by having coarse verrucae, some of which are high and somewhat pointed, with no negative reticulum developed (Frederiksen, 1980b).

Botanical affinity: Bryophyta or Pteridophyta sensu lato, possibly Oleandraceae, Polypodiaceae, or Pteridaceae (Frederiksen, 1980b).

Polypodiisporonites favus Potonié, 1931

Plate 4, figure 10

Discussion: *Polypodiisporonites favus* is distinguished by having low, rounded, moderately large verrucae which are so closely spaced that a negative reticulum is formed around them. *Polypodiisporonites afavus* has smaller verrucae than *P. favus*, *P. alienus* has high and pointed verrucae with little to no development of a negative reticulum, and *Verrucatosporites prosecundus* has verrucae or botryoidal ornamentation arranged in broad irregular rows perpendicular to the monolete mark (Elsik, 1968b; Frederiksen, 1980b).

Botanical affinity: Probably Polypodiaceae sensu lato (Frederiksen, 1980b).

Genus *Reticuloidosporites*
Pflug in Thomson and Pflug, 1953

Reticuloidosporites pseudomurii
Elsik, 1968 sensu lato

Plate 4, figure 5

Discussion: Jardine (2011) did not subdivide monolete reticulate spores, assigning them all to *Reticuloidosporites* spp. A broad species concept for *R. pseudomurii* is used here which includes monolete spores with a faint, irregular reticulum, allowing for a range of variation in the size of the lumina.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

Reticuloidosporites sp. A

Plate 4, figures 8, 9

Discussion: This type of monolete spore is reniform and reticulate, with lumina circa 1–2 µm in diameter separated by thin muri. Only two specimens have been observed. The size range of the observed specimens is circa 51–67 µm. The monolete mark is only slightly marginate. *Reticuloidosporites pseudomurii* is more faintly and irregularly reticulate than *Reticuloidosporites* sp. A. *Microfoveolatosporis pseudodentatus* is punctate rather than reticulate.

Botanical affinity: Bryophyta or Pteridophyta sensu lato.

5.4. Gymnosperm pollen

Class Pinopsida

Plate 5, figure 4

Discussion: This study will follow Pocknall and Nichols (1996), Nichols (2002), Jardine (2011), and Smith (2020) in not speciating bisaccate pollen grains in the Paleogene of North America. If assigned to fossil form genera, the majority of well-oriented specimens would be best placed in *Pinuspollenites* (Raatz, 1938). Morphological criteria used to differentiate between some modern genera in Class Pinopsida like *Abies*, *Picea*, and *Pinus* (e.g., Kapp and others, 2000) appear to break down in these Paleocene samples, with morphological intermediates somewhat common. Further discussion of this pollen type is given in Smith (2020). There appears to be little biostratigraphic or paleoecological value in splitting most bisaccate pollen in the Wilcox Group, with the exception of rare specimens which can be more confidently assigned to a modern genus.

Botanical affinity: Class Pinopsida (Smith, 2020).

Paleoecology: Probably temperate upland forest, although modern pine trees do occur in lowland warm temperate swamps in the southeastern United States (Frederiksen, 1985).

Genus *Classopollis* Pflug, 1953 emend. Pocock and Jansonius, 1961

Classopollis classoides Pflug, 1953 emend. Pocock and Jansonius, 1961

Plate 5, figures 9, 10

Discussion: Pocknall and Nichols (1996) identified similar pollen types from the upper Paleocene of the Powder River Basin as "*Corollina* sp." Since that publication, Traverse (2004) published a formal proposal to conserve *Classopollis* against what would otherwise be its senior synonym, *Corollina*. The taxonomic history of *Classopollis* and other similar or synonymous form genera is complex (e.g., Pocock and Jansonius, 1961). *Classopollis torosus* is similar to *C. classoides* and may be conspecific (Couper, 1958; Chaloner, 1962); we agree with Srivastava (1976) that the disappearance of the holotype of *C. torosus* does not permit a confident determination of the potential synonymy of the two species.

Botanical affinity: Family Cheirolepidiaceae, division Pinophyta (Srivastava, 1976; Traverse, 2004).

Paleoecology: Probably salt marsh, xeric coastal, based on previously published interpretations (e.g., Hughes and Moody-Stuart, 1967; Upchurch and Doyle, 1981; Escapa and Leslie, 2017; Berry, 2022) and high relative abundances in these samples. Smith and others (2024) provide more extensive discussion of the paleoecology.

Stratigraphic comments: Although mainly a Mesozoic group, Pocknall and Nichols (1996) considered that their upper Paleocene specimens were in situ. Following arguments made in more detail in Smith and others (2024), we also consider the Paleocene occurrences of *C. classoides* in these samples as in situ, with the final extinction of the genus occurring possibly in the Ypresian in the northern Gulf of America coastal plain (Fairchild and Elsik, 1969).

Genus *Cycadopites* Wodehouse, 1933

Discussion: *Cycadopites* is distinguished from other monocolpate pollen genera like *Arecipites*, *Liliacidites*, and *Monocolpopollenites* by having a colpus which extends the full length of the grain and is open at the ends (Nichols and others, 1973).

Cycadopites follicularis Wilson and Webster, 1946 sensu lato

Plate 5, figure 3

Discussion: *Cycadopites follicularis* has a psilate to faintly scabrate sculpture. A broad species concept is used here to include specimens outside the quite narrow size range given in the original description (39–42 µm long). Psilate to faintly scabrate grains of *Cycadopites* <50 µm in length have been assigned to *C. follicularis*; psilate to faintly scabrate grains of *Cycadopites* >50 µm in length have been assigned to *Cycadopites giganteus*. Some of the smaller, faintly scabrate specimens assigned to *C. follicularis* here could arguably be separated as *Cycadopites scabratus* (Stanley, 1965); we did not find separating these types useful and they have been included in *C. follicularis* sensu lato.

Botanical affinity: Cycadaceae (Wodehouse, 1933).

Paleoecology: Probably lowland forest or marsh (Wakefield and Monteil, 2002; Akkiraz and others, 2008; Smith, 2020).

Cycadopites giganteus Stanley, 1965

Plate 5, figure 2

Discussion: *Cycadopites giganteus* was originally described by Stanley (1965) as being 50–72 µm long; the similar species *Cycadopites follicularis* is smaller.

Botanical affinity: Cycadaceae (Wodehouse, 1933).

Paleoecology: Probably lowland forest or marsh (Smith, 2020).

Genus *Ephedripites* Bolkovitina, 1953 from Potonié, 1958

Ephedripites (*Distachyapites*) *eocenipites* (Wodehouse, 1933) Krutzsch, 1961 sensu lato

Plate 5, figures 11, 12

Discussion: See Smith (2020) for detailed information on the taxonomy of this species.

Botanical affinity: Ephedraceae, probably *Ephedra* (Smith, 2020).

Paleoecology: Arid scrub (Smith, 2020).

Genus *Gnetaceaepollenites* Thiergart, 1938

Gnetaceaepollenites jansonii (Pocock, 1964) de Lima, 1980 sensu lato

Plate 5, figure 13; Plate 6, figure 1

Selected synonymy:

Equisetosporites jansonii
(Pocock, 1964, Plate 1, figs. 26, 27)

Equisetosporites barghoornii
(Pocock, 1964, Plate 1, fig. 21)

Ephedra voluta
(Stanley, 1965, Plate 40, figs. 10, 11)

Ephedripites jansonii
(Muller, 1968, Plate 2, fig. 9)

Gnetaceaepollenites jansonii
(de Lima, 1980, Plate 3, fig. 11)

Ephedripites jansonii
(Nichols, 2002, not illustrated)

Ephedripites subgenus *Spiralipites* spp.
(Jardine, 2011, Plate 3, fig. 6)

Gnetaceaepollenites sp. A
(Smith, 2020, Plate 2.4, figs. 5–8)

Discussion: This pollen type includes ephedroid pollen grains with plicae that do not merge at the polar extremities as with modern *Ephedra*, but loop around the ends of the grain. There is substantial variability in the total size of these grains, the number and arrangement of plicae, and the orientation of the plicae relative to the long axis. It should be noted that because these grains are considered to have an affinity with the Ephedraceae, the equatorial axis is considered the long axis parallel to the plicae. Nichols (2002) synonymized *Equisetosporites jansonii* with *Ephedra voluta*, giving the species a broad circumscription. *Equisetosporites jansonii* was originally described as being circa 82–90 µm long with 14 to 15 parallel ribs and *E. voluta* was originally described as being circa 48 µm long with three ridges (i.e., ribs). Pocock (1964) described a species of ephedroid pollen, *Equisetosporites barghoornii*, which is similar to *G. jansonii* in all respects except its smaller size (longitudinal axis ca. 43 µm long in the holotype specimen). *Equisetosporites barghoornii* is also considered synonymous with *G. jansonii* sensu lato. Smith (2020) described smaller (16–24 µm long) but otherwise similar ephedroid pollen from the Eocene southern Gulf of America and identified them informally as "*Gnetaceaepollenites* sp. A." This study will follow Han and others (2016) and assign ephedroid pollen with unfused plicae to *Gnetaceaepollenites*. This pollen type appears to exhibit a continuous range of variation with respect to size and plicae number, so Nichol's (2002) broad definition of *G. jansonii* will be followed here. If considered useful in other sections, *G. jansonii* could be split into subspecies based on size or plicae number. *Gnetaceaepollenites* sp. B in Smith (2020) differs significantly from *G. jansonii* sensu lato in having plicae which undulate in a sinusoidal pattern.

Botanical affinity: Ephedraceae.

Paleoecology: Probably arid tropical to subtropical scrub (Smith, 2020).

Stratigraphic comments: Frederiksen (1988) placed the top of *G. jansonii* sensu lato (as *Ephedripites* subgenus *Spiralipites* spp.) somewhat questionably in the Eocene or Oligocene.

Gnetaceaepollenites sp. B

Plate 6, figure 2

Discussion: The single specimen of this type observed in this study is slightly larger than the specimen identified as *Gnetaceaepollenites* sp. B by Smith (2020); the specimen in this study has an equatorial length (i.e., long axis) of circa 45 µm and the specimen of *Gnetaceaepollenites* sp. B in Smith (2020) has an equatorial length of 34 µm. Both specimens are considered conspecific as they are otherwise similar, with plicae which are unfused at the ends of the grain and undulate in a sinusoidal pattern. *Gnetaceaepollenites undulatus* is a similar species described from the Upper Cretaceous of South America with undulating plicae; the holotype specimen in Regali and others (1974, Plate 12, fig. 6) is less elongate than the two observed specimens of *Gnetaceaepollenites* sp. B. The observation of more specimens would help to clarify whether *Gnetaceaepollenites* sp. B should be synonymized with *G. undulatus*.

Botanical affinity: Ephedraceae.

Paleoecology: Probably arid tropical to subtropical scrub (Smith, 2020).

Genus *Inaperturopollenites* Pflug and Thomson in Thomson and Pflug, 1953

Inaperturopollenites hiatipites (Wodehouse, 1933) Nichols, 2010

Plate 5, figure 7

Discussion: We will follow Nichols (2010) and consider that North American pollen similar to that produced by modern *Taxodium* is best identified as *Inaperturopollenites hiatipites*; other authors (e.g., Jardine, 2011) instead identify this species as *Cupressacites hiatipites*. *Inaperturopollenites hiatus* is a similar species mainly identified in European strata and is arguably conspecific with *I. hiatipites*. Nichols (2010) stated that *I. hiatus* is distinguished by having a thicker and smoother exine than *I. hiatipites*, but expressed some uncertainty about the potential synonymy of the two species pending a redescription of *I. hiatus* from the type material.

Botanical affinity: Cupressaceae–Taxaceae–Taxodiaceae, possibly *Taxodium* or *Glyptostrobus* (Jardine 2011).

Paleoecology: The common presence of *Taxodium* (bald cypress) trees in modern swamps along the northern Gulf of America coastal plain makes it tempting to interpret *I. hiatipites* pollen as derived from similar paleoenvironments. However, Cupressaceae–Taxaceae–Taxodiaceae pollen is nondescript and modern pollen is generally not identifiable at the species level. Harrington (2008) observed that *I. hiatipites* (identified as *Cupressacites hiatipites*) was much more common in marginal marine samples with a large pollen source area than lignite samples with more local swamp palynofloras in the Paleocene and Eocene of the northern Gulf of America coastal plain, suggesting that *I. hiatipites* was a common constituent of regional lowland forest vegetation but not as common in swamp paleoenvironments.

Genus *Picea* Dietrich, 1824

Picea sp.

Plate 5, figure 1

Discussion: The single observed specimen of this type is quite similar to pollen from extant *Picea*. Characteristics which help to distinguish this specimen of *Picea* pollen from other bisaccate pollen types include the large size of the pollen grain (ca. 126 µm in length measured from the end of one saccus to the other in lateral equatorial view in this specimen), the fine reticulum on the sacci, sacci which are borne low with respect to the corpus equator, and a very obtuse angle where the sacci meet the corpus on the distal side where the germinal area is located (Traverse, 2007; Klymiuk and Stockey, 2012; Leopold and Zaborac-Reed, 2014). When the angle of the distal sacci-corpus attachment approaches 180°, as in this pollen grain, the outline of the grain is an uninterrupted oval in both polar and equatorial view, as Elsik (1969) noted. *Piceaepollenites* and *Piceapollis* are both pollen form genera which have been used to accommodate fossil pollen referable to *Picea*; the highly obtuse angle of attachment is given as a primary criterion for distinguishing *Piceapollis* from other bisaccate genera (Jansonius and Hills, 1976, cards 1993, 1996). This study will use the modern genus, as in situ *Picea* pollen has been found in seed cones dating to the Lower Cretaceous on Vancouver Island (Klymiuk and Stockey, 2012).

Botanical affinity: *Picea*.

Paleoecology: Modern *Picea* has a cool temperate to boreal distribution. Elsik (1969) interpreted the presence of *Picea* pollen as indicative of cool temperate conditions. The single specimen observed here was likely transported from a more temperate paleoenvironment in the continental interior.

Genus *Podocarpus* Persoon, 1807

Podocarpus? spp.

Plate 5, figure 5

Discussion: Two specimens of this bisaccate pollen type has been observed, both in polar view. Stanley (1965, p. 280) provided discussion on the criteria used to differentiate *Podocarpus* pollen from other similar bisaccate pollen in the Paleocene of North Dakota. These include thin, usually wrinkled bladders, a coarsely ornamented cap, and a furrow that is sharply separated from the bladders. Although many species of *Podocarpus* produce pollen with relatively large bladders like the two specimens observed in our samples (e.g., Kapp and others, 2000, p. 27), not all extant species have bladders proportionally larger than those in *Pinus*. Boulter and Chaloner (1970) expressed some reservations about the identification of fossil *Podocarpus* pollen in the Neogene of Europe related to the similarity of fossil *Pinus* and *Podocarpus* pollen. Frederiksen (1980b) identified somewhat similar pollen from the Eocene to Oligocene of Mississippi and Alabama as *Podocarpus*. *Podocarpidites* is a form genus for pollen similar to modern *Podocarpus* but also possibly derived from other genera in the Podocarpaceae (Jansonius and Hills, 1976, card 2055).

Botanical affinity: Possibly *Podocarpus*, possibly also another genus in the Podocarpaceae or Pinaceae.

Genus *Sequoiapollenites*
Potonié, 1958

Sequoiapollenites sp.

Plate 5, figure 8

Discussion: This study will follow Jardine (2011) and not speciate *Sequoiapollenites* pollen, which is distinguished by being inaperturate and possessing a prominent ligula or papilla. Nichols (2010), in redescribing *I. hiatipites*, noted that a small or obscure papilla may be present in *I. hiatipites* and modern *Taxodium*, but that there is taxonomic value in distinguishing pollen with a prominent papilla.

Botanical affinity: Cupressaceae–Taxaceae–Taxodiaceae, possibly *Sequoia* (Pocknall and Nichols, 1996; Jardine, 2011).

Genus *Tsuga* (Endlicher, 1847) Carrière, 1855

Tsuga sp.

Plate 5, figure 6

Discussion: This study will follow Frederiksen and others (1983) and assign Paleogene pollen of this type to the modern genus *Tsuga* rather than a form genus. Palynodata Inc. and White (2008) list 107 fossil and modern species of *Tsuga*. Only a single specimen has been observed.

Botanical affinity: Modern *Tsuga* has a cool temperate distribution; its presence in the Wilcox Group may be a result of long-distance transport from higher latitudes.

Paleoecology: Probably temperate uplands.

5.5. Monocolpate angiosperm pollen

Genus *Arecipites* Wodehouse, 1933 emend.
Anderson, 1960 sensu lato

Discussion: *Arecipites* was somewhat vaguely defined by Wodehouse (1933); Anderson (1960) emended *Arecipites* to include punctate or finely reticulate monocolpate pollen with a tapering colpus. The emendation of *Arecipites* by Nichols and others (1973) includes psilate and punctate pollen with a tectate exine and excludes reticulate pollen. We will not use the emendation of *Arecipites* by Nichols and others (1973) as it would exclude species like *Arecipites tenuiexinous* which are finely reticulate (e.g., Korasidis and others, 2023, Plate 1, figs. 9–14). A broad definition of *Arecipites* is used here which includes scabrate as well as punctate and finely reticulate forms. In practice the distinction between scabrate, punctate, and finely reticulate sculpture is often ambiguous in light microscopy; therefore, we consider that excluding finely reticulate forms from *Arecipites* is overly arbitrary.

Arecipites pertusus (Elsik in Stover and others, 1966) Nichols and others, 1973

Plate 6, figure 13

Discussion: This species has ornamentation in the form of punctae tending to be linearly aligned and fine rugulae; the original description by Stover and others (1966) described these rugulae as pseudovermiculate.

Botanical affinity: Possibly Arecaceae–Magnoliaceae (Stover and others, 1966).

Stratigraphic comments: Tschudy (1973b) gave the range of *A. pertusus* (as *Calamuspollenites pertusus*) in the Mississippi Embayment from slightly above the top of the Nanafalia Formation (Thanetian) to the lowermost Claibornian (Ypresian) (Dockery, 1996). *Calamuspollenites pertusus* was rarely observed well below the Selandian-Thanetian boundary in both the Jerome Olinick No. 16 and Moczygemba VT No. 11 wells, indicating a significant downward range extension for *A. pertusus* in the onshore Wilcox Group of Texas.

Arecipites spp. (punctate or scabrate)

Plate 6, figures 9, 10

Discussion: The type species of *Arecipites*, *Arecipites punctatus*, was described as having a smooth to minutely pitted (i.e., punctate) sculpture and ranging from 23–25 µm in length (Wodehouse, 1933). Nichols (2010) reexamined the holotype specimen and redescribed *A. punctatus*, restricting the species to scabrate and visibly columellate forms with a marginate colpus. The *Arecipites* spp. (punctate or scabrate) in this study have punctate to scabrate sculpture, are generally not visibly columellate, and do not generally have marginate colpi. Jardine (2011) did not identify *Arecipites* spp. below the genus level. *Arecipites tenuiexinous* is here distinguished from *Arecipites* spp. (punctate or scabrate) by being micro-reticulate.

Botanical affinity: Possibly Arecaceae, based on the botanical affinity given for morphologically similar *Arecipites* pollen in Nichols and Brown (1992).

Paleoecology: Possibly arid tropical scrub, based on the interpreted paleoecology for *Arecipites tenuiexinous* given in Smith (2020).

Arecipites tenuiexinous Leffingwell, 1970 sensu lato

Plate 6, figure 11

Discussion: *Arecipites tenuiexinous* was originally described by Leffingwell (1970) as micro-reticulate, with lumina circa 0.5 µm in diameter. Although Leffingwell (1970) distinguished *A. tenuiexinous* from *A. punctatus* based on the larger size of *A. tenuiexinous*, the range of size variation permissible for *A. punctatus* was not clearly defined in the original description by Wodehouse (1933). *Arecipites tenuiexinous* is here distinguished from *A. punctatus* by having clearly micro-reticulate sculpture. Anderson (1960) considered that some of the finely reticulate, monocolpate pollen in his samples were synonymous with *Monocolpites reticulatus* and transferred the species to *Arecipites* as *Arecipites reticulatus* (van der Hammen, 1954; Anderson, 1960). However, the holotype illustration of *M. reticulatus* (van der Hammen 1954, Plate 2) shows a pollen grain with a colpus that does not reach the ends of the grain and is expanded at the ends. Anderson (1960) described his specimens as having a colpus which extends to the ends of the grains and is never expanded at the ends. We therefore consider that Anderson's (1960) specimens are not conspecific with *M. reticulatus*. Leffingwell (1970) considered that Anderson's (1960) specimens identified as *A. reticulatus* are distinguished from *A. tenuiexinous* on the basis of the larger size of *A. tenuiexinous*. This is problematic even if Anderson's (1960) specimens are considered conspecific with *M. reticulatus*, as the holotype specimen of *M. reticulatus* was described as 33 µm in size (van der Hammen, 1954), and *A. tenuiexinous* was described as 25–30 µm by 18–23 µm (Anderson, 1960). We therefore use a broad definition of *A. tenuiexinous* which includes similar but smaller forms identified by Anderson (1960) as *A. reticulatus*. The circumscription of *A. tenuiexinous* given here is somewhat different from Smith (2020), as Smith (2020) included types with punctate sculpture in *A. tenuiexinous*. Admittedly this distinction is often ambiguous.

Botanical affinity: Arecaceae (Nichols and Brown, 1992).

Paleoecology: Possibly arid tropical scrub (Smith, 2020).

Genus *Liliacidites* Couper, 1953

Liliacidites spp.

Plate 6, figures 4, 12

Discussion: This study will follow Jardine (2011) and not speciate pollen in this genus. Palynodata Inc. and White (2008) list 155 species of *Liliacidites*.

Botanical affinity: Possibly Arecaceae (Jardine, 2011).

Genus *Longapertites*
van Hoeken-Klinkenburg, 1964

Longapertites aff. *vaneendenburgi*
Germeraad and others, 1968

Plate 6, figure 3

Discussion: This type of *Longapertites* has sculpture intermediate between the fine perforations in *L. vaneendenburgi* and the foveolate to reticulate sculpture in *Longapertites proxapertioides* (Germeraad and others, 1968; van der Hammen and Garcia de Mutis, 1966). The observed specimens are all larger than the maximum size range given in the original description for *L. proxapertioides* of 60 µm, and more consistent with the size range given for *L. vaneendenburgi* of 59–83 µm. Frederiksen (1988) and Jardine (2011) did not identify *Longapertites* below the genus level. Zetter and others (2001) noted that some specimens identified as *Longapertites* are actually folded halves of *Proxapertites* specimens. If that is the case, some or all of the specimens identified as *Longapertites* aff. *vaneendenburgi* here may be synonymous with *Proxapertites magnus*; their sculpture is essentially indistinguishable.

Botanical affinity: Possibly Arecaceae (Germeraad and others, 1968), although Jaramillo and others (2010) gave the affinity of various *Longapertites* and *Proxapertites* species as the Annonaceae.

Paleoecology: Possibly back-mangrove, based on the paleoecology indicated for *Proxapertites* spp. in Akkiraz and others (2008).

Nupharipollis Krutzsch, 1970

Discussion: *Nupharipollis* accommodates monocolpate, echinate pollen similar to that produced by modern *Nuphar*, with "…rather heavy spines" according to the generic description translated by Jansonius and Hills (1976, card 1785). *Nymphaeaepollenites* is a similar form genus, probably best distinguished by having a rounder shape and more delicate echinae. Jansonius and Hills (1976, card 1785) note that the two genera are also distinguished on the basis of size, but the size range permissible in *Nupharipollis* was not clearly described. *Monogemmites*, despite the genus name, also includes some monocolpate, echinate pollen, but the echinae are finer and shorter in *Monogemmites* than *Nupharipollis* (Jansonius and Hills, card 1693).

Nupharipollis sp.

Plate 6, figure 8

Discussion: The type species *Nupharipollis echinatus* is larger (ca. 56 µm long in the holotype specimen) than the single observed specimen of *Nupharipollis* in our samples (ca. 37 µm long) (Krutszch, 1970). *Nupharipollis echinatus* is also more thick-walled and coarsely echinate. *Nupharipollis mortonensis* is similar but the echinae or projections were described as more variable, sometimes including blunt-tipped echinae, papillae, and baculae (Pocknall and Mildenhall, 1984). We have left the specimen unspeciated because the range of variation of this type in the Wilcox Group is unknown.

Botanical affinity: Probably *Nuphar*.

Paleoecology: Probably freshwater aquatic based on the ecology of modern *Nuphar*.

Genus *Proxapertites*
van der Hammen, 1956

Proxapertites magnus
Muller and others 1987, sensu lato

Plate 6, figure 5

Discussion: Jaramillo and Dilcher (2001) provide helpful information for species level identification of some *Proxapertites* species. Muller and others (1987) originally described *P. magnus* as having perforate ornamentation with lumina <1 µm in diameter. A broad species concept is used here to include specimens which have some lumina >1 µm in diameter; the overall ornamentation can be described as punctate-foveolate. It was sometimes difficult to separate *P. magnus* and *Longapertites* aff. *vaneendenburgi* in these samples. Elsik (1968a, 1974) described two similar species, *Annona*? *paleocenica* and *Annona*? *foveoreticulata*. Frederiksen (1980) treated both of these species as synonymous with *Proxapertites* and did not speciate the genus. Although Elsik (1974) did not explicitly state the difference between these two species, the holotype specimen of *Annona*? *foveoreticulata* (Elsik, 1974, Plate 1, figs. 16–17) is clearly and coarsely reticulate while the holotype specimen of *Annona*? *paleocenica* (Elsik, 1968a, Plate 5, fig. 3) appears more ambiguously punctate-foveolate. Specimens identified as *P. magnus* here are probably more or less synonymous with *Annona*? *paleocenica*, but we hesitate to consider *P. magnus* a junior synonym as the pollen morphology is more clearly delineated in Muller and others (1987). Tschudy (1973b, Plate 3, figs. 1–4) identified some specimens of *Proxapertites* spp. which are substantially different from pollen identified as *P. magnus* here in being clearly and coarsely reticulate rather than punctate-foveolate.

Botanical affinity: Possibly Annonaceae or Arecaceae (Zetter and others, 2001; Jaramillo and others, 2010).

Paleoecology: Possibly back-mangrove, based on the paleoecology indicated for *Proxapertites* spp. in Akkiraz and others (2008).

Genus *Spinizonocolpites*

Spinizonocolpites aff. *baculatus*
Muller, 1968

Plate 6, figure 6

Discussion: The single observed specimen of this type is similar to *S. baculatus* sensu stricto, differing mainly in that the projections are mainly bifurcate at the tips rather than baculate.

Botanical affinity: Probably *Nypa*, based on the similarity to *S. baculatus* (Muller, 1968).

Paleoecology: Probably mangrove swamp, based on the modern ecology of *Nypa* (Gee, 2001).

Stratigraphic comments: Although Gee (2001) considered that *Spinizonocolpites* ranged from the early to late Eocene along the northern Gulf of America coastal plain, Jardine (2011) identified *Spinizonocolpites echinatus* from the Paleocene Calvert Bluff Formation in the Wilcox Group of Texas. Crabaugh and Elsik (2000) placed the base of the Calvert Bluff Formation slightly above the Selandian-Thanetian boundary in nannofossil zone NP6 of Martini (1971). The single observed specimen of *Spinizonocolpites* aff. *baculatus* was observed at 4964.67 ft (1513.23 m) in the Moczygemba VT No. 11 well, in lower zone NP6.

Spinizonocolpites breviechinatus
Jaramillo and Dilcher, 2001

Plate 6, figure 7

Discussion: The single observed specimen of this species is similar to *Spinizonocolpites echinatus*, differing mainly in having smaller and more relatively wide-based spines. The exine is finely punctate or micro-reticulate. This may be the first documented occurrence of this species outside of South America, with the caveat that other authors may have identified this type in North America as *S. echinatus*.

Botanical affinity: Probably *Nypa*.

Paleoecology: Probably mangrove swamp, based on the modern ecology of *Nypa* (Gee, 2001).

Stratigraphic comments: See comments for *Spinizonocolpites* aff. *baculatus*. The single observed specimen of *S. breviechinatus* at 4935.17 ft (1504.24 m) in Moczygemba VT No.11 is in lower NP6.

5.6. Tricolpate angiosperm pollen

Genus *Clavatricolpites* Pierce, 1961

Clavatricolpites sp. B

Plate 8, figures 13, 14

Discussion: This species is tricolpate or ambiguously tricolporoidate, prominently clavate, equatorial diameter circa 20 µm. Nexine circa 0.5–1.0 µm thick, sexine composed of free-standing clavae circa 2.5 µm long. Oblate, amb subcircular. Colpi deeply incised, widely gaping.

Discussion: *Clavatricolpites* sp. A and *Clavatricolpites* aff. *gracilis* as described in Smith (2020) are both larger and in other ways morphologically dissimilar to this pollen type. *Ilexpollenites* is a similar form genus but is restricted to tricolporate forms. If pores are present in *Clavatricolpites* sp. B, they are not clearly visible, and we hesitate to assume their presence.

Botanical affinity: Eudicots, possibly *Ilex* L. (Aquifoliaceae). The modern pollen of *Ilex*, although tricolporate, is morphologically similar, and the pores may be obscure (Kapp and others, 2000).

Genus *Cupuliferoidaepollenites*
Potonié and others, 1950 from Potonié, 1960

Cupuliferoidaepollenites spp.

Plate 7, figures 6, 7

Discussion: *Cupuliferoidaepollenites* encompasses tricolpate, psilate, prolate pollen with well-rounded poles. Although not specifically stated in the generic description, the genus is generally limited to small (<20 µm long polar axis) pollen types, similar in size to the type species *Cupuliferoidaepollenites liblarensis*. This study will follow Jardine (2011) and not speciate the genus. Pollen identified as *Psilatricolpites* spp. (prolate) are larger (>20 µm long polar axis) than *Cupuliferoidaepollenites* spp. and pollen identified as *Eucommia*? spp. are larger than *Cupuliferoidaepollenites* spp. and have apparently unequal colpi. Only two specimens of this type with a polar axis length of <20 µm have been observed in these Lower Wilcox samples; they are probably conspecific with *C. librarensis*, although the species was described as "highly refractive" in the original description translated by Jansonius and Hills (1976). It is unclear to us what this means other than that the exine is psilate. The refractive index of pollen is not determinable in routine light microscopy.

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Eucommia*? Oliver, 1890

Eucommia? spp.

Plate 7, figures 1–3

Discussion: This pollen type is synonymous with *Eucommia*? sp. A in Smith (2020) and *Eucommia* spp. in Jardine (2011). *Eucommia*? spp. have been grouped together with tricolpate pollen because generally the pollen grains appear tricolpate, but rarely pores are faintly visible (Jardine, 2011). Only pollen with visibly unequal colpi are included in this pollen type (Smith, 2020). The apparently unequal colpi are in reality of equal length but characteristically appear unequal as the result of compression; the exine is psilate to scabrate (Pocknall and Nichols, 1996). *Psilatricolpites* spp. (prolate) includes some similar pollen with colpi of equal length; it was considered preferable to separate specimens with apparently unequal colpi from those with apparently equal colpi. The morphology of the specimens found here is essentially the same as described for *Eucommia*? *leopoldae* (Frederiksen and others, 1983) by Pocknall and Nichols (1996), but this study will follow Jardine (2011) and not speciate the genus.

Botanical affinity: Possibly *Eucommia* (Eucommiaceae).

Paleoecology: Possibly in part moist temperate upland forest; Ramírez-Arriaga and others (2014) suggested a cloud forest paleoecology for unspeciated specimens of *Eucommia* from Eocene and Oligocene strata near Pueblo, Mexico. The wide paleogeographic distribution of Eucommiaceae plants in the Paleogene suggests a correspondingly broad set of paleoecological tolerances.

Genus *Fraxinoipollenites*
Potonié, 1951 from Potonié, 1960

Fraxinoipollenites spp. (micro-reticulate)

Plate 8, figures 1–4

Discussion: This pollen type includes prolate, tricolpate pollen with finely reticulate (lumina <1 µm in diameter) sculpture. *Tricolpites* is distinguished by being oblate to spheroidal. Further discussion of the taxonomic issues with previously described species of *Fraxinoipollenites* is provided in Smith (2020).

Botanical affinity: Eudicots, lower affinity uncertain (Smith, 2020).

Genus *Insulapollenites* Leffingwell, 1970

Insulapollenites rugulatus
Leffingwell, 1970

Plate 8, figures 10–12

Discussion: Pocknall and Nichols (1996) discuss this species in detail.

Botanical affinity: Angiospermae, possibly Sapindaceae or Myrtaceae (Pocknall and Nichols, 1996).

Stratigraphic comments: *Insulapollenites rugulatus* is well known as a biostratigraphically important Paleocene marker in the Western Interior of North America (e.g., Leffingwell, 1970; Pocknall, 1987; Pocknall and Nichols, 1996). In the Powder River Basin of Wyoming and Montana, *I. rugulatus* first appears near the base of the Paleocene *Pistillipollenites mcgregorii* subzone and has its last appearance just below the Paleocene–Eocene boundary (Pocknall, 1987). Harrington and others (2004) noted the presence of *I. rugulatus* in lowermost Eocene strata from the Red Hot Truck Stop locality in Meridian, Mississippi, but speculated the species may have been reworked from Paleocene sediments. Zarra and others (2019) place T *I. rugulatus* at circa 57.7 Ma near the top of the Lower Wilcox in nannofossil zone NP8. The base of *I. rugulatus* in the Lower Wilcox of Texas may be slightly above B *Pistillipollenites mcgregorii* in lower NP6 or upper NP5, although the rarity of the taxon reduces confidence in the timing of the event (see discussion in section 3.2).

Genus *Myocolpopollenites*
Elsik in Stover and others, 1966

Myocolpopollenites reticulatus
Elsik in Stover and others, 1966

Plate 8, figure 9

Discussion: This tricolpate pollen species is easily distinguished by its coarse reticulum and pseudosyncolpate triradiate crests.

Botanical affinity: Angiospermae, lower affinity uncertain (Stover and others, 1966).

Stratigraphic comments: Tschudy (1973b) interpreted the range of *M. reticulatus* in the Mississippi Embayment as restricted to the Wilcox Group, ranging from the Nanafalia Formation (Selandian-Thanetian) to the Pendleton Formation (age equivalent to the Thanetian Tuscahoma Formation) (Wasem and Wilbert, Jr., 1943; Dockery, 1996).

Genus *Psilatricolpites* Pierce, 1961

Psilatricolpites spp. (prolate)

Plate 7, figures 4, 5

Discussion: This pollen type includes psilate to faintly scabrate, prolate pollen of unknown lower botanical affinity. *Cupuliferoidaepollenites* is also a form genus for psilate, prolate, tricolpate pollen. Although not specifically mentioned in the original description, *Cupuliferoidaepollenites* is generally reserved for small (<20 µm polar axis length) pollen grains (e.g., Jardine, 2011), and all pollen identified as *Psilatricolpites* spp. (prolate) in this study are over 20 µm in length. Pollen identified as *Psilatricolpites* sp. A by Smith (2020) are distinguished by being oblate rather than prolate. This type is similar to pollen identified as *Eucommia*? spp. with obscure pores, differing in that the colpi in *Psilatricolpites* spp. (prolate) are apparently equal in length. We considered grouping this pollen type with *Eucommia*? spp. but decided to identify them separately because the colpi do not have the appearance of being unequal in length.

Botanical affinity: Angiospermae, lower affinity unknown, possibly *Eucommia*.

Genus *Retitrescolpites* Sah, 1967

Discussion: *Retitrescolpites* includes oblate to spheroidal, reticulate, tricolpate pollen. *Retitrescolpites* is more coarsely reticulate (>1 µm) than the similar genus *Tricolpites* but is otherwise similar.

Retitrescolpites anguloluminosus (Anderson, 1960) Frederiksen, 1979

Plate 7, figures 25–29

Discussion: More information regarding the taxonomy of this species is presented in Smith (2020).

Botanical affinity: Eudicots, lower affinity unknown, but possibly Hamamelidaceae or Oleaceae (Smith, 2020).

Retitrescolpites spp.

Plate 7, figures 20–24

Discussion: Coarsely reticulate (lumina >1 µm in diameter), oblate, tricolpate pollen not assignable to *Retitrescolpites anguloluminosus* has not been speciated. The morphologies are somewhat variable in the coarseness of the reticulum, the relative thickness of the muri, the shape of the lumina, and the total diameter of the grain, but these variations appear to be generally gradational. Many specimens are quite similar to *Tricolpites hians*, differing only in being more coarsely reticulate, while others approached the morphology of *R. anguloluminosus*. Specimens identified by Jardine and Harrington (2008, Plate 2, fig. 25, Plate 3, figs. 1, 30) as *Rousea* sp., Tricolpate sp. 1, and *Retitrescolpites* sp. 1 all fall under the circumscription of *Retitrescolpites* spp. as defined here. Jardine (2011, Plate 8, figs. 5–6) later considered that all three of these specimens should be assigned to *Tricolpopollenites geranioides*. However, in the original description for *T. geranioides* (as *Tricolpites geranioides*), the species was described as subprolate to prolate, with lumina 3–4 µm across, and with an equatorial diameter of 37–47 µm (Couper, 1960). Jardine's (2011) pollen type is spheroidal rather than subprolate, has lumina 1–3 µm wide, and has an equatorial diameter of 24–38 µm. A specimen identified here as *Retitrescolpites* sp. in Plate 7, figure 24 is substantially larger (ca. 37 µm diameter) than other specimens identified as *Retitrescolpites* spp. in this study; if additional specimens of this type are observed in other sections the type may be worth speciating separately. The lumina in this specimen tend to decrease in size near the colpi margines, but not prominently or consistently; an alternative generic identification for this specimen would be *Rousea*.

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Retitricolpites* van der Hammen, 1956 from van der Hammen and Wymstra, 1964

Discussion: Following reasoning given in Smith (2020), *Retitricolpites* is here restricted to prolate, reticulate, tricolpate pollen with lumina diameter

>1 µm. *Retitricolpites* as circumscribed here is much less common in the Wilcox Group than in the Ypresian section of the IODP 364 core in the Yucatán Peninsula, and the presence of *Retitricolpites* spp. here may represent more thermophilic vegetation in the Wilcox Group. Elsik (1968b, Plate 23, fig. 16) provided an image of a prolate, coarsely reticulate, tricolpate pollen grain he identified as *Tricolpites hians* Stanley 1965, but *Tricolpites* as emended by Jarzen and Dettmann (1989) is restricted to finely reticulate, oblate to subprolate forms. The informal species listed below have been differentiated following Smith (2020) on the basis of the maximum lumina diameter.

Retitricolpites sp. A

Plate 8, figure 5

Discussion: This informally named species is synonymous with *Retitricolpites* sp. A of Smith (2020), which includes reticulate, prolate, tricolpate pollen with lumina 1–2 µm in diameter.

Botanical affinity: Angiospermae, lower affinity unknown.

Retitricolpites sp. B

Plate 8, figure 6

Discussion: This informally named species is synonymous with *Retitricolpites* sp. B of Smith (2020), which includes reticulate, prolate, tricolpate pollen with lumina 2–4 µm in diameter.

Botanical affinity: Angiospermae, lower affinity unknown.

Retitricolpites sp. C

Plate 8, figure 7

Discussion: This informally named species is here grouped with *Retitricolpites* sp. C of Smith (2020), which includes reticulate, prolate, tricolpate pollen with lumina >4 µm in size.

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Rousea* Srivastava, 1969

Rousea aff. *crassimurina* Pocknall and Nichols, 1996

Plate 8, figure 8

Discussion: The single specimen of *Rousea* aff. *crassimurina* observed in these samples is similar to *R. crassimurina* sensu stricto, differing mainly in its larger size, 42 µm in equatorial diameter versus 12–25 µm in equatorial diameter for *R. crassimurina* sensu stricto (Pocknall and Nichols, 1996). The amb is circular and the reticulum is heterobrochate, with a coarser reticulum (ca. 2 µm lumina diameter) in the mesocolpium, fining towards the apocolpium and colpi margines. The lumina have a circular to elongate or rounded polygonal shape. The muri are relatively thick, approaching a foveolate sculpture. The colpi are deeply incised, broadly gaping, and have psilate margines. *Rousea crassimurina* was described as being prolate to subspheroidal; it is not possible to determine the P/E ratio for a specimen observed in polar view using routine microscope slide mounting techniques and *Rousea* aff. *crassimurina* may be oblate. Also, *R. crassimurina* was described as being duplibaculate, and this feature was not visible on *Rousea* aff. *crassimurina*. Zetter and others (2011) discussed some pollen identified as *R. crassimurina* from the Paleocene of North Dakota which are also not visibly duplibaculate. *Rousea subtilis* (Srivastava, 1969), the type species of the genus, is larger and more coarsely reticulate than *Rousea* aff. *crassimurina*. *Rousea linguiflumena* (Pocknall and Nichols, 1996) is smaller and more finely reticulate than *Rousea* aff. *crassimurina*. The *Rousea* sp. A of Smith (2020) is distinguished by having a colpus membrane and lacking colpi margines. *Rousea spatium* (Korasidis and others, 2023) is distinguished by having more prominently thickened colpi margines and thinner muri.

Botanical affinity: Angiospermae, possibly Salicaceae based on the similarity to modern *Salix* spp. with a heterobrochate reticulum (e.g., Kapp and others, 2000; Zetter and others, 2011; Maciejewska-Rutkowska and others, 2021).

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

Discussion: *Scabratricolpites* includes all scabrate, tricolpate pollen. The genus is broadly defined and is best reserved for pollen which cannot be placed in a more narrowly defined form genus and with unknown lower botanical affinities. Scabrate sculpture is here defined as an indistinctly roughened surface in light microscopy, which in reality may contain multiple sculptural elements only observable in scanning electron microscopy. The distinction between scabrate and psilate sculpture is gradational and may partly result from variable preservation of pollen grains.

Scabratricolpites spp. (non-prolate)

Plate 7, figures 8–11

Discussion: The pollen type includes scabrate tricolpate pollen which is oblate to spherical. This type likely includes poorly preserved tricolpate pollen where the surface sculpture has been corroded, and some specimens may be pollen otherwise referable to *Tricolpites asper*, *Tricolpites hians*, or other oblate, tricolpate species where the original surface sculpture is not clearly observable. This pollen type is roughly synonymous with pollen identified by Elsik (1968b, Plate 23, figs. 2–6) as "*Tricolpopollenites* sp."

Botanical affinity: Angiospermae, lower affinity uncertain.

Genus *Striatopollis* Krutzsch, 1959

Striatopollis grahamii Smith, 2020

Plate 8, figure 15

Discussion: This rarely observed striate, tricolpate pollen type is morphologically indistinguishable from Ypresian pollen described as *Striatopollis grahamii* in Smith (2020). The observation of this species in the Lower Wilcox extends the temporal range of the species downwards to the Selandian and the geographic range to Texas in addition to the Yucatán Peninsula. The best preserved of the two observed specimens (Plate 8, fig. 15) shows some kinks and bulges around the colpi at the equator that may indicate the presence of cryptic pores, but the pollen is considered tricolpate because the pores are not clearly present. An alternative identification, if the grain is considered tricolporate, would be *Striatricolporites* aff. *conspicuus* (e.g., Smith, 2020, Plate 3.8, fig. 7). *Ailanthipites berryi* is somewhat similar but *A. berryi* is reticulate-striate with clearly observable pores.

Botanical affinity: Possibly *Crudia* (Fabaceae) (Smith, 2020).

Paleoecology: Tropical lowland forest (Smith, 2020).

Genus *Striatricolpites* (van der Hammen, 1956) González Guzmán, 1967

Discussion: Although arguably, *Striatricolpites* is invalid as a form genus (Jansonius and Hills, 1976; Smith, 2020); it is useful in accommodating non-prolate, striate, tricolpate pollen grains which cannot be more narrowly placed in another existing pollen form genus. *Striatopollis* is restricted to prolate, striate, tricolpate pollen grains.

Striatricolpites sp. A

Plate 8, figure 16

Discussion: A single specimen of this type has been observed. It is oblate, finely striate, and tricolpate, with widely gaping, somewhat ragged, non-marginate colpi and no observable pores. Scabrate colpus membranes partially fill the colpi. The equatorial diameter is circa 29 µm. *Ailanthipites nonprolatus* is somewhat similar and is distinguished mainly by being tricolporate (Frederiksen and others, 1983). It is possible *Striatricolpites* sp. A is tricolporate but the pores are not clearly visible on this specimen, in which case it is probably conspecific with *A. nonprolatus*.

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Tricolpites* Cookson, 1947 from Couper, 1953 emend. Jarzen and Dettmann, 1989

Tricolpites asper Frederiksen, 1978

Plate 7, figures 12, 13

Discussion: *Tricolpites asper* differs from *Tricolpites hians* in having more shallowly incised colpi with rougher colpi edges (Jardine, 2011). There appears to be some morphological integradation with *T. asper* and *T. hians* and arguably there may not be much practical value in separating them.

Tricolpites hians Stanley, 1965 sensu lato

Plate 7, figures 14–16, 18, 19

Discussion: Stanley (1965) originally described *T. hians* as being oblate, tricolpate, and microreticulate, with lumina circa 0.2–0.3 µm in diameter. The equatorial diameter was given as between 18–20 µm and the exine was described as circa 1 µm thick. The colpi were described as long, straight, and open. Elsik (1968b) reassigned *T. hians* to the genus *Tricolpopollenites* and broadened the species concept to include specimens with an equatorial diameter ranging from 8 to 28 µm and lumina up to 1 µm in diameter, as well as specimens with ragged or marginate colpi and prolate specimens. This study will in part follow the broadened species concept of Elsik (1968b), excepting that prolate specimens fall outside the circumscription of *Tricolpites* as emended by Jarzen and Dettmann (1989) and are excluded. Also, *Tricolpites asper* is distinguished from *T. hians* by having shallower colpi with more ragged margines. This study will follow Pocknall and Nichols (1996) and consider *Tricolpites parvus* and *Tricolpites varius* to be junior synonyms of *T. hians*. *Tricolpites reticulatus* is more strongly trilobate than *T. hians*.

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

Tricolpites reticulatus
Cookson, 1947 from Couper, 1953 emend.
Jarzen and Dettmann, 1989

Plate 7, figure 17

Discussion: *Tricolpites reticulatus* is distinguished from *Tricolpites hians* by being more strongly trilobate, with more strongly concave sides to the colpi in polar view (Jardine, 2011). This study will follow Wanntorp and others (2004) and consider *Tricolpites microreticulatus* a junior synonym of *T. reticulatus*. Only one specimen was observed in this study (Plate 7, fig. 17). *Bombacacidites*? aff. *nanobrochatus* (e.g., Plate 12, fig. 17) is somewhat similar but more strongly trilobate, more finely reticulate, and thinner-walled, with more widely gaping, shorter colpi (and obscure pores).

Botanical affinity: Probably *Gunnera* (Gunneraceae) (Wanntorp and others, 2004; Jardine, 2011).

5.7. Tricolporate angiosperm pollen

Genus *Aesculiidites* Elsik, 1968

Aesculiidites circumstriatus
(Fairchild in Stover and others, 1966)
Elsik, 1968

Plate 11, figures 14–17

Discussion: This species is easily distinguished by its circumstriate ornamentation. *Aesculiidites circumstriatus* has been grouped with tricolporate pollen following Jardine (2011), but this species may be either tricolpate or tricolporate.

Botanical affinity: Possibly Hippocastanoideae (Sapindaceae) (Elsik, 1968b; Pocknall and Nichols, 1996; Jardine, 2011).

Stratigraphic comments: Gregory and Hart (1995b) have an observed base of *A. circumstriatus* in the Thanetian of the Wilcox Group in Louisiana, below the base of *Pistillipollenites mcgregorii*. *Aesculiidites circumstriatus* appears to range through our studied sections of the Lower Wilcox, well below the Selandian-Thanetian boundary.

Genus *Ailanthipites* Wodehouse, 1933

Discussion: The sculpture of *Ailanthipites* was originally described by Wodehouse (1933, p. 512) as "…reticulate-pitted with the pits elongate and linearly arranged forming a sort of thumb-print pattern." Nichols (2010) distinguished the similar genus *Rhuspollenites* from *Ailanthipites* on the basis of their sculpture, with *Ailanthipites* having a foveolate rather than reticulate sculpture. It is not clear to us why the sculpture of *Ailanthipites* was redescribed as foveolate. Wodehouse (1933) interpreted the sculpture of *Ailanthipites* as reticulate. According to Punt and others (2007), foveolae are defined as more or less rounded depressions over 1 µm in diameter. The sculpture of the type species, *Ailanthipites berryi*, was redescribed and imaged by Nichols (2010). The depressions Nichols (2010) described as foveolae are both less than 1 µm in diameter and elongate, in some cases up to 10 µm in length. Whether these depressions are lumina of a reticulum, foveolae, or punctae depends on the size of the holes, how widely the holes are separated and whether they form a network-like pattern using the terminology of Punt and others (2007). In the type species *A. berryi* the depressions are quite small, and even the high-quality images provided by Nichols (2010, Plate 16, figs. 9–10) are somewhat ambiguous regarding the fine structure. Scanning electron microscopy of *A. berryi* specimens from the type locality would help to clarify the issue. *Rhuspollenites* is probably best reserved for more coarsely reticulate-striate pollen where the lumina and muri are larger and more clearly defined in light microscopy. *Aesculiidites* is distinguished from *Ailanthipites* by having striate ornamentation with the elongated elements parallel to the equatorial axis rather than parallel to the polar axis as in *Ailanthipites*. *Striatopollis* and *Striatricolpites* are restricted to striate, tricolpate pollen.

Ailanthipites berryi Wodehouse, 1933 sensu lato

Plate 11, figures 10–12

Discussion: A broad species concept is used here to include morphologies which Pocknall and Nichols (1996) identified as "*Ailanthipites* sp. cf. *A. berryi*."

Botanical affinity: Eudicots, possibly Anacardiaceae, Leguminosae, Sapindaceae, or Simarubaceae (Pocknall and Nichols, 1996).

Ailanthipites nonprolatus Frederiksen in Frederiksen and others, 1983

Plate 11, figure 13

Discussion: *Ailanthipites nonprolatus* is distinguished from other species in *Ailanthipites* by being relatively small (19–25 µm in the original description) and oblate spheroidal to subprolate rather than prolate. Only a single specimen has been observed.

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Bombacacidites* Couper, 1960

Discussion: Although technically *Bombacacidites* pollen is tricolporate, the pores are often not clearly visible and the grains appear to have three short colpi with no pores. *Intratriporopollenites* is a similar genus; Nichols (2010) stated that *Intratriporopollenites* is distinguished from *Bombacacidites* by being vestibulate, with clearly developed endannuli and sculpture which may be infrareticulate but is never suprareticulate as in *Bombacacidites*.

Bombacacidites? aff. *nanobrochatus* Frederiksen in Frederiksen and others, 1983

Plate 12, figure 17

Discussion: This rarely observed type resembles in outline other species of *Bombacacidites* with a subtriangular amb, but the colpi are unusually long for the genus and there is no indication of the typical colpi margines seen in *Bombacacidites* pollen. The size range in the three observed specimens is circa 24–30 µm in diameter. *Bombacacidites nanobrochatus* is similar in having a very finely reticulate (lumina diameter <0.5 µm), homobrochate sculpture, and a subtriangular amb, but *B. nanobrochatus* has a thicker, clearly columellate exine and relatively shorter colpi which are marginate (Frederiksen and others, 1983). There is some uncertainty about the generic identification because in some respects this type departs from the morphology of typical *Bombacacidites*. Also, although the pores in *Bombacacidites* are often obscure, the apertures in *Bombacacidites*? aff. *reticulatus* appear simply colpate. *Tricolpites reticulatus* is somewhat similar but has longer, less widely gaping colpi, a trilobate amb which is less strongly subtriangular, and a thicker, visibly columellate exine (e.g., Plate 7, fig. 17).

Botanical affinity: Possibly Bombacoideae.

Bombacacidites bombaxoides Couper, 1960 sensu lato

Plate 12, figures 19, 20

Discussion: *Bombacacidites bombaxoides* is distinguished from *Bombacacidites nacimientoensis* by being more finely reticulate at the apocolpium (i.e., the polar region) and from *Bombacacidites nanobrochatus* by being more coarsely reticulate with a heterobrochate reticulum. In their original descriptions, the lumina for *B. bombaxoides* are described as being circa 1 µm in diameter and the lumina for *B. nacimientoensis* are described as being circa 2 µm in diameter (Anderson, 1960; Couper, 1960). The brochi (i.e., the lumina and half the width of adjacent muri) for *B. nanobrochatus* were described as <0.5 µm in diameter. These three species are morphologically gradational; some cutoff in lumina size must be applied consistently if the species are differentiated. Elsik (1968b) emended *B. nacimientoensis* and restricted the size range of the apocolpial lumina to 1–2 µm. Frederiksen and others (1983), on the other hand, excluded specimens with apocolpial lumina <1.5 µm from *B. nacimientoensis*. We consider this unjustified as the emendation of *B. nacimientoensis* in Elsik (1968b) clearly includes specimens with apocolpial lumina between 1.0–1.5 µm, and Frederiksen and others (1983) did not formally emend *B. nacimientoensis*. An additional question is whether specimens similar to *B. nacimientoensis* but more coarsely reticulate (>2 µm lumina diameter) should be included in *B. nacimientoensis* or split as a separate species. Following Jaramillo and Dilcher (2001), who included specimens with lumina >4 µm in diameter in *B. nacimientoensis*, a broad species definition of *B. nacimientoensis* is used here which includes specimens with apocolpial lumina 1–4 µm in diameter. *Bombacacidites bombaxoides* is similar but more finely reticulate than *B. nacimientoensis*, with apocolpial lumina 0.5–1.0 µm in diameter. *Bombacacidites nanobrochatus* has apocolpial lumina <0.5 µm in diameter. A broad species concept is used here following Smith (2020), which includes specimens smaller than the quite narrow range given by Couper (1960) for *B. bombaxoides* of 41–44 µm equatorial diameter.

Botanical affinity: Malvaceae, probably Bombacoideae. The botanical affinity for

B. bombaxoides and other species of *Bombacacidites* is discussed in Smith (2020).

Paleoecology: Ramírez-Arriaga and others (2014) gave the paleoecology of *Bombacacidites* spp. as tropical deciduous forest.

Bombacacidites nacimientoensis
(Anderson, 1960) Elsik, 1968 sensu lato

Plate 12, figures 21, 22

Discussion: *Bombacacidites nacimientoensis* is distinguished from other species of *Bombacacidites* by its subtriangular shape and heterobrochate reticulum with lumina 1–4 µm in diameter (see discussion for *B. bombaxoides*). A broad species concept is used here which includes specimens slightly smaller and larger than the 35–39 µm range given by Anderson (1960).

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Bombacacidites nanobrochatus
Frederiksen in
Frederiksen and others, 1983 sensu lato

Plate 12, figure 18

Discussion: *Bombacacidites nanobrochatus* is distinguished from other species of *Bombacacidites* by its subtriangular shape and heterobrochate reticulum with lumina <0.5 µm in diameter (see discussion for *B. bombaxoides*). *Bombacacidites*? aff. *nanobrochatus* is distinguished primarily by having longer, non-marginate colpi, and secondarily by having a thinner exine which is not visibly columellate. Only a single specimen of this type has been observed.

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Stratigraphic comments: *Bombacacidites nanobrochatus* was originally described from the Middle Eocene of California (Frederiksen and others, 1983) and has been observed in the Ypresian in the southern Gulf of America (Smith, 2020). No Paleocene occurrences are recorded in Palynodata Inc. and White (2008); this Paleocene occurrence appears to be the oldest occurrence of *B. nanobrochatus* sensu lato in the published literature.

Bombacacidites reticulatus
(Groot and Groot, 1962) Srivastava, 1972

Plate 12, figures 11–14

Discussion: Species of *Bombacacidites* are commonly distinguished by the coarseness of the reticulum in the apocolpium, the total diameter of the grain, the shape of the amb, and whether the reticulum is heterobrochate (Smith, 2020). Specimens of *B. reticulatus* sensu lato observed in this study are heterobrochate with lumina in the apocolpium circa 1–3 µm in diameter, a circular to subcircular amb, and a total diameter of 24–35 µm. Jardine (2011) noted that *B. reticulatus* is distinguished from other species of *Bombacacidites* in the Paleogene of the U.S. Gulf Coast by having a circular or nearly circular amb. *Bombacacidites brevis* also has a circular amb, but has a finer, homobrochate reticulum, and has only been identified from South and Central America (Smith, 2020). Srivastava's (1972a) specimens of *B. reticulatus* had a reticulum with lumina 3–5 µm in diameter and a total diameter of 26–34 µm, while Jardine's (2011) specimens had a reticulum with lumina 1–3 µm in diameter and a total diameter of 26–31 µm. Nichols (2010) redescribed pollen originally identified as *Tilia crassipites* by Wodehouse (1933), placing the species in *Bombacacidites* as *Bombacacidites crassipites*. *Bombacacidites crassipites* as redescribed and imaged by Nichols (2010) is quite similar to *B. reticulatus* and may be a senior synonym in part of *B. reticulatus*, but this relatively new combination has not been widely used in the literature.

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Bombacacidites sp. C

Plate 12, figures 15, 16

Discussion: This species of *Bombacacidites* is informally named *Bombacacidites* sp. C to avoid confusion with other species described in Smith (2020). This species is distinguished by its roughly circular amb and homobrochate reticulum (lumina ca. 1–4 µm in diameter); in other words, there is no significant, consistent increase in lumina size in the apocolpium compared to the mesocolpium. *Bombacacidites fereparilis* is nearly homobrochate but has a more triangular amb (Frederiksen and others, 1983). *Bombacacidites brevis* has a subcircular amb and a homobrochate reticulum but is more finely reticulate (Smith, 2020). *Bombacacidites reticulatus* is heterobrochate but otherwise similar. The few specimens of *Bombacicidites* sp. C observed in this study are morphologically variable, particularly in the coarsensess of the reticulum and colpi length; the type may be worth formally naming as a new species if it is observed in higher abundance in other sections.

Botanical affinity: Malvaceae, probably Bombacoideae.

Paleoecology: Tropical deciduous forest.

Genus *Cupuliferoipollenites* Potonié, 1951 from Potonié, 1960

Discussion: *Cupuliferoipollenites* accommodates small, prolate to prolate spheroidal, psilate to faintly scabrate, tricolporate pollen. Although not specifically stated in the description, the genus is generally restricted to small forms broadly similar to modern *Castanea* pollen (e.g., Jardine, 2011). The upper size limit (21 µm) of the type species *Cupuliferoipollenites pusillus* can be considered the approximate upper size limit of the genus. The generic description is also somewhat vague regarding the morphology of the pores, which were described as "short equatorial rugae" in the translation provided by Jansonius and Hills (1976). *Cupuliferoidaepollenites* is similar but tricolpate. *Siltaria* is distinguished from *Cupuliferoipollenites* in this study primarily by having large, lalongate pores, and secondarily by being more clearly columellate and larger.

Cupuliferoipollenites spp.

Plate 10, figures 21–23

Discussion: This study will follow Jardine (2011) and not speciate pollen referable to *Cupuliferoipollenites*. Only three specimens of *Cupuliferoipollenites* were observed in our samples, all in Moczygemba VT No. 11.

Botanical affinity: Probably Fagaceae, possibly Fabaceae (Frederiksen and others, 1983; Jardine, 2011).

Genus *Favitricolporites* Sah, 1967 emend. Srivastava, 1972a

Favitricolporites baculoferus (Pflug in Thomson and Pflug, 1953) Srivastava, 1972

Plate 13, figures 2–5

Discussion: This tricolporate species is distinguished by its retipilate sculpture and fine reticulum. The pores are small and often indistinguishable, especially in polar view (e.g., Srivastava, 1972a; Jardine, 2011); because of the distinctive retipilate sculpture, even apparently tricolpate pollen grains of this type have been included in *F. baculoferus*.

Botanical affinity: Angiospermae, lower affinity uncertain.

Genus *Holkopollenites* Fairchild in Stover and others, 1966 emend. Christopher and Prowell, 2002

Discussion: The emendation of *Holkopollenites* by Christopher and Prowell (2002) broadened its circumscription to allow a wider variety in shape, colpi length, wall thickness, and orientation of the nexinal channels.

Holkopollenites sp. A

Plate 10, figures 4–7

Discussion: This species is essentially syn-on-ymous with "cf. *Symplocoipollenites*" pollen described by Elsik (1968b) and Jardine (2011). Jardine (2011) distinguished cf. *Symplocoipollenites* from *Holkopollenites chemardensis* by being less sharply punctate, having less deeply incised colpi, possessing convex rather than straight or concave sides of the amb, and possessing generally finer nexinal striations. As emended by Christopher and Powell (2002), this pollen type can be accommodated within *Holkopollenites*. Jardine (2011) noted that transitional forms between his cf. *Symplocoipollenites* and *H. chemardensis* were encountered, strengthening the argument that the two species should be placed in the same genus. Jardine (2011) also noted the similarity of this type with *Nyssapollenites* spp. These two types are primarily distinguished here based on the presence or absence of nexinal striations; *Nyssapollenites* as defined here does not have nexinal striations and *Holkopollenites* does have nexinal striations.

Holkopollenites chemardensis
Fairchild in Stover and others, 1966

Plate 10, figure 3

Discussion: Only a single specimen of *H. chemardensis* has been observed in these samples. *Holkopollenites* sp. A is distinguished primarily by having significantly convex sides of the amb; the colpi are also less deeply incised in *Holkopollenites* sp. A. Jardine (2011) noted that morphological intermediates are present between *H. chemardensis* and his "cf. *Symplocoipollenites*" type (i.e., *Holkopollenites* sp. A). The nexinal striations are weakly developed in the single observed specimen of *H. chemardensis*.

Genus *Intratriporopollenites*
Pflug and Thomson in Thomson and Pflug, 1953
emend. Nichols, 2010 sensu lato

Discussion: Nichols (2010) emended *Intratriporopollenites* to include tetracolporate as well as tricolporate pollen.

Intratriporopollenites vescipites
(Wodehouse, 1933) Nichols, 2010

Plate 12, figures 6–10

Discussion: *Intratriporopollenites vescipites* is here considered synonymous with specimens identified by Pocknall and Nichols (1996) as "*Intratriporopollenites* sp. cf. *Tilia tetraforaminipites*." Nichols (2010) considered that Pocknall and Nichol's (1996) species was synonymous with *I. vescipites*, although Nichols (2010) described *I. vescipites* as infrareticulate, while Pocknall and Nichols' (1996) specimens were described as being scabrate, granulate, or possibly minutely punctate. Jardine (2011) agreed with Nichols (2010) that there was no utility in separating tetraporate specimens of *I. vescipites* as *Intratriporopollenites tetraforaminipites*. In some specimens of *I. vescipites* observed in this study, a very fine infrareticulum is barely visible; other scabrate or finely granulate specimens with no visible infrareticulum have also been included in *I. vescipites*, following Pocknall and Nichols (1996). Both tricolporate and tetracolporate types of this species have been observed in our samples. *Intratriporopollenites pseudinstructus* and *Tilia instructa* are similar but *I. vescipites* is distinguished by having narrower endannuli, more protruding ora, and a thinner exine.

Botanical affinity: Malvaceae, probably within the former families Bombacaceae, Sterculiaceae, or Tiliaceae (Nichols, 2010).

Genus *Lanagiopollis* Morley, 1982 sensu lato

Discussion: Jardine (2011) provides an extensive discussion of *Lanagiopollis*, including comparisons with other similar pollen form genera and information about species differentiation. Although strictly *Lanagiopollis* is limited to pollen grains >60 µm in diameter (Morley, 1982), in practice pollen grains as small as 20 µm with similar morphology have been included in the genus (e.g., Srivastava, 1972a). *Nyssapollenites* is similar but is distinguished by having infrapunctate rather than reticulate or rugulate sculpture (Morley, 1982; Jardine, 2011). In some pollen grains with very fine sculpture, it is difficult to determine whether the sculpture was infrapunctate or reticulate; a secondary characteristic used to distinguish *Lanagiopollis* and *Nyssapollenites* in these samples is that *Lanagiopollis* spp. have more prominently marginate, widely gaping colpi than *Nyssapollenites* spp.

Lanagiopollis cribellata (Srivastava, 1972) Frederiksen, 1988 sensu lato

Plate 9, figures 6–8

Discussion: *Lanagiopollis cribellata* is mainly distinguished from other species of *Lanagiopollis* in the Paleogene Gulf Coast by having a relatively thin exine (ca. 1 µm thick), thickened colpi margines, and a sculpture which is finely reticulate and homobrochate or punctate (lumina or punctae ca. 0.5 µm thick) (Jardine, 2011). A broad species concept is used to include specimens larger than the original size range of 20–38 µm given by Srivastava (1972a); specimens in this study reach up to circa 50 µm in diameter. Some of the specimens identified by Elsik (1968b) as *Tricolporopollenites kruschii* are synonymous with *L. cribellata* (Srivastava, 1972a; Jardine, 2011). Some pollen otherwise similar to *L. cribellata* sensu stricto (e.g., Plate 9, fig. 8) have fine sculpture which is perhaps better described as punctate rather than reticulate; these have been included in *L. cribellata* because they are otherwise similar to clearly reticulate forms, particularly in having more prominent colpi margines than *Nyssapollenites* spp.

Botanical affinity: Possibly *Alangium* (Frederiksen and others, 1983; Frederiksen, 1988).

Paleoecology: If the botanical affinity is with *Alangium*, the genus has a mainly tropical modern distribution in Africa and Asia. However, the geographic range and climatic tolerance of *Alangium* was broader in the Paleogene and its presence is not necessarily indicative of tropical conditions (Eyde and others, 1969).

Lanagiopollis lihoka (Srivastava, 1972) Frederiksen, 1988

Plate 9, figures 9–11

Discussion: *Lanagiopollis lihoka* is similar to *L. cribellata*, but is heterobrochate, with lumina ranging from 0.75–3.00 µm in diameter (Srivastava, 1972a). The reticulum is coarsest in the mesocolpia and finer toward the apocolpia and colpi, although this difference in the coarseness of the reticulum may be slight.

Botanical affinity: Possibly *Alangium* (Frederiksen and others, 1983; Frederiksen, 1988).

Paleoecology: Broad paleoecological tolerances.

Lanagiopollis spp.

Plate 9, figures 12–15

Discussion: Pollen assignable to *Lanagiopollis* sensu lato, but falling outside the circumscription of previously described species of *Lanagiopollis*, have been grouped together here. This includes, in particular, pollen grains similar to *L. cribellata* but having straight-sided rather than convex sides.

This taxon is synonymous in part with the *Nyssa kruschii* group of Jardine (2011). This type appears to be synonymous in part with specimens identified as "*Holkopollenites* (?) sp." by Elsik (1968b, Plate 30, figs. 4–6) which lack the nexinal striations diagnostic of *Holkopollenites* sensu stricto.

Botanical affinity: Possibly *Alangium*.

Paleoecology: Broad paleoecological tolerances.

Genus *Nyssapollenites* Thiergart, 1938 from Potonié, 1960

Discussion: Following the original description translated by Jansonius and Hills (1976), *Nyssapollenites* is restricted to oblate to spheroidal, rounded subtriangular, infrapunctate, tricolporate pollen. The colpi have more or less thickened margines. Two similar form genera in the Wilcox Group are *Holkopollenites* and *Lanagiopollis*; *Holkopollenites* can be distinguished by possessing nexinal channels running more or less parallel to the grain sides, and *Lanagiopollis* can be distinguished by having reticulate or rugulate rather than infrapunctate sculpture (Jansonius and Hills, 1976; Jardine, 2011). The nomenclature of fossil nyssoid pollen is complicated; in particular, the pollen form species *Pollenites kruschii* has often been used to accommodate nyssoid pollen, as well as morphologically and botanically unrelated pollen forms (Eyde, 1991). *Pollenites kruschii* was transferred to *Tricolporopollenites* by Thomson and Pflug (1953), transferred to the modern genus *Nyssa* by Frederiksen (1980b), transferred to *Nyssapollenites* by Jardine and Harrington (2008), and included in the "*Nyssa kruschii* group" of Jardine (2011). Multiple form subspecies have been described. *Pollenites kruschii* is problematic due to the "…lack of detailed description and illustrations for *P. kruschii*" (Srivastava, 1972a). Eyde (1991, p. 81) aptly described *P. kruschii* as a "…monumental nomenclatural mess." Therefore, we have avoided identifying pollen in this study using that form species name.

Nyssapollenites pulvinus (Potonié, 1931) Frederiksen, 1980

Plate 10, figures 1, 2

Discussion: According to Jardine (2011), this species is distinguished from other species of *Nyssapollenites* by its distinctly punctate to microreticulate ornamentation and its prominently thickened pores, and distinguished from *Lanagiopollis* spp. by being generally smaller, with narrower colpi and ora. Reticulate ornamentation falls outside the circumscription of *Nyssapollenites* sensu stricto, but the genus name will be kept for taxonomic continuity.

Botanical affinity: Nyssaceae or Cornaceae (Frederiksen, 1980b).

Nyssapollenites spp.

Plate 9, figures 1–5

Discussion: This pollen type is synonymous with *Nyssapollenites* spp. and, in part, the *Nyssa kruschii* group of Jardine (2011). Jardine (2011) described several species of *Nyssapollenites* and similar genera. Jardine's (2011) *Nyssa kruschii* group included *Rhoipites angustus*; we prefer to identify prolate *R. angustus* type pollen separately and leave most *Nyssapollenites* spp. unspeciated rather than use the nomenclaturally problematic *N. kruschii* (see discussion for the genus *Nyssapollenites* above). Specimens identified as *Nyssapollenites* here are oblate and, aside from *N. pulvinus*, punctate rather than reticulate. According to Frederiksen (1980b), *Nyssa kruschii* is finely reticulate, not punctate. No specimens referable to *Nyssapollenites paleocenicus* were observed in our samples, and Jardine (2011) observed only a single specimen of *N. paleocenicus* from the eastern Gulf Coast. Jardine (2011) gave similar biostratigraphic ranges for the *Nyssa kruschii* group and *Nyssapollenites* spp. Attempts to subdivide *Nyssapollenites* consistently, aside from separating *N. pulvinus*, proved unproductive in these samples. Some pollen identified as *Nyssapollenites* spp. in this study have ambiguously infrapunctate or micro-reticulate sculpture, but clearly reticulate pollen types have been excluded from *Nyssapollenites*.

Botanical affinity: Possibly Nyssaceae or *Alangium* based on morphological resemblance to modern *Nyssa* and *Alangium* pollen.

Paleoecology: Possibly swamp (see discussion in Chapter 4).

Genus *Punctatricolporites*
Kedves, 2000 emend. Smith, 2020

Punctatricolporites spp. (prolate)

Plate 10, figure 8

Discussion: This rare pollen type includes prolate, punctate (generally infrapunctate), tricolporate pollen. This type is similar to *Nyssapollenites* spp., but prolate pollen falls outside the generic circumscription of *Nyssapollenites* sensu stricto. No specimens similar to the *Punctatricolporites* sp. A of Smith (2020) were observed in this study. Not enough specimens were observed to justify speciating this genus.

Genus *Retitricolporites* van der Hammen, 1956
from Van der Hammen and Wijmstra, 1964

Discussion: *Retitricolporites* includes all reticulate, tricolporate pollen grains. As with some other broadly defined form genera, it is best reserved for pollen types which cannot be more narrowly placed in another form genus. Smith (2020) provides more detailed taxonomic discussion about the ambiguity regarding the generic differentiation between various reticulate, tricolporate pollen form genera, particularly *Caprifoliipites*, *Horniella*, and *Rhoipites*. To maintain taxonomic continuity, previously described species assigned to these form genera will not be transferred to *Retitricolporites*, with the understanding that generic distinctions between these three genera have not been consistently maintained in the literature.

Retitricolporites spp.

Plate 10, figures 24–28

Discussion: A heterogenous group of tricolporate, reticulate pollen has been provisionally identified here as *Retitricolporites* spp. This morphotype was difficult to meaningfully subdivide and serves as a wastebasket taxon, similar to *Horniella* spp. and *Caprifoliipites* spp. in Jardine (2011). Some specimens of *Retitricolporites* spp. in this study are finely reticulate and somewhat similar to our *Rhoipites angustus* type but significantly smaller (<20 µm). Other specimens are larger than 20 µm in diameter but differ from *Rhoipites cryptoporus* and the *R. angustus* type in various ways.

Botanical affinity: Angiospermae, lower affinity uncertain.

Rhoipites Wodehouse, 1933

Rhoipites cryptoporus Srivastava,
1972 sensu lato

Plate 10, figure 29; Plate 11, figures 1–6

Discussion: A broad species concept is used here to include specimens falling slightly outside the range of variation in size, exine thickness, and margo thickness described by Srivastava (1972a). The size of the lumina was originally described as circa 1–2 µm in diameter; Jardine (2011) also included more finely reticulate specimens with lumina 0.5–1.0 µm in diameter. The reticulum was described as heterobrochate, fining towards the colpi, but this fining of the reticulum can be quite subtle, for example, in the holotype and paratype specimens (Srivastava, 1972a, Plate 21, figs. 1–11). *Rhoipites capax* is more coarsely reticulate, with lumina 3–4 µm in diameter, and *Rhoipites latus* has polygonal to longitudinally elongate lumina rather than more or less circular lumina as in *R. cryptoporus* (Jardine, 2011). *Rhoipites angustus* is distinguished most easily by being more finely and evenly reticulate.

Botanical affinity: Angiospermae, lower affinity unknown.

Rhoipites aff. *latus* Frederiksen, 1980

Plate 11, figure 7

Discussion: The single observed specimen of this type is similar to *Rhoipites latus* in being tricolporate, coarsely reticulate, prolate, fairly large (ca. 38 µm in our specimen compared to 34–44 µm in *R. latus*), with more or less round, distinct ora, marginate colpi, and polygonal to longitudinally elongate lumina. *Rhoipites* aff. *latus* differs from *R. latus* mainly in having thinner muri which are not visibly duplibaculate. *Rhoipites capax* is spheroidal to subprolate rather than prolate (Frederiksen 1988).

Botanical affinity: As noted by Frederiksen (1980b), *R. latus* is similar to modern pollen of *Parthenocissus* (Vitaceae). The specimen of *Rhoipites* aff. *latus* in our study is also similar to modern *Parthenocissus* pollen, for example *Parthenocissus hirsuta* (e.g., Wodehouse, 1932).

Rhoipites angustus type

Plate 10, figures 15–20

Discussion: This morphological type includes spheroidal to prolate, finely reticulate, tricolporate pollen with round pores described by Frederiksen (1980b) as *Rhoipites angustus*. A broad species concept is used here which includes similar pollen types falling slightly outside the range of variation given by Frederiksen (1980b) in pollen size, pore diameter, colpi length, and exine thickness. In Frederiksen's (1980b, p. 55) remarks regarding *R. angustus*, he noted that *Nyssa kruschii* "…is spheroidal to oblate, but otherwise it is similar to *Rhoipites angustus* in many respects." Jardine (2011) included pollen falling under the circumscription of both *R. angustus* and *N. kruschii* in his *Nyssa kruschii* group. Our *R. angustus* type is similar in including prolate and oblate tricolporate pollen with small, round pores, but it does not include infrapunctate pollen. Based on reasoning provided in the generic description for *Nyssapollenites*, we consider *N. kruschii* a nomen dubium.

Botanical affinity: Possibly Cornaceae, Nyssaceae, or Anacardiaceae (Frederiksen, 1980b). We doubt the botanical affinity is with *Nyssa* as this type is reticulate, but the *R. angustus* type may be an early relative in the family Nyssaceae.

Genus *Scabratricolporites* Roche and Schuler, 1976

Discussion: *Scabratricolporites* includes all scabrate, tricolporate grains. Such a broadly defined genus is best reserved for pollen types which cannot be more narrowly placed in another existing genus. Frederiksen (1980b) used a broader definition of *Siltaria* which is essentially synonymous with *Scabratricolporites*; this study will maintain the narrower original definition of *Siltaria* in Traverse (1955). *Cupuliferoipollenites* includes psilate, prolate, tricolporate pollen. Although not mentioned in the original description, the type species *Cupuliferoipollenites pusillus* is small (15–21 µm), and Jardine (2011) considered that *Cupuliferoipollenites* was restricted to small pollen. *Nyssapollenites* includes spherical to oblate, tricolporate pollen with endannulate ora, long, narrow colpi, and an infrapunctate exine (Jansonius and Hills, 1976). Jardine (2011) described *Araliaceoipollenites* as incorporating tricolporate pollen with a columellate and granulate exine, although the original description is narrower; Jansonius and Hills (1976) noted that *Araliaceoipollenites* may be a junior synonym in part of *Tricolporopollenites*. *Tricolporopollenites*, as Jardine (2011) noted, technically includes nearly all tricolporate pollen. We consider *Tricolporopollenites* too broadly defined to be useful as a form genus.

Scabratricolporites spp.

Plate 10, figures 9–14

Discussion: This morphological type includes tricolporate pollen with variably developed colpi margines and more or less circular ora. The grains may be prolate, spheroidal, or oblate and are usually observed in equatorial view. The sculpture is indistinctly scabrate. The *Rhoipites angustus* type in this study is similar but finely reticulate; many specimens identified here as *Scabratricolporites* spp. may be related but have a reticulum too fine to be clearly observable in light microscopy. Some specimens identified by Elsik (1968b, Plate 34, figs. 1–2, 4) as *Tricolporopollenites kruschii* are not visibly reticulate or infrapunctate and may be synonymous with *Scabratricolporites* spp., assuming the surface sculpture was scabrate in light microscopy and the ambiguity in the surface sculpture is not due to photographic limitations. *Scabratricolporites* spp. is a wastebasket taxon and likely represents pollen from a heterogenous group of plants with nondescript, overlapping morphologies in light microscopy. The relative abundance of this type in the assemblages may in part reflect the average state of preservation of the pollen grains, with poorly preserved assemblages having more tricolporate pollen with indistinguishable, ambiguously roughened surface sculpture.

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Siltaria* Traverse, 1955

Discussion: *Siltaria* includes finely scabrate or punctate, distinctly columellate, tricolporate pollen grains with long colpi and large, elliptical, lalongate ora.

Siltaria scabriextima Traverse, 1955 sensu lato

Plate 11, figures 8, 9

Discussion: A broad species concept is used here which includes specimens smaller than 25 µm that Frederiksen (1980b) and Jardine (2011) identified as "*Siltaria* cf. *S. scabriextima*." Traverse (1955) did not clearly restrict the size range permissible for *S. scabriextima*, giving an average polar axis length of 32 µm. *Siltaria hanleyi* is perforate (i.e., punctate) (Pocknall and Nichols, 1996).

Botanical affinity: Traverse (1955) noted that the genus *Siltaria* has features intermediate between modern *Quercus* and *Castanea* pollen, both in the family Fagaceae.

Genus *Spinaepollis* Krutzsch 1961

Spinaepollis spinosa (Potonié, 1931) Krutzsch, 1961

Plate 11, figure 20; Plate 12, figures 1–4

Discussion: Although this species is tricolporate, the apertures are often not visible and the grains may appear tricolpate or even inaperturate. Even if the apertures are not clearly visible, the echinae are fairly distinctive.

Botanical affinity: Angiospermae, lower affinity unknown (Jardine, 2011).

Genus *Symplocos* Jacquin, 1760

Symplocos? *virginiensis* group sensu Frederiksen, 1988

Plate 11, figures 18, 19

Discussion: The modern genus *Symplocos* is mainly peroblate, brevitricolporate, and vestibulate; the ornamentation is variable, commonly punctate to micro-reticulate in specimens assigned to this genus from the Paleogene U.S. Gulf Coast (Barth, 1979; Jardine, 2011). This study will follow Frederiksen (1980b, 1998) and Jardine (2011) in assigning the pollen to the modern genus, with a question mark to indicate some uncertainty as to whether the fossil pollen have an affinity with the modern genus or more broadly with the Symplocaceae. We will follow Frederiksen (1988) and combine *Symplocos*? *contracta* and *Symplocos*? *virginiensis* into a combined *Symplocos*? *virginiensis* group.

Botanical affinity: Symplocaceae, possibly *Symplocos*.

Stratigraphic comments: This taxon has an Upper Paleocene to Oligocene range in the northern Gulf of America coastal plain (Frederiksen, 1988).

Genus *Verrutricolporites*
van der Hammen and Wymstra, 1964

Verrutricolporites sp. A

Plate 13, figure 1

Discussion: The single observed specimen of this type is prolate, with low, rounded, closely spaced verrucae circa 1–2 µm in diameter. The polar axis length is circa 26 µm and the equatorial diameter is circa 14 µm. The narrow spaces between the verrucae form a negative reticulum. The pores are faintly visible as invaginations on the colpi margines. *Verrutricolpites* sp. A in Smith (2020) is somewhat similar but is tricolpate and larger. The type species *Verrutricolporites rotundiporus* has a prominent circular pore and is spherical rather than prolate.

Botanical affinity: Angiospermae, lower affinity unknown.

5.8. Stephanocolpate angiosperm pollen

Genus *Retistephanocolpites*
Leidelmeyer, 1966

Retistephanocolpites sp. A

Plate 13, figures 13, 14

Discussion: The two observed stephanocolpate, reticulate pollen in this study are similar to tricolpate, reticulate pollen grains identified here as *Tricolpites hians*, aside from being tetracolpate.

Botanical affinity: Angiospermae, lower affinity unknown.

Scabrastephanocolpites van der Hammen
and de Mutis, 1966

Discussion: This genus includes all scabrate, stephanocolpate pollen grains.

Scabrastephanocolpites spp.

Plate 13, figures 6, 7

Discussion: This pollen type has four or five colpi lacking margines, a scabrate exine, and a circular amb. Jardine (2011) described a "Pentacolpate pollen sp. 1" but that species differs in having longer, marginate colpi, as well as a different exine morphology. Van der Hammen and Garcia de Mutis (1966) described several species distinguished in part by the number of colpi, but the number of colpi in modern stephanocolpate pollen can be intraspecifically variable. Due to the rarity and lack of clear biostratigraphic value in this type, it has not been subdivided. *Quadrapollenites vagus* is distinguished most easily by having prominently marginate colpi; *Q. vagus* is also stephanocolporate, but the pores are generally indistinct (Jardine, 2011). Elsik (1968b, Plate 26, figs. 5–10) identified several apparently non-marginate, tetracolpate pollen specimens as *Q. vagus*; these are similar to specimens identified here as *Scabrastephanocolpites* spp.

Botanical affinity: Angiospermae, lower affinity unknown.

Genus *Stephanocolpites*
van der Hammen, 1954

Stephanocolpites sp. A

Plate 13, figure 11

Discussion: The single observed specimen of this type is considered conspecific with two specimens identified as "*Polycolpites* sp." by Frederiksen (1980b, Plate 11, figs. 7–8) from the lower Yazoo Clay Formation of Mississippi. The specimen has six deeply incised colpi with prominent margines. The mesocolpia are notably straight and flat-topped, giving the amb a distinctive polygonal, stellate shape. The diameter of the amb is circa 45–51 µm, depending on the direction of measurement. The exine is finely punctate in our specimen; Frederiksen (1980b) also included forms with granulate to verrucate sculpture in his "*Polycolpites* sp." type. We have changed the generic identification because as originally described by Couper (1953), *Polycolpites* is restricted to pollen with more than six colpi, and as emended by Saxena (1982), *Polycolpites* is restricted to pollen similar to the type species *Polycolpites clavatus* (Couper, 1953) with a circular to polygonal amb, more than three colpi, and clavate sculpture. We agree with arguments made by Saxena (1982) that the original descriptions for *Polycolpites* and *Stephanocolpites* are overly broad for pollen form genera, but we could find no other more narrowly defined form genus which accommodates punctate, stephanocolpate pollen. If more specimens of this type were observed, we would consider creating a new form genus for this distinct but rare type, possibly "*Punctastephanocolpites*" using the nomenclatural system of van der Hammen (1956); the placement of this type in *Stephanocolpites* is provisional.

Botanical affinity: Angiospermae, possibly Bruniaceae, Escalloniaceae, Linaceae, or Pedaliaceae (Frederiksen, 1980b).

5.9. Stephanocolporate angiosperm pollen

Genus *Lanagiopollis* Morley, 1982

aff. *Lanagiopollis lihoka* (Srivastava, 1972)
Frederiksen, 1988 (4-colporate)

Plate 13, figure 12

Discussion: The single observed specimen of this type resembles *L. lihoka* in all respects except for being tetracolporate rather than tricolporate.

Botanical affinity: Possibly *Alangium*, based on the similarity with *L. lihoka* sensu stricto (Frederiksen and others, 1983; Frederiksen, 1988).

Paleoecology: Probably similar to *L. lihoka*; broad climatic tolerances, in part tropical.

Genus *Quadrapollenites* Stover in
Stover and others, 1966 emend. Elsik, 1968b

Quadrapollenites vagus Stover in
Stover and others, 1966 emend. Elsik, 1968b

Plate 13, figures 8–10

Discussion: *Quadrapollenites vagus* is distinguished by its psilate exine and its marginate colpi. Although the genus was originally restricted to tetracolporate pollen (hence the name), Elsik (1968b) emended the genus to include tetracolpate forms as well as tricolpate or tricolporate and 5-colpate or 5-colporate forms. The specimens observed in this study do not have clearly distinguishable pores and are mostly tetracolpate, with one 5-colpate specimen observed. A similar stephanocolpate morphological type, *Scabrastephanocolpites* spp., is distinguished by having non-marginate colpi.

Botanical affinity: Angiospermae, lower affinity unknown.

5.10. Diporate angiosperm pollen

Genus *Retidiporites*
Varma and Rawat, 1963

Retidiporites sp. A

Plate 13, figure 15

Discussion: The single observed pollen grain of this type is elliptical and diporate, with annulate pores; the length of the grain is circa 39 µm. The grain is somewhat poorly preserved but the sculpture appears micro-reticulate. Elsik (1968a, 1968b) briefly described a diporate, reticulate pollen type from the Wilcox Group which he tentatively assigned to the modern genus *Ruppia*. The specimen in this study does not closely resemble modern *Ruppia* pollen, which are heteropolar and have three pores, or arguably two pores with a leptoma at the convex distal pole (Harley, 2004). Elsik's (1968a, 1968b) *Ruppia* pollen type is also more coarsely reticulate than *Retidiporites* sp. A.

Botanical affinity: Angiospermae, lower affinity unknown.

5.11. Triporate angiosperm pollen

Betulaceae–Myricaceae type

Plate 15, figures 1–7

Discussion: Smith (2020) and Jardine (2011) provide descriptions and discussion of this informally named pollen type. *Momipites* is distinguished by having less strongly annulate or tumescent pores and by being less densely granulate. *Trivestibulopollenites* spp. is distinguished from the Betulaceae–Myricaceae type by being vestibulate but is otherwise fairly similar. These Betulaceae–Myricaceae type pollen grains are usually triporate, but very rarely 4-porate types have been observed (e.g., Plate 15, fig. 5). Modern genera in the Betulaceae and Myricaceae occasionally produce 4-porate pollen (Blackmore and others, 2003).

Botanical affinity: Eudicots, probably mainly Betulaceae or Myricaceae, possibly in part Casuarinaceae (Pocknall and Nichols, 1996; Jardine, 2011).

Paleoecology: Swamp. Harrington (2008) noted extremely high abundances of Betulaceae–Myricaceae type pollen in swamp samples from the Paleocene and Eocene in Mississippi and Alabama and suggested that the ecology may be similar to extant coastal stands of *Myrica* shrubs along the Atlantic coast of the United States (Crawford and Young, 1998).

Genus *Brosipollis* Krutzsch, 1968

Brosipollis striata Frederiksen, 1988

Plate 16, figure 13

Discussion: Further information is provided in Smith (2020). Only a single specimen was observed in our samples.

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

Paleoecology: Probably lowland tropical to warm temperate forest.

Genus *Caryapollenites* Raatz,
1937 from Potonié, 1960

Discussion: Species identification for *Caryapollenites* and the similar form genus *Momipites* in the Paleogene Gulf of America is largely determined by the position of the pores and the presence or absence of areas of thinned exine on the pollen grains (Nichols and Ott, 1978, 2006). A morphological continuum between specimens with equatorial pores, slightly subequatorial pores, and significantly subequatorial pores has been observed. For this reason, the species identification of some specimens is difficult to determine with certainty, particularly in specimens not observed in direct polar view. The type species of the genus, *Caryapollenites simplex*, closely resembles modern *Carya* pollen (Jansonius and Hills, 1976, card 404; Jardine, 2011); *C. simplex* was not observed in our samples.

Caryapollenites aff. *imparalis*
Nichols and Ott, 1978

Plate 14, figure 32

Discussion: *Caryapollenites* aff. *imparalis* is similar to *C. imparalis* in all respects except that only one pore is located off the equator. This taxon represents a morphological intermediate between *C. imparalis* and *Momipites coryloides*. *Caryapollenites* aff. *imparalis* is similar to *Caryapollenites prodromus* but lacks a circumpolar ring of thinned exine.

Botanical affinity: Juglandaceae, based on the botanical affinity given for *Caryapollenites imparalis* sensu stricto in Nichols and Ott (1978).

Paleoecology: Broad climatic and ecological tolerance. The comments here will serve to cover all species of *Caryapollenites* and *Momipites* in this study. *Caryapollenites* and *Momipites* in the Paleocene Wilcox Group are morphologically similar and both represent pollen from the family Juglandaceae. These genera represent ancestors of modern *Carya* and the *Engelhardia* complex (Nichols, 1973; Nichols and Ott, 1978; Frederiksen, 1985). Modern *Carya* (i.e., hickory) trees are extant and widespread in temperate regions of North America and Asia, while extant members of the *Engelhardia* complex live in lowland forests of tropical southeastern Asia. Pollen of this type is common in the Paleocene–Eocene of North America and has been found abundantly in lignite layers as well as clastic marginal marine deposits (Nichols, 1973; Frederiksen, 1985). Akkiraz and others (2008) interpreted the paleoecology of Eocene *Momipites* pollen from Turkey as lowland-riparian. In lower latitudes of the Americas in the Paleogene, *Momipites* may be mainly restricted to montane environments (Ramírez-Arriaga and others, 2014; Smith, 2020), but in more temperate regions the genus appears to have been widely distributed in both coastal and hinterland environments. In the Paleocene of Mississippi and Alabama, Harrington (2008) found *Caryapollenites–Momipites* to be much more common in marginal marine samples than swamp samples, but this pollen type has also been found in high abundances in peat swamp paleoenvironments in the Americas and Europe (Frederiksen, 1985).

Caryapollenites imparalis
Nichols and Ott, 1978

Plate 14, figure 33

Discussion: *Caryapollenites imparalis* is distinguished from other species of *Caryapollenites* by having two subequatorial pores and no region of thinned exine (Nichols and Ott, 2006).

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *C. imparalis* in the Rocky Mountains and Great Plains region is at the base of zone P4 in the Paleocene (Nichols and Ott 1978, 2006). The published ranges for *Momipites–Caryapollenites* spp. in the Rocky Mountains and Great Plains region do not perfectly correspond with observed ranges in the Lower Wilcox.

Caryapollenites inelegans Nichols and Ott, 1978

Plate 14, figure 34

Discussion: *Caryapollenites inelegans* is distinguished from other species of *Caryapollenites* by having three subequatorial pores and lacking a region of thinned exine.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *C. inelegans* in the Rocky Mountains and Great Plains region is at the base of zone P5 in the Paleocene (Nichols and Ott, 1978, 2006).

Caryapollenites prodromus Nichols and Ott, 1978

Plate 14, figure 35

Discussion: *Caryapollenites prodromus* has one subequatorial pore and a circumpolar ring of thinned exine. In *Caryapollenites wodehousei* two pores are located off the equator, and in *Caryapollenites veripites* all three pores are located off the equator (Nichols and Ott, 2006).

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *C. prodromus* in the Rocky Mountains and Great Plains region is in the middle part of Paleocene zone P3 and the last occurrence is in the upper part of Paleocene zone P4 (Nichols and Ott, 1978, 2006).

Caryapollenites veripites (Wilson and Webster, 1946) Nichols and Ott, 1978

Plate 14, figures 37, 38

Discussion: *Caryapollenites veripites* is distinguished by having three subequatorial pores and a circumpolar ring of thinned exine. *Carya viridi-fluminipites* (Wodehouse, 1933; Wilson and Webster, 1946) is somewhat similar, but the illustration of *C. viridi-fluminipites* provided by Wodehouse (1933, fig. 29) shows no evidence of a circumpolar ring of thinned exine, and *C. viridi-fluminipites* is considerably larger (36–39 µm) than *C. veripites*.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *C. veripites* in the Rocky Mountains and Great Plains region is at the base of zone P5 in the Paleocene (Nichols and Ott, 1978, 2006). The first occurrence of *C. veripites* is a primary marker in the Lower Wilcox in the Selandian, zone Paly 4a, nannofossil zone NP5 (Zarra and others, 2019).

Caryapollenites wodehousei
Nichols and Ott, 1978

Plate 14, figure 36

Discussion: *Caryapollenites wodehousei* is distinguished by having two subequatorial pores and a circumpolar ring of thinned exine.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *C. wodehousei* in the Rocky Mountains and Great Plains region is at the base of zone P4 in the Paleocene (Nichols and Ott, 1978, 2006).

Caryapollenites–Momipites spp.

Plate 14, figure 31

Discussion: Pollen identified here as *Caryapollenites–Momipites* spp. has not been speciated in cases where it is not possible to determine the position of the pores due to poor preservation, suboptimal orientation or folding, or obscuring organic material.

Genus *Choanopollenites* Stover in Stover and others, 1966

Discussion: *Choanopollenites* includes triaperturate pollen with a triangular amb, often with concave sides. The apertures may be more circular (pores) or elongate (colpi). Exine stratification is conspicuous and the apertures are compound. The sexine is thicker than the nexine and greatly thickened around the apertures. The sculpture may be psilate, scabrate, or punctate. Arguably some of the species in *Choanopollenites* with elongate apertures could be considered tricolpate or tricolporate, but this study will follow Jardine (2011) and group *Choanopollenites* with triporate genera in the systematic taxonomy.

Choanopollenites aff. *eximius* Stover in Stover and others, 1966

Plate 16, figures 4, 9

Discussion: This rarely observed type is similar to *C. eximius* sensu stricto, but the specimens observed here have diameters between circa 47–58 µm, substantially smaller than the size range given in the original description for *C. eximius* of 71–82 µm (Stover and others, 1966). This type is synonymous with specimens identified as *Choanopollenites* sp. cf. *Choanopollenites eximius* by Jardine (2011).

Botanical affinity: Normapolles complex (Tschudy, 1975).

Stratigraphic comments: *Choanopollenites eximius* sensu stricto was originally described from the Wilcox Group by Stover and others (1966) and has biostratigraphic value, although the true top and bottom occurrences in our sections of *C.* aff. *eximius*, if present, are difficult to ascertain with certainty due to its low abundance in these sections.

Choanopollenites alabamicus (Srivastava, 1972) Frederiksen, 1979

Plate 15, figures 20, 21; Plate 16, figures 1–3

Discussion: *Choanopollenites transitus* was considered a junior synonym of *C. alabamicus* by Frederiksen (1979) and Jardine (2011).

Discussion: Tschudy (1973a) gave a range for *C. transitus* from the Campanian to the Paleocene; Frederiksen (1979) gave a range for *C. alabamicus* from the Danian to the Thanetian.

Botanical affinity: Normapolles complex (Tschudy, 1975).

Genus *Momipites* Wodehouse, 1933 emend. Nichols, 1973

Momipites amplus (Leffingwell, 1970) Nichols, 1973

Plate 14, figure 28

Discussion: *Mompites amplus* is characterized by having convex sides and a circumpolar ring of thinned exine. *Momipites anellus* is similar but smaller; the size range in the original description of *M. anellus* was 18–27 µm and the size range in the original description of *M. amplus* was 29–37 µm (Leffingwell, 1970; Nichols and Ott, 1978). Specimens in the intermediate size range between 27 and 29 µm have also been placed in *Momipites amplus*.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: *Momipites amplus* was originally described from the Paleocene Fort Union Formation in Wyoming; Nichols and Ott (2006) do not provide a more specific stratigraphic range for this species.

Momipites anellus Nichols and Ott, 1978

Plate 14, figures 25–27

Discussion: *Momipites leffingwellii* is distinguished from *M. anellus* by having straight to concave sides of the amb. *Momipites amplus* is similar but larger.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The base of *M. anellus* in the Rocky Mountains and Great Plains region is at the base of zone P3 in the Paleocene (Nichols and Ott, 2006).

Momipites coryloides Wodehouse, 1933 (20–27 μm)

Plate 14, figures 4–7

Discussion: Nichols and Ott (1978) described a species, *Momipites wyomingensis*, which is distinguished from *M. coryloides* only by its smaller size (19–27 μm in diameter in the original description). There is an increase in size of *Momipites* spp. over time in the Wind River Basin, with Paleocene specimens generally smaller than Eocene specimens (but larger than modern *Alfaroa–Engelhardia* pollen), so there is biostratigraphic utility in separating the types based on size (Nichols and Ott, 1978). However, measured specimens of *M. coryloides* from the type locality ranged from 20–35 μm in size (Nichols, 2010). We therefore consider *M. wyomingensis* a junior synonym of *M. coryloides*; similar reasoning was given in Smith (2020). *Momipites coryloides* is here informally split on the basis of size in order to maintain the biostratigraphic utility of separating this pollen type, and the smaller type (<27 μm in diameter) is essentially synonymous with the concept of *M. wyomingensis* proposed by Nichols and Ott (1978). Pollen similar to *M. coryloides* but smaller (<20 μm in diameter) has been identified separately as *Momipites tenuipolus*; although a circular region of thinned exine is present in most specimens of *M. tenuipolus*, it is not always present, so the primary distinction between *M. coryloides* and *M. tenuipolus* is size (Anderson, 1960).

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The smaller variety of *M. coryloides*, formerly known as *M. wyomingensis*, has a lowest occurrence at the base of Paleocene zone P2 in the Rocky Mountains and Great Plains region (Nichols and Ott, 2006). *Momipites coryloides* (20–27 μm) is one of the most common range-through taxa in our samples.

Momipites coryloides Wodehouse, 1933 (>27 μm)

Plate 14, figures 8, 9

Discussion: See above comments for *M. coryloides* (20–27 μm).

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The larger variety of *M. coryloides* has its first appearance in the Eocene of the Rocky Mountains and Great Plains region according to Nichols and Ott (2006). Specimens of *M. coryloides* over 27 μm in diameter were rare but occasionally present in our Lower Wilcox samples. There is likely biostratigraphic utility in changes in the relative abundance of the two types in the onshore Wilcox Group of Texas, but the true stratigraphic base of *M. coryloides* (>27 μm) is well below the Paleocene–Eocene boundary.

Momipites dilatus
(Fairchild in Stover and others, 1966) Nichols, 1973

Plate 14, figures 14–16

Discussion: *Momipites dilatus* is distinguished by its greatly expanded atria. It was sometimes difficult to distinguish between *M. dilatus* and concave specimens of *Momipites waltmanensis*.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The highest occurrence of *M. dilatus* was used by Elsik and Crabaugh (2001) as a marker for the top of the Lower Wilcox. We have placed T *M. dilatus* in the Thanetian, NP7, based on its observed top in Moczygemba VT No. 11.

Momipites inaequalis Anderson, 1960

Plate 14, figure 12

Discussion: *Momipites inaequalis* is typically characterized by having sides of unequal length (Nichols and Ott, 1978), although the original description by Anderson (1960) includes specimens with sides of equal length as well. This study will restrict the circumscription of *M. inaequalis* to pollen with clearly unequal sides. Only one specimen of *M. inaequalis* sensu stricto was observed in these samples; a single specimen of *Momipites* with unequal sides and expanded atria has been identified separately as *Momipites* cf. *inaequalis*.

Botanical affinity: Juglandaceae.

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *M. inaequalis* in the Rocky Mountains and Great Plains region is at or below the base of the Paleocene and the last occurrence is at the top of the Paleocene zone P2 (Nichols and Ott, 1978, 2006).

Momipites cf. *inaequalis* Anderson, 1960

Plate 14, figure 13

Discussion: The single observed specimen of this type is similar to *Momipites inaequalis* sensu stricto in having sides of unequal length, differing in having expanded atria similar to *Momipites dilatus*. Anderson (1960) specifically excluded *Momipites* pollen with protruding or thickened pores from *M. inaequalis*.

Botanical affinity: Juglandaceae.

Paleoecology: Broad climatic and ecological tolerance.

Momipites leffingwellii Nichols and Ott, 1978

Plate 14, figures 29, 30

Discussion: *Momipites leffingwellii* is distinguished from the similar species *M. anellus* by having straight to concave sides of the amb. This species is extremely rare in our samples, and Jardine (2011) did not identify any specimens of *M. leffingwellii* from the Wilcox or Midway Groups in the northern Gulf of America coastal plain.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *M. leffingwellii* in the Rocky Mountains and Great Plains region is at or below the base of the Paleocene and the last occurrence is in the Paleocene zone P3 (Nichols and Ott, 1978, 2006).

Momipites rotundus
(Leffingwell, 1970) Nichols, 1973 sensu lato

Plate 14, figures 17–20

Discussion: *Momipites rotundus* is differentiated from most other species of *Momipites* by having three circular areas of thinned exine and a convex triangular amb. Nichols and Ott (1978) described a similar species, *Momipites ventifluminis*, which differs from *M. rotundus* only on the basis of size; *M. rotundus* was originally described as having a diameter of 24 to 34 µm (Leffingwell, 1970) and *M. ventifluminis* was described as having a diameter of 21 to 27 µm, with a modal diameter of 24.5 µm. Clearly there is a substantial overlap in the size ranges of the two species. One approach to this problem would be to restrict *M. ventifluminis* to specimens smaller than the size range given for *M. rotundus*. However, this would exclude specimens with the modal size given for *M. ventifluminis* from *M. ventifluminis*. We therefore consider *M. ventifluminis* as originally described, a junior synonym of *M. rotundus*, and we use a broad species concept for *M. rotundus* which includes pollen with a diameter less than 27 µm. If it is considered useful in future studies to separate the morphotypes on size, *M. rotundus* could be split informally, two subspecies of *M. rotundus* could be separated, or the two species could be formally emended to remove the overlap in size ranges. In these samples, only two specimens of *M. rotundus* larger than 27 µm were observed (e.g., Plate 14, fig. 20), so the larger morphotype has not been identified separately. *Maceopolipollenites granulatus* (Simpson, 1961; Elsik and Crabaugh, 2001) is also similar to *M. rotundus*; Simpson (1961) described *M. granulatus* (syn. *Engelhardtia granulata*) as having large granules and a dark triradiate mark which broadens towards the equator between the three circular areas of thinned exine. Leffingwell (1970) gave a somewhat different description for his specimens of *M. granulatus*, describing *M. granulatus* as possessing crescent-shaped rather than circular areas of thinned exine. Some specimens identified here as *M. rotundus* have somewhat crescent-shaped areas of thinned exine, but there appears to be a continuous range of morphological variation, even within individual pollen grains (e.g., Plate 14, fig. 19). This taxonomic uncertainty is unfortunate because Crabaugh and Elsik (2000) used the last appearance of *M. granulatus* as a marker event for the Big Shale in the Wilcox subsurface (Thanetian age). Jardine (2011) did not identify any specimens of *M. granulatus* in his Wilcox Group samples.

Botanical affinity: Juglandaceae.

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *M. ventifluminis* in the Rocky Mountains and Great Plains region is in the Paleocene zone P3 (Nichols and Ott, 1978, 2006).

Momipites tenuipolus Anderson, 1960

Plate 14, figures 1–3

Discussion: *Momipites tenuipolus* is distinguished by its small size (14–20 µm) and usually by possessing a circular to irregularly shaped area of thinned exine. Anderson (1960) stated that most but not all specimens of *M. tenuipolus* have an area of thinned exine. *Momipites anellus* also has an area of thinned exine, but this area is a circular ring around a central island of normally thickened exine (Nichols and Ott, 1978). There is some overlap with the size range given for *Momipites wyomingensis* (19–27 µm), which we have named as *M. coryloides* (20–27 µm); we restrict *M. coryloides* to pollen grains greater than 20 µm in diameter. If considered useful in future studies, *Momipites tenuipolus* could be separated into forms with a circular area of thinned exine and forms lacking a clear circular area of thinned exine, either by formal emendation of *M. tenuipolus*, the creation of two subspecies of *M. tenuipolus*, or the use of informal nomenclature.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Momipites triorbicularis
(Leffingwell, 1970) Nichols, 1973

Plate 14, figures 21, 22

Discussion: *Momipites triorbicularis* is distinguished by having a triangular to concavely triangular amb and three round spots of thinned exine on one pole.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *M. triorbicularis* in the Rocky Mountains and Great Plains region is in the upper part of the Paleocene zone P3 and the last occurrence is in the middle part of the Paleocene zone P5 (Nichols and Ott, 2006).

Momipites triradiatus type
sensu Jardine (2011)

Plate 14, figures 23, 24

Discussion: This type of *Momipites* is characterized by triradiate thickenings or folds; three thinned spots of exine may also be present on one or both hemispheres. Jardine (2011) provides more discussion on the morphology and taxonomy of this group. *Momipites actinus* is somewhat similar, but *M. actinus* lacks triradiate thickenings; instead, the exine in *M. actinus* is thinned into a triradiate shape with rays pointed towards the interporal areas, somewhat resembling a trilete mark. No specimens of *M. actinus* have been observed.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Momipites waltmanensis
Nichols and Ott, 1978

Plate 14, figures 10, 11

Discussion: *Momipites waltmanensis* is distinguished from most other *Momipites* species by having straight to concave sides of the amb and by lacking polar modification. *Momipites strictus* is arguably in part synonymous with *M. waltmanensis*. The original description for *M. strictus* by Frederiksen and Christopher (1978) includes specimens with straight to slightly convex sides, while the original description for *M. waltmanensis* by Nichols and Ott (1978) includes specimens with straight to concave sides. Other characteristics described by Frederiksen and Christopher (1978) for *M. strictus*, including the presence of an annulus and thinned areas of exine, are described as present in most but not all specimens. Jardine (2011) stated that *M. strictus* is distinguished from *M. waltmanensis* by having straight sides of the amb, but *M. waltmanensis* as originally described also includes pollen grains with straight sides. If straight-sided pollen of this type is restricted to *M. strictus*, many specimens identified here as *M. waltmanensis* would be transferred to *M. strictus*. Jardine (2011) considered *Momipites flexus* (Frederiksen, 1979) a junior synonym of *M. waltmanensis*.

Botanical affinity: Juglandaceae (Nichols and Ott, 1978).

Paleoecology: Broad climatic and ecological tolerance.

Stratigraphic comments: The first occurrence of *M. waltmanensis* in the Rocky Mountains and Great Plains region is at the base of the Paleocene zone P2 (Nichols and Ott, 2006).

Genus *Nudopollis* Pflug in Thomson and Pflug, 1953

Nudopollis aff. *endangulatus* (Pflug in Thomson and Pflug, 1953) Pflug, 1953

Plate 15, figure 13

Discussion: The single observed specimen of this type is similar to a pollen grain identified by Elsik (1968b, Plate 36, fig. 8) as *Nudopollis thiergartii*; Frederiksen (1979, p. 155) considered that grain to be a transitional form between *N. thiergartii* and *N. endangulatus*. *Nudopollis thiergartii* and *N. endangulatus* are distinguished by the shape of the inner contour, which is circular in *N. thiergartii* and triangular in *N. endangulatus*. *Nudopollis terminalis* is distinguished from *N. endangulatus* by having a convex rather than straight-sided or concave amb (Jardine, 2011). The single observed specimen in our samples has a convexly subtriangular inner contour which approaches a circular shape and closely resembles *N. endangulatus* sensu stricto. However, in the original description for *N. endangulatus* translated by Jansonius and Hills (1976, card 1783), the exine was described as chagrinate, but our observed specimen is finely and evenly granulate.

Botanical affinity: Normapolles complex (Tschudy, 1975).

Stratigraphic comments: Frederiksen (1979) tentatively gave the range of *N. endangulatus* in the Gulf Coast as from the Midwayan to lower Sabinian provincial stages, equivalent to the Paleocene and possibly lower Eocene (Dockery, 1996).

Nudopollis terminalis (Pflug and Thomson in Thomson and Pflug, 1953) Pflug, 1953

Plate 15, figures 9–12

Discussion: *Nudopollis thiergartii* is similar but is distinguished by having a circular rather than triangular inner contour (Jardine, 2011).

Botanical affinity: Normapolles complex (Tschudy, 1975).

Genus *Pistillipollenites* Rouse, 1962

Pistillipollenites mcgregorii Rouse, 1962

Plate 16, figures 10–12

Discussion: Although the pores in this triporate species are often difficult to observe, the gemmate sculpture is distinctive.

Botanical affinity: Probably Gentianaceae, possibly *Macrocarpaea* (Taylor, 1988). Rouse (1962) also noted the similarity of *P. mcgregorii* and pollen produced by *Rusbyanthus*, a genus which was later subsumed into *Macrocarpaea* by Weaver (1974).

Paleoecology: If the botanical affinity is with *Macrocarpaea*, possibly montane tropical forest, based on the modern distribution of the genus in the Neotropics (Vieu and others, 2022).

Stratigraphic comments: The base and top of *P. mcgregorii* are both important markers in the deepwater Wilcox Group (Zarra and others, 2019).

Genus *Plicapollis* Pflug, 1953 emend. Tschudy, 1975

Plicapollis vacuus Tschudy, 1975

Plate 15, figures 14, 15, 17

Discussion: *Plicapollis vacuus* is distinguished from *Plicapollis usitatus* and *Plicapollis retusus* by the virtual absence of aggregates of bacula in the exogerminal, thinner walls, and generally smaller size; *Plicapollis rusticus* has prominent verrucate sculpture (Tschudy, 1975).

Botanical affinity: Normapolles group.

Stratigraphic comments: The three observed specimens of *Plicapollis vacuus* in this study are interpreted as reworked from Cretaceous sediments; Tschudy (1975) gave the stratigraphic distribution of *P. vacuus* as in the Coffee Sand and McNairy Sand Member of the Cretaceous Ripley Formation.

Genus *Pseudoplicapollis* Krutzsch in Góczán and others, 1967

Pseudoplicapollis limitata Frederiksen, 1978

Plate 15, figure 16

Discussion: *Pseudoplicapollis limitata* is a triporate pollen species distinguished by distinct, narrow plicae with rounded ends (Frederiksen, 1978; Jardine, 2011). Only a single specimen was observed in our samples. Frederiksen (1978) considered *Pseudoplicapollis* sp. A in Tschudy (1975) synonymous with *P. limitata*.

Botanical affinity: Normapolles complex (Tschudy, 1975).

Stratigraphic comments: Frederiksen (1978) gave the range of *P. limitata* on the eastern Gulf of America coastal plain as from the Nanafalia Formation to the Wilcox Group, equivalent to nannofossil zones NP6–NP11 according to Dockery (1996).

Genus *Thomsonipollis* Krutzsch, 1960 emend. Elsik, 1968b

Discussion: Elsik (1968b) provides a detailed description of *Thomsonipollis*. There is an invaginate nexinous swelling around the apertures, forming a distinct ring; this is the single most distinctive and important diagnostic character. The number of apertures varies from one to nine according to Elsik (1968b). The type species *Thomsonipollis magnificus* is usually triporate, although the original description by Elsik (1968b) does not specify the number of pores. The ornamentation is also variable, including tectate-psilate and intectate-granulate morphologies. *Thomsonipollis* may be a member of the Normapolles group, which became extinct around the end of the Eocene (Jansonius and Hills, 1976; Friis, 1983).

Thomsonipollis magnificus (Pflug and Thomson, 1953 from Krutzsch, 1960) emend. Elsik, 1968b

Plate 16, figures 5–8

Discussion: *Thomsonipollis magnificus* is distinguished from *Thomsonipollis sabinetownensis* by having baculate rather than psilate or scabrate surface ornamentation. This study will follow Jardine (2011) and group together specimens referable to *Thomsonipollis magnificoides* (Krutzsch, 1960) with *T. magnificus*. Nearly all specimens of *T. magnificus* in this study are triporate with equatorial pores, but rarely specimens with more than three pores or subequatorial pores were observed. Very rarely, a triangular feature described by Elsik (1968b) as a fold, but which arguably represents an area of thinned exine, is developed.

Botanical affinity: Possibly Rubiaceae (Elsik, 1968b).

Paleoecology: Lenz and others (2021) interpreted *T. magnificus* as a component of mangrove paleoenvironments in the Eocene of Germany.

Stratigraphic comments: Changes in the relative abundance of *T. magnificus*, including the highest common occurrence in the Ypresian, are used as biostratigraphic markers for the deepwater Wilcox in Zarra and others (2019). The first appearance of *T. magnificus* in Texas may be in the Maastrichtian (Kumar, 2019).

Genus *Trivestibulopollenites* Pflug in Thomson and Pflug, 1953

Trivestibulopollenites spp.

Plate 15, figure 8

Discussion: Jardine (2011) provides discussion on this pollen type, which is distinguished from the Betulaceae–Myricaceae type by being vestibulate. *Alnus verus* is distinguished by possessing arci and commonly having more than three pores. This type was very rare in our samples, although it was sometimes difficult to determine with certainty whether some similar pollen grains were vestibulate. Only pollen with clearly visible vestibula were identified as *Trivestibulopollenites*; morphologically similar types lacking clearly visible vestibula have been grouped with the Betulaceae–Myricaceae type.

Botanical affinity: Probably Betulaceae, possibly *Betula*. Modern *Betula* pollen is vestibulate and triporate (Blackmore and others, 2003).

Genus *Trudopollis* Pflug, 1953

Trudopollis plenus Tschudy, 1975

Plate 15, figures 18, 19

Discussion: Jardine (2011) provides detailed comments about this genus and species. Four specimens of *T. plenus* were observed in our samples.

Botanical affinity: Normapolles complex (Tschudy, 1975).

Stratigraphic comments: Tschudy (1975) gave a restricted upper Paleocene range for *T. plenus* in the Mississippi Embayment (Naborton and Naheola Formations). Frederiksen (1991) observed the base of *T. plenus* in the Danian in South Carolina. The biostratigraphic value of *T. plenus* appears to be limited in the onshore Wilcox Group of Texas due to the rarity of the species.

Genus *Tschudypollis* Nichols, 2002

Discussion: Nichols (2002) erected a new genus, *Tschudypollis*, to accommodate some reticulate, triporate pollen types previously considered to have an affinity with the Proteaceae and assigned to the form genus *Proteacidites*.

Tschudypollis retusus (Anderson, 1960) Nichols, 2002 sensu lato

Plate 16, figures 14, 15

Discussion: *Tschudypollis retusus* is distinguished by its triporate morphology, small size, and heterobrochate reticulum, with the reticulum coarser near the equator. *Tschudypollis retusus* is similar to *Tschudypollis thalmannii*, also identified in the literature as *Proteacidites thalmannii* and *Symplocos*? *thalmannii* (e.g., Anderson, 1960; Frederiksen, 1980b; Jardine, 2011). Anderson (1960) originally described both species but did not clearly state how *T. retusus* and *T. thalmannii* are distinguished; *T. retusus* was described as finely reticulate and *T. thalmannii* was described as coarsely reticulate. Also, *T. retusus* was described as having small, circular pores and *T. thalmannii* was described as having circular or lolongate pores. Later authors appear to consider the lolongate pores in *T. thalmannii* as short colpi and use the presence of short colpi as the primary feature distinguishing *T. thalmannii* from *T. retusus*; Martin and Harris (1974), for example, excluded *T. thalmannii* from *Proteacidites* based on the species having short colpi and Frederiksen (1980b) transferred the species to *Symplocos* questionably as *Symplocos*? *thalmannii* also based on the presence of short colpi. Nichols (2002) restricted his genus *Tschudypollis* to triporate forms but included pollen identified by Anderson (1960) as *Proteacidites thalmannii* in *Tschudypollis*. Arguably, if *P. thalmaniii* is brevitricolporate or simply brevitricolpate it cannot be accommodated in *Tschudypollis*. In the original description of *P. retusus*, the pollen are described as finely and irregularly reticulate with lumina diameter circa 0.5 µm. The reticula in the pollen identified as *T. retusus* here are morphologically variable but generally have some lumina >1 µm, with the reticulum usually becoming coarser in the mesoporia. In this study, we have restricted the use of *P. thalmannii* to clearly tricolporate forms (which were not observed) and broadened the circumscription of *T. retusus* to include more coarsely reticulate forms.

Botanical affinity: Possibly Proteaceae (Stanley, 1965); alternatively, *Symplocos* (Frederiksen, 1980b).

Stratigraphic comments: *Tschudypollis retusus* sensu stricto is indicative of a Coniacian-Maastrichtian age (Nichols and others, 1982, 1985; Kumar, 1992) and *T. retusus* pollen may be reworked here. Alternatively, the pollen identified here as *T. retusus* may represent a morphotype identified by other researchers as *Symplocos*? *thalmannii* and be in situ. Frederiksen (1980b) observed *S. thalmannii* in Middle Eocene to Lower Oligocene strata from the northern Gulf of America coastal plain and expressed uncertainty as to whether they were reworked from Cretaceous strata. Because of the uncertainty regarding its stratigraphic range, *Tschudypollis retusus* has not been marked as reworked in the counts.

5.12. Stephanoporate angiosperm pollen

Genus *Alnus* Miller, 1754

Alnus scotica Simpson, 1961

Plate 17, figure 4

Discussion: This species of *Alnus* is distinguished by possessing a ring of thickened exine on one hemisphere (Pocknall and Nichols, 1996; Jardine, 2011). Only one specimen was observed in our samples.

Botanical affinity: *Alnus* (Betulaceae). Pocknall and Nichols (1996) noted that three extant species of *Alnus* native to Japan also possess a ring of thickened exine on one hemisphere.

Paleoecology: Lowland-riparian or upland, temperate to tropical (see comments for *Alnus verus*).

Stratigraphic comments: Jardine (2011) noted the presence of *A. scotica* in the Paleocene and Eocene along the northeastern Gulf of America coastal region. Pocknall and Nichols (1996) also noted the rare presence of *A. scotica* (syn. *Alnipollenites scoticus*) in the Paleocene "*Caryapollenites* Assemblage Zone" in the Fort Union Formation of Montana and Wyoming.

Alnus verus (Potonié, 1931)
Martin and Rouse, 1966 sensu lato

Plate 17, figures 1–3

Discussion: See Smith (2020) for discussion of the taxonomy of *A. verus*. A broad species concept is used here following Jardine (2011) which allows for substantial variation in pore number; the specimens observed in this study have between four to six pores.

Botanical affinity: *Alnus* (Betulaceae).

Paleoecology: Lenz and others (2021) considered that Eocene *Alnus* pollen from Germany may represent temporarily inundated freshwater wetland habitats. Akkiraz and others (2008) interpreted the paleoecology of Eocene *Alnus* pollen from Turkey as microthermal and lowland-riparian. Ramírez-Arriaga and others (2014) interpreted the paleoecology of Eocene-Oligocene *Alnus* pollen from central Mexico as cloud forest (i.e., tropical montane forest).

Stratigraphic comments: Increased abundances of *Alnipollenites* (i.e., *Alnus*) spp. were used by Zarra and others (2019) as an indicator for their Paly Zone 3 in the Selandian. They also found some utility in separating specimens with seven and eight pores in the Wilcox; only a single specimen with more than six pores was observed in these Lower Wilcox samples, so specimens with more than six pores have not been identified separately in this study.

Genus *Juglans* Linnaeus, 1753

Juglans nigripites Wodehouse, 1933

Plate 17, figure 8

Discussion: This study will follow Nichols (2010) and Jardine (2011) and assign pollen similar to extant *Juglans* that is polyporate-heteroporal with over 9 pores to the modern genus rather than the form genus *Juglanspollenites*. Arguably polyporate-heteropolar pollen is not fully stephanoporate (i.e., with only equatorial pores), but this study will follow Jardine (2011) and group *J. nigripites* with stephanoporate pollen.

Botanical affinity: *Juglans* (Juglandaceae).

Paleoecology: Probably moist temperate upland forest. Ramírez-Arriaga and others (2014) considered *Juglanspollenites* pollen (with probable botanical affinity with *Juglans* sensu stricto) from the Eocene to Oligocene of Mexico represented a cloud forest paleoecology. Graham (1998) also interpreted the paleoecology of Miocene-Pliocene *Juglans* pollen from Guatemala as cloud forest.

Stratigraphic comments: The earliest previously recorded occurrence of *J. nigripites* in the Gulf of America that we are aware of was in the Eocene Tallahatta Formation (Jardine, 2011). The single specimen observed in the Edmond Olinick No. 1 ditch cutting samples may be caved from upsection.

Genus *Malvacipollis* Harris, 1965

Malvacipollis spp. (Euphorbiaceae type)

Plate 17, figures 9, 10

Discussion: Pores in these pollen grains are often obscure and some may be subequatorial. Smith (2020) provides more information on this pollen type. Jardine (2011) observed broadly similar stephanoporate, echinate pollen and identified them as *Compositoipollenites* based on the presence of larger, more "thorn-like" echinae. We respectfully disagree with this identification and consider *Malvacipollis* a more suitable form genus. The original description of *Compositoipollenites* translated by Jansonius and Hills (1976, card 542) includes only triporate or tricolporate pollen (the colpi were described as questionably present), and the pollen observed by Jardine (2011) has either four or six pores and no observable colpi. The size and shape of the echinae in the genus description for *Malvacipollis* is not described and therefore the morphology of the echinae cannot be used as a criterion to differentiate *Malvacipollis* and *Compositoipollenites* without formal emendation. The pollen form genus name *Malvacipollis* is somewhat misleading, as it includes species with botanical affinity to the Euphorbiaceae as well as species with affinity to the Malvaceae sensu lato (e.g., Frederiksen and others, 1983; Smith, 2020). The name *Compositoipollenites* is similarly misleading if used for pollen types not referable to the Asteraceae (i.e., Compositae), even if the pollen species falls under the morphological umbrella of *Compositoipollenites*; for example, *Compositoipollenites grandiannulatus*, which Frederiksen and others (1983) suggested may have an affinity with the Sterculioideae in the family Malvaceae sensu lato. The *Malvacipollis* spp. observed in our samples have spines which are a simple extension of an outer homogenous exine layer, similar to some modern Euphorbiaceae pollen, rather than spines with thickened exine underneath and columellae extending into the base of the spines, similar to some modern Sterculioideae in Malvaceae sensu lato (Martin, 1974; Frederiksen and others, 1983; Smith, 2020). It is not clear to us whether the morphology of the spines in Jardine's (2011) specimens corresponds to the Euphorbiaceae or Malvaceae type.

Botanical affinity: Euphorbiaceae (Smith, 2020).

Paleoecology: Probably lowland tropical forest (Smith, 2020).

Genus *Ulmipollenites* Wolff 1934

Ulmipollenites krempii (Anderson, 1960) Frederiksen, 1979 emend. Smith, 2020

Plate 17, figures 5–7

Discussion: See Smith (2020) for a detailed discussion of this species. Specimens in this study generally had four or five, and rarely three, equatorial pores. Anderson (1960) described a species, *Ulmipollenites, tricostatus*, which was distinguished from triporate specimens of *U. krempii* by having a more triangular outline and more distinct "beaded" arci; we consider *U. tricostatus* a synonym in part of *U. krempii* as emended by Smith and others (2020b).

Botanical affinity: Ulmaceae (Pocknall and Nichols, 1996; Jardine, 2011; Smith, 2020).

Paleoecology: Probably moist lowland-riparian forest (Akkiraz and others, 2008), although in south-central Mexico, Eocene-Oligocene occurrences of *Ulmipollenites krempii* have been interpreted as indicators of montane tropical forest (Ramírez-Arriaga and others, 2014). The high relative abundance of *U. krempii* in some samples suggests a more proximal, lowland source in the Wilcox Group.

5.13. Pantoporate angiosperm pollen

Genus *Chenopodipollis*
Krutzsch, 1966

Discussion: Although the original description of *Chenopodipollis* restricted the genus to spherical, pantoporate, punctate pollen grains, in practice pollen grains with a non-punctate sculpture (at least in light microscopy) and botanical affinity with the Amaranthaceae have also been included in *Chenopodipollis* (e.g., Nichols and Brown, 1992; Ramírez-Arriaga and others, 2014). Smith (2020) described specimens of *Chenopodipollis* which appear psilate to scabrate in light microscopy but are micro-granulate, micro-echinate, and micro-punctate in scanning electron microscopy.

Chenopodipollis spp.

Plate 17, figures 11–13

Discussion: These specimens are generally referable to the form genus *Chenopodipollis* and generally have a botanical affinity with the Amaranthaceae. This form genus is often not identified to the species level in the Paleogene of North America (e.g., Frederiksen, 1980; Nichols and Brown, 1992; Nichols, 2002; Jardine, 2011). The surface sculpture ranges from scabrate to punctate. The *Chenopodipollis* pollen in our samples and in other Paleogene studies in the southeastern United States generally have pores which are both fewer in number and distributed more irregularly (e.g., Elsik, 1968a, Plate 15, figs. 9–12; Gregory and Hart, 1995b, Plate 10, fig. 5; Jardine, 2011, Plate 5, fig. 30) than typical modern Amaranthaceae pollen (e.g., Angelini and others, 2014; El Ghazali, 2021).

Botanical affinity: Probably Amaranthaceae, based on previous interpretations of the botanical affinity of *Chenopodipollis* spp. in the Wilcox Group. The morphologies do appear to depart somewhat from typical modern Amaranthaceae pollen in having fewer and more irregularly distributed pores. Somewhat similar pantoporate pollen is also produced by the Caryophyllaceae, which are grouped with the Amaranthaceae in the order Caryophyllales (e.g., Jordan and Macphail, 2003).

Paleoecology: Possibly coastal marsh or coastal arid scrub (Smith, 2020).

Genus *Erdtmanipollis* Krutzsch, 1962

Erdtmanipollis pachysandroides
Krutzsch, 1962 sensu lato

Plate 17, figure 14

Discussion: The crotonoid reticulum of this pantoporate pollen type is quite distinctive. *Erdtmanipollis pachysandroides*, the type species of the genus, was described as circa 25–35 µm in diameter. A similar species, *Pachysandra cretacea*, was distinguished by Stanley (1965) from *E. pachysandroides* only on the basis of a wider size range, 20–40 µm in diameter rather than 25–35 µm in diameter. *Pachysandra cretacea* is here considered a junior synonym of *E. pachysandroides*. The single specimen observed in this study has a diameter between 35–40 µm depending on the direction of measurement (although probably originally spherical, the shape has likely been altered taphonomically). A broad species definition is used here for *E. pachysandroides* to include specimens slightly larger and smaller than the original size range given.

Botanical affinity: Probably Buxaceae; pollen of the extant genus *Pachysandra* is quite similar to *E. pachysandroides* (e.g., Hesse and others, 2009, p. 166), hence the species name.

Stratigraphic comments: *Pachysandra*-type pollen ranges from the Upper Cretaceous to recent (Srivastava, 1969).

Thymelaeaceae? sp. A

Plate 17, figure 15

Discussion: The observed specimens of this type are spherical and hollow, with reticulate surface ornamentation. The lumina are mostly circa 1–2 µm in diameter, but some scattered lumina, which may be pores, are significantly larger, circa 3–4 µm in diameter. They closely resemble specimens identified by Elsik (1968b, Plate 15, fig. 14) as "Thymelaeaceae?" Modern pollen from the family Thymelaeaceae is generally pantoporate and often, but not always, crotonoid (Herber, 2002); the specimens in this study are not crotonoid.

Botanical affinity: Possibly Thymelaeaceae (Elsik, 1968b).

Genus *Wodehouseia* Stanley, 1961

Discussion: This genus has been grouped together with the pantoporate (i.e., periporate) pollen types following Jardine (2011), although some species have apertures that are better described as colpi (Wiggins, 1976).

Wodehouseia spinata Stanley, 1961

Plate 17, figure 16

Discussion: Detailed information about the morphology of *W. spinata* is provided in Tekleva and others (2019).

Botanical affinity: Eudicots, lower affinity unknown (Tekleva and others, 2019).

Stratigraphic comments: The top of *Wodehouseia spinata* is at the K/Pg boundary in the Western Interior of the United States and in the early Paleocene, zone P1, in Canada (Bercovici and others, 2012). The two specimens observed in these Lower Wilcox samples are probably reworked from Cretaceous strata.

5.14. Triprojectate angiosperm pollen

Genus *Aquilapollenites* Rouse, 1957

Aquilapollenites spinulosus Funkhouser, 1961

Plate 18, figure 4

Discussion: The single observed specimen of *A. spinulosus* in our samples is poorly preserved and partially obscured by organic matter. *Aquil-*

apollenites attenuatus is similar but distinguished by being punctate, having shorter equatorial protrusions, and having echinae grouped into definite areas (Funkhouser, 1961).

Botanical affinity: Probably Angiospermae. Jarzen (1977) speculated that the botanical affinity of *Aquilapollenites* may lie within the order Santalales.

Stratigraphic comments: Pocknall (1987) placed the top of *A. spinulosus* in his *Pistillipollenites mcgregorii* zone, above the base of *P. mcgregorii*. If the chronology of events is similar in the Lower Wilcox, the top of *A. spinulosus* is above the base of *P. mcgregorii* in the late Selandian or Thanetian. Fairchild and Elsik (1969, p. 84) stated that *Aquilapollenites* spp. in the Paleogene Gulf Coast are "…reworked from the Upper Cretaceous into the Lower Tertiary, but occur consistently in the Midway and Lower Wilcox." The biostratigraphic utility of this species and *Aquilapollenites* spp. in general in these sections is limited due to its rarity.

Aquilapollenites aff.
attenuatus Funkhouser, 1961

Plate 18, figures 1, 2

Discussion: This type resembles *Aquilapollenites attenuatus* sensu stricto in being isopolar tridemicolpate and having a punctate to micro-reticulate surface with spinules. However, *A. attenuatus* sensu stricto has spinules which are clearly grouped into definite areas of the grain, while our specimens have spinules which are less clearly organized. *Aquilapollenites spinulosus* (Funkhouser, 1961) is similar but is neither punctate nor micro-reticulate. *Integricorpus reticulatus* (Mtchedlishvili, 1965; Stanley, 1970) is strioreticulate.

Botanical affinity: Probably Angiospermae. Jarzen (1977) speculated that the botanical affinity of *Aquilapollenites* may lie within the order Santalales.

Genus *Integricorpus*
Mtchedlishvili and others, 1961

Integricorpus reticulatus
(Mtchedlishvili, 1965) Stanley, 1970

Plate 18, figure 3

Discussion: Tschudy and Leopold (1970) considered that the similar species *Aquilapollenites reticulatus* (Stanley, 1961) is a junior synonym of *I. reticulatus*. The specimens in this study, although somewhat poorly preserved, compare favorably with SEM images of *I. reticulatus* provided by Farabee and Skvarla (1988, Plate 1, figs. 1–4). *Aquilapollenites mchedlishvilii* may also be a junior synonym of *I. reticulatus* (Hofmann and Zetter, 2007). *Aquilapollenites* aff. *attenuatus* and *A. spinulosus* are distinguished most obviously by being echinate.

Botanical affinity: Probably Angiospermae. Jarzen (1977) speculated that the botanical affinity of *Aquilapollenites* may lie within the order Santalales.

Stratigraphic comments: *Integricorpus reticulatus* survived the K/Pg extinction event and is found in the Paleocene of North America (Nichols and Brown, 2002).

5.15. Jugate angiosperm pollen

Genus *Ericipites* Wodehouse, 1933

Ericipites spp.

Plate 18, figure 5

Discussion: This study will follow Pocknall and Nichols (1996) and Jardine (2011) and not attempt to identify these grains to species level. The individual grains in the tetrahedral tetrads are psilate or scabrate and tricolporate, although the pores and particularly the colpi are often difficult to observe.

Botanical affinity: Probably Ericaceae (Pocknall and Nichols, 1996; Jardine, 2011).

Paleoecology: Modern Ericaceae plants are common and diverse in montane zones as well as heathlands and mainly prefer acidic soil (Stevens and others, 2004).

5.16. Fungi

Genus *Callimothallus* Dilcher, 1965 from Jansonius and Hills, 1977

Callimothallus spp.

Plate 20, figures 4, 5

Discussion: *Callimothallus* is distinguished from other fossil ascocarp form genera by having a radiate body and porate cells (Saxena and Tripathi, 2011). In many specimens only a few cells are porate, and some fragmentary specimens identified as *Phragmothyrites* may actually be specimens of *Callimothallus*. In this study, if any of the cells in a microthyriaceous fungal body are porate, the specimen has been identified as *Callimothallus* spp.

Biological affinity: Microthyriales (Saxena and Tripathi, 2011).

Genus *Dicellaesporites* Elsik, 1968

Dicellaesporites spp.

Plate 18, figures 16, 17;
Plate 19, figures 1–3

Discussion: This type includes inaperturate, psilate to scabrate, uniseptate fungal spores with two cells. *Fusiformisporites* also includes dicellate fungal spores but is limited to forms with striate or other longitudinal features. A variety of morphological types have been observed which have not been split due to their rarity. Most specimens have cells which are symmetrical to each other and evenly tapering towards the ends of the grain.

Biological affinity: Probably phylum Ascomycota, lower affinity unknown. The majority of fungal spores found in palynological preparations are produced by the Ascomycota; other groups of fungi like the Basidiomycota generally produce very small spores (Kalkutgar and Jansonius, 2000). If a lower affinity for fungal spore types in this study is unknown it is provisionally referred to the Ascomycota.

Genus *Dicellaeporisporites* Kalkutgar, 1997

Dicellaeporisporites sp. A

Plate 19, figure 7

Discussion: This fungal spore type is psilate, elliptical, and divided equally into two halves with a pore at the end of each cell, placed symmetrically at the long axes of the ellipse. Only one specimen of this type has been observed in our samples. *Dicellaeporisporites poratus* (Kalkutgar, 1997) and *Dicellaeporisporites siglerae* (Kalkutgar, 1997; Kalkutgar and Jansonius, 2000) have a constriction at the septum in the middle of the spore. *Dicellaeporisporites delitschiapites* (Kalkutgar and Sigler, 1995; Kalkutgar, 1997) has lateral germinal slits rather than pores.

Biological affinity: Probably Ascomycota.

Genus *Diporisporites* van der Hammen, 1954 emend. Elsik, 1968a

Discussion: This genus includes unicellate fungal spores with two pores on opposite ends of the grains.

Diporisporites hammenii Elsik, 1968

Plate 18, figures 14, 15

Discussion: Elsik (1968a) originally described *D. hammenii* from the Paleocene of Texas and gave the size range for the long axis as 11–14 µm. The single observed specimen in this study is slightly larger (ca. 15 µm long) but otherwise similar to *D. hammenii* sensu stricto.

Biological affinity: Probably Ascomycota.

Diporisporites sp. A

Plate 18, figure 11

Discussion: The single observed specimen of this type is circular in outline and psilate, with two circular pores at the center of the spore on opposite sides. *Diporisporites hammenii* is much smaller and fusiform (Elsik, 1968a).

Biological affinity: Probably Ascomycota.

Diporisporites sp. B

Plate 18, figure 12

Discussion: The single observed specimen of this type is asymmetrically fusiform in shape, with two pores on each end of the long axis of the spore. One pore is smaller and more clearly defined than the other and the long axis of the spore is circa 35 µm in diameter.

Biological affinity: Probably Ascomycota.

Fungal hyphae

Plate 20, figures 6, 7

Discussion: A variety of fungal hyphae were observed in the assemblage. No apparent biostratigraphic or paleoecological value was found in subdividing the morphologies, but a more detailed morphometric and statistical analysis of fungal hyphae in these samples may be the subject of future research.

Biological affinity: Fungi, lower affinities unknown, various.

Fusiformisporites Rouse, 1962

Fusiformisporites crabbii Elsik, 1968

Plate 19, figures 4–6

Discussion: As emended by Elsik (1968a), *Fusiformisporites* includes inaperturate, dicellate fungal spores with elongate striae, ribs, ridges, or costae oriented parallel to the long axis of the spore. The inner surface of the cell wall is psilate to punctate or scabrate and there is a two-layered equatorial septum. The type species of *Fusiformisporites*, *Fusiformisporites crabbii*, was originally described by Rouse (1962); our specimens are essentially morphologically indistinguishable. A similar species, *Fusiformisporites pseudocrabbii*, was originally described by Elsik (1968a) from the Wilcox Group. *Fusiformisporites pseudocrabbii* appears to be distinguished from *F. crabbii* primarily by having rows of punctae parallel to the longitudinal ribs of the spore; *F. pseudocrabbii* was not observed in our samples.

Biological affinity: Shumilovskikh and others (2017) provided strong arguments for the affinity of *F. crabbii* with the extant fungal species *Megalohypha aqua-dulces*.

Paleoecology: The morphologically similar *Megalohypha aqua-dulces* was originally identified from submerged wood in tropical forest streams in Panama and Thailand (Ferrer and others, 2007) and is considered as a paleoclimatic indicator for warm, humid conditions and decaying, submerged wood, although the possibility exists that *M. aqua-dulces* may also live in marine environments (Shumilovskikh and others, 2017).

Genus *Inapertisporites* van der Hammen, 1954

Discussion: The genus *Inapertisporites* originally included all fungal spores without an aperture. Elsik (1968a) emended *Inapertisporites* and restricted the genus to inaperturate, psilate fungal spores with one cell and no septae. Saxena and others (2021) discuss emendations of *Inapertisporites* by various authors, some of whom restrict *Inapertisporites* to psilate forms and others who include spores with a variety of surface sculpture. Pending a more comprehensive revision of the taxonomy of the Amerosporae, the summary diagnosis of *Inapertisporites* by Saxena and others (2021, p. 842) will be used: "Inaperturate, shape and size variable, spore wall psilate to variously ornamented."

Inapertisporites spp.

Plate 18, figures 6, 7

Discussion: This fungal spore type includes inaperturate, nonseptate, unicellate spores. All specimens of *Inapertisporites* observed in our samples were psilate, and the vast majority were small, thin-walled, and approximately spherical. More elliptical forms were rare, and non-psilate forms referable to *Inapertisporites* were not observed. Fungal spore clusters identified as *Microsporonites* in this study are morphologically indistinguishable from *Inapertisporites*, aside from being grouped into clusters, and many specimens of *Inapertisporites* may have originally been grouped in clusters before being disaggregated.

Biological affinity: Probably Ascomycota.

Microsporonites Jain, 1968 emend.
Kalkutgar and Jansonius, 2000

Microsporonites spp.

Plate 18, figures 8–10

Discussion: This fungal spore type includes psilate, nonseptate, inaperturate, approximately spherical fungal spores which are observed in loosely organized clusters of two or more. The cell walls are closely appressed, but the spores do not appear to share cell walls. This morphological type resembles isolated spores identified here as *Inapertisporites*, some of which may have originally been in clusters. *Polyadosporites* is another form genus for clusters of psilate to scabrate, inaperturate or monoporate fungal spores; *Polyadosporites* is distinguished from *Microsporonites* by having cells which share septa rather than cells which have discrete, separate walls (Kalkutgar and Jansonius, 2000).

Biological affinity: Probably Ascomycota.

Genus *Monoporisporites*
van der Hammen, 1954

Monoporisporites spp.

Plate 18, figures 18, 19

Discussion: This type includes monoporate, aseptate fungal spores. The specimens of *Monoporisporites* in this study were spherical to elliptical and psilate, with a single annulate pore, and a size range of circa 10–30 µm. Although a range of subdividable morphologies were observed, *Monoporisporites* has not been speciated here due to its low abundance in these samples.

Biological affinity: Probably Ascomycota.

Genus *Multicellites*
Kalkutgar and Jansonius, 2000

Multicellites? sp. A (echinate)

Plate 19, figure 9

Discussion: The single observed specimen of this type is multicellate, with approximately eight cells, and no observable apertures. The generic identification and cell count is somewhat uncertain due to obscuring organic matter overlying the spore. The distinguishing feature of this type is a single row of small echinae ornamenting each cell, aligned perpendicularly to the long axis of the spore.

Biological affinity: Probably Ascomycota.

Genus *Pesavis*
Elsik and Jansonius, 1974

Pesavis tagluensis
Elsik and Jansonius, 1974

Plate 19, figures 16–18

Discussion: This fungal spore species is easily distinguished by having a stalked central cell and two lateral, multicellate crescentic branches, with secondary hyphae-like projections arising from the cells.

Biological affinity: Probably Ascomycota. Elsik and Jansonius (1974) noted that modern conidia of *Engelhardtiella alba* (Funk, 1973), a fungal mycoparasite, are similar to spores in the genus *Pesavis*.

Stratigraphic comments: Elsik and Jansonius (1974) described the range of *P. tagluensis* as roughly Paleocene to Eocene. Gregory and Hart (1995a) provided a range chart for the Wilcox Group showing the base of *P. tagluensis* in the Thanetian, slightly younger than the base of *Pistillipollenites mcgregorii*. The true base of P. *tagluensis* in our sections is somewhat questionable due to the rarity of the taxon, but the observed base of *P. tagluensis* in Jerome Olinick No. 16 and Moczygemba VT No. 11 suggests a base slightly below *P. mcgregorii*.

Phragmosporae spp.

Plate 19, figures 11–15

Discussion: Phragmosporae spp. include fungal spores with three or more transversely septate cells (Saxena and others, 2021). Numerous separate morphotypes were observed; two have been identified separately in this study. A comprehensive morphometric study of this group is considered outside the scope of this study but may be the subject of future research. Typical specimens were elongated and tapering at one or both ends. It is not possible to confidently assign fragmentary specimens of multicellate, transversely septate fungal spores to fossil form genera, as it is not possible to determine whether apertures are present at the ends of the spore. This type of fungal spore could be accommodated within the broad original generic concept of *Pluricellaesporites* (van der Hammen, 1954), but the genus concept as used by Jansonius and Kalkutgar (2000) limits the circumscription of *Pluricellaesporites* to multicellate, monoporate fungal spores.

Biological affinity: Probably Ascomycota.

Phragmosporae sp. A

Plate 19, figure 10

Discussion: The single specimen of this type is quite distinct. The spore is quite large, circa 61 by 31 µm, and composed of four cells, with no apertures. The two cells on each end of the long axis of the spore are large and hemispherical, while the two cells in the middle are elongated perpendicular to the long axis and roughly rectangular.

Biological affinity: Probably Ascomycota.

Phragmosporae sp. B

Plate 19, figure 8

Discussion: The single specimen of this type is distinguished by having highly asymmetrical cells, with the cell on one end greatly enlarged and terminating in a spine. The opposite end tapers gradually and the cells become smaller. Four cells are present. The long axis of the spore is circa 41 µm.

Biological affinity: Probably Ascomycota.

Genus *Phragmothyrites* Edwards, 1922 emend. Kalgutkar and Jansonius, 2000

Phragmothyrites spp.

Plate 20, figures 2, 3

Discussion: Saxena and Tripathi (2011) provide extensive discussion of *Phragmothyrites* and related form genera used for ascocarps produced by the Microthyriaceae. Two morphological types have been observed in our Lower Wilcox samples: *Phragmothyrites*, which lacks cell pores, and *Callimothallus*, which possesses pores in at least some cells.

Biological affinity: Microthyriaceae (Saxena and Tripathi, 2011).

Staurosporae sp.

Plate 20, figure 1

Discussion: Staurosporae includes pluricellate fungal spores with more than one axis, particularly spores with a stellate morphology (Saxena and others, 2021). Only a single, somewhat poorly preserved and nearly opaque specimen of this type has been observed.

Biological affinity: Probably Ascomycota.

5.17. Algae

Genus *Botryococcus* Kützing, 1849

Botryococcus braunii Kützing, 1849

Plate 20, figure 8

Discussion: The specimens of *Botryococcus* observed in this study do not appear to be meaningfully distinguishable from the algal remains of the modern species *Botryococcus braunii*. Using a morphological species concept, *Botryococcus braunii* has a remarkably long stratigraphic record, ranging from the Ordovician to present (Palynodata Inc. and White, 2008).

Biological affinity: *Botrococcus braunii*.

Paleoecology: Lacustrine (Guy-Ohlson, 1992).

Foraminiferal test linings

Plate 20, figure 9

Discussion: No attempt has been made to morphologically subdivide the rare foraminiferal test linings observed in these samples.

Biological affinity: Phylum Foraminifera (Mikhalevich, 2013).

Paleoecology: Almost certainly brackish or marine; the only truly freshwater extant foraminifera are single-chambered monothalamids (Holzmann and others, 2021), and all foraminiferal test linings observed in this study are multi-chambered organic linings.

Genus *Ovoidites*
Potonié, 1951 ex Krutzsch, 1959

Discussion: There appears to be some disagreement in the literature about the morphological circumscription of *Ovoidites*. In the description by Krutzsch (1959), translated by Jansonius and Hills (1976), no mention is made of the surface sculpture. Potonié (1966) provided an emended diagnosis of *Ovoidites* also translated by Jansonius and Hills (1976) which restricted *Ovoidites* to forms with a reticulate tectum. In this study we will use the broader circumscription of *Ovoidites* outlined by Rich and others (1982) which includes forms with a variety of surface sculpture; similar forms with a coarse reticulum are arguably better placed in the form genus *Schizosporis*.

Ovoidites spp.

Plate 20, figure 15

Discussion: Specimens of *Ovoidites* in this study were very rare and most specimens were poorly preserved, resulting in somewhat ambiguous psilate or scabrate sculpture. If speciated, most of these specimens could be placed in *Ovoidites elongatus* or *Ovoidites minoris*. A single specimen with somewhat better preservation (Plate 20, fig. 15) has a faintly developed, sparse rugulate sculpture and resembles Miocene specimens identified by Worobiec (2014, Plate 1, fig. 2) as "*Ovoidites* sp. 1." Due to their rarity in these samples the genus has not been speciated.

Biological affinity: Probably Zygnemataceae in the Zygnematophyceae, possibly in part Desmidiaceae in the Zygnematophyceae (Rich and others, 1982; Grenfell, 1995; Worobiec, 2014).

Paleoecology: Lacustrine, freshwater marsh (Rich and others, 1982).

Genus *Pediastrum* Meyen, 1829

Pediastrum spp.

Plate 20, figures 13, 14

Discussion: No attempt was made to identify *Pediastrum* spp. to the species level, due to the rarity and generally poor preservation of the observed specimens. Zamaloa and Tell (2005) provide discussion on the taxonomy and morphology of several fossil *Pediastrum* species.

Botanical affinity: *Pediastrum* (Hydrodictyaceae).

Paleoecology: Freshwater (Worobiec, 2014).

Genus *Pseudoschizaea* Thiergart and Frantz, 1962 from Potonié, 1966

Pseudoschizaea circula (Wolff, 1934)
Christopher, 1976

Plate 20, figures 10–12

Discussion: Christopher (1976) describes the taxonomy and morphology of *Pseudoschizaea* in detail.

Botanical affinity: *Pseudoschizaea* spp. are commonly believed to represent algal remains, possibly from the Zygnemataceae (e.g., Christopher, 1976; Grenfell, 1995; Mudie and others, 2021), although Scott (1992) suggested they may be invertebrate eggs.

Paleoecology: Mudie and others (2021) considered that *Pseudoschizaea* represents freshwater algal spores.

Genus *Pterospermopsis* Wetzel, 1952

Pterospermopsis spp.

Plate 21, figure 3

Discussion: *Pterospermopsis* spp. includes algal phycoma similar to those produced by extant *Pterosperma*, hence the name. Fossil forms of this type have been identified as *Pterospermopsis* as well as *Pterospermella* (Eisenack, 1972); we will follow Sarjeant (1976) and consider *Pterospermella* a junior synonym of *Pterospermopsis*. We prefer to use *Pterospermopsis* rather than the extant genus *Pterosperma* because the extant genus includes forms that depart from the morphology of *Pterospermopsis*, in particular a form genus for the motile phase of *Pterosperma*, *Pterosphaera* (Jørgensen, 1900), which has a more complex morphology with many intersecting alae defining quadrangular or polygonal fields (Parke and others, 1978). The acritarch genus *Catillopsis* (Drugg, 1970) is somewhat similar to *Pterospermopsis*, particularly when the "operculum" is not visible, but differs in that the outer layer or wing is fibrous and extends over the ventral side of the body.

Botanical affinity: *Pterosperma* (Pterospermataceae) (Takahashi and Matsuoka, 1981).

Paleoecology: Marine (Parke and others, 1978).

Pterospermopsis? sp. A

Plate 21, figure 2

Discussion: The single observed specimen of this type is somewhat similar to *Pterospermopsis* in having a subcircular central body with equatorial encircling wings. However, this type has a prominently thickened zone at the edge of the central body along the wing border. Also, the wing is unusually small relative to the central body and is not undulate as is common with more typical *Pterospermopsis* in our assemblages (e.g., Plate 21, fig. 3).

Botanical affinity: Possibly *Pterosperma* (Pterospermataceae).

Paleoecology: Probably marine.

Genus *Schizocystia* Cookson and Eisenack, 1962

Schizocystia rugosa Cookson and Eisenack, 1962

Plate 21, figure 5

Discussion: *Schizocystia laevigata* is considered synonymous with *S. rugosa* following reasoning given by Zippi (1998); both psilate and rugulate forms are included within *S. rugosa*. The three specimens observed in this study are essentially psilate, and if the two species are split, they would be assigned to *S. laevigata*. These zygospores tend to split into separated halves along a line of dehiscence. The specimens observed in this study are separated halves, which may indicate they represent zygospores which have successfully germinated (Zippi, 1998).

Botanical affinity: Zygnemataceae (Zippi, 1998).

Paleoecology: Freshwater (Zippi, 1998).

Genus *Stigmozygodites* Krutzsch and Pacltová, 1990

Stigmozygodites spp.

Plate 21, figure 4

Discussion: This genus has not been speciated due to their extreme rarity in these samples; only two specimens have been observed. Worobiec (2014) provided extensive discussion of the taxonomy, ecology, and stratigraphic distribution of *Stigmozygodites*.

Botanical affinity: Zygnemataceae, possibly *Zygnema* (Worobiec, 2014).

Paleoecology: Shallow freshwater to brackish. The presence of this type has been used as a marker for "...clean, oxygen-rich, shallow stagnant, mesotrophic to eutrophic, open water in habitats subject to seasonal warming" (Worobiec, 2014, p. 126).

Genus *Tasmanites* Newton, 1875

Tasmanites sp. A

Plate 21, figure 8

Discussion: Schopf and others (1944) provide extensive discussion of the taxonomic history of *Tasmanites*. The single specimen of this type observed in our Lower Wilcox samples is relatively small for the genus, circa 28 µm in diameter, and circular in plan view, originally presumably spherical. The surface sculpture is composed of regularly arranged punctae approaching a reticulate sculpture formed by pore canals, as well as overlying small verrucae. The presence of small verrucae is unusual for the genus but otherwise the specimen resembles other modern and fossil *Tasmanites* specimens (e.g., Wall, 1962; Boalch and Guy-Ohlsen, 1992).

Botanical affinity: Although *Tasmanites* was originally described from fossil specimens, the affinity with certain modern prasinophyte algae previously identified as *Pachysphaera* has been so well established that the fossil genus is considered a senior synonym. *Tasmanites* therefore has an exceptionally long stratigraphic record from the Precambrian to the present (Boalch and Guy-Ohlsen, 1992; Guy-Ohlsen and Boalch, 1992).

Paleoecology: Marine (Wall, 1962).

Genus *Tetraporina* Naumova, 1939 emend. Lindgren, 1980

Discussion: The most notable characteristic of *Tetraporina* is its quadrate, tetrahedral or parallelepipedal shape; as emended by Lindgren (1980) *Tetraporina* includes forms with and without pores.

Tetraporina spinifera
Lindgren, 1980 sensu lato

Plate 21, figure 6

Discussion: *Tetraporina spinifera* is distinguished from other species of *Tetraporina* by having short spines at the corners of the algal body and a single-layered wall. A broad species concept is used here to include specimens smaller than the original size range for *T. spinifera* of 40–63 µm. *Tetraporina denticulata* is similar to *T. spinifera* but has a two-layered wall (Lindgren, 1980).

Botanical affinity: Probably Zygnemataceae, possibly Chlorophyceae (Lindgren, 1980; Grenfell, 1995).

Paleoecology: Freshwater (Zippi 1998).

Tetraporina sp. (psilate)

Plate 21, figure 7

Discussion: It was not considered useful to subdivide psilate *Tetraporina* specimens which lack notable distinguishing features of ornamentation such as echinae. This type includes forms which Elsik (1968a) identified as *Tetraporina horologia*. Only one specimen of this type was observed in these samples.

Botanical affinity: Zygnemataceae, possibly *Mougeotia* (Grenfell, 1995).

Paleoecology: Freshwater (Zippi, 1998).

5.18. Acritarchs

Genus *Baltisphaeridium* Eisenack, 1958

Discussion: Detailed discussion of the taxonomy of *Baltisphaeridium* and related genera is provided in Sarjeant and Stancliffe (1994).

Baltisphaeridium aff. *distentum* Playford, 1977

Plate 21, figures 9–11

Discussion: This acritarch type is similar to *Baltisphaeridium distentum* sensu stricto as described by Playford (1977), differing mainly in having shorter and narrower spines; the spines in *B. distentum* were described as 20–40 µm long. *Baltisphaeridium infulatum* is similar but has weakly microgranular rather than psilate spines (Wall, 1965).

Biological affinity: Acritarcha, incertae sedis.

Stratigraphic comments: Although this type is similar to *B. distentum*, which was described from Devonian strata (Playford, 1977), the generally good preservation and light color of these sporomorphs indicate they may be in situ.

Genus *Catillopsis* Drugg, 1970

Catillopsis abdita? Drugg, 1970

Plate 21, figure 1

Discussion: *Catillopsis abdita* was originally described from the Wilcox Group of Alabama. There is some uncertainty in the identification of the two specimens observed because the circular to semicircular apertures described by Drugg (1970) were not clearly observable, the wings appear fibrous but are not well preserved, and it is not clear that the wings extend over the ventral side of the body. *Pterospermopsis* is similar but distinguished by having a non-fibrous wing which does not extend over the ventral side of the body and by lacking an aperture. These specimens are somewhat similar to a specimen of *C. abdita* photographed by Drugg (1970, fig. 17f) where the wing has been partially stripped away.

Biological affinity: Acritarcha, incertae sedis (Drugg, 1970).

Genus *Comasphaeridium*
Staplin and others, 1965 emend.
Sarjeant and Stancliffe, 1994

Comasphaeridium sp. A

Plate 21, figure 14

Discussion: The single observed specimen of this type has a spherical central body circa 15 µm in diameter surrounded by very thin, hairlike spines. Detailed taxonomic discussion of *Comasphaeridium* and related genera is provided by Sarjeant and Stancliffe (1994).

Botanical affinity: Acritarcha, incertae sedis (Sarjeant and Stancliffe, 1994).

Genus *Micrhystridium*
Deflandre, 1937 emend.
Sarjeant and Stancliffe, 1994

Micrhystridium? sp. A

Plate 21, figures 12, 13

Discussion: The specimens of *Micrhystridium*? sp. A observed in this study are perfectly psilate in light microscopy, with very thin walls and a single-walled central body circa 15–25 µm in diameter. Generally, between 8–20 slender, acuminate spines arise from the central body. The spines are hollow, tapered, and in communication with the central body. The shape of the central body is irregular and is modified by the spines; all observed specimens of this type have been folded or compressed to some extent. Specimens identified as *Baltisphaeridium* aff. *distentum* here are quite similar but are distinguished by having a more perfectly spherical central body which generally does not appear to be in communication with the spines. Despite the difference in generic assignment, the morphological similarity of the two species suggests a similar biological affinity. The generic identification is somewhat questionable due to the size and shape of the central body. As emended by Sarjeant and Stancliffe (1994), *Micrhystridium* includes acritarchs usually <20 µm diameter whose outline in optical section is not significantly modified by the base of the spines. *Dorsennidium* is somewhat similar to *Micrhystridium*? sp. A but is restricted to forms with 4–10 spines (Sarjeant and Stancliffe, 1994; Stancliffe and Sarjeant, 1996).

Biological affinity: Acritarcha, incertae sedis (Sarjeant and Stancliffe, 1994).

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Appendix 1. Plates

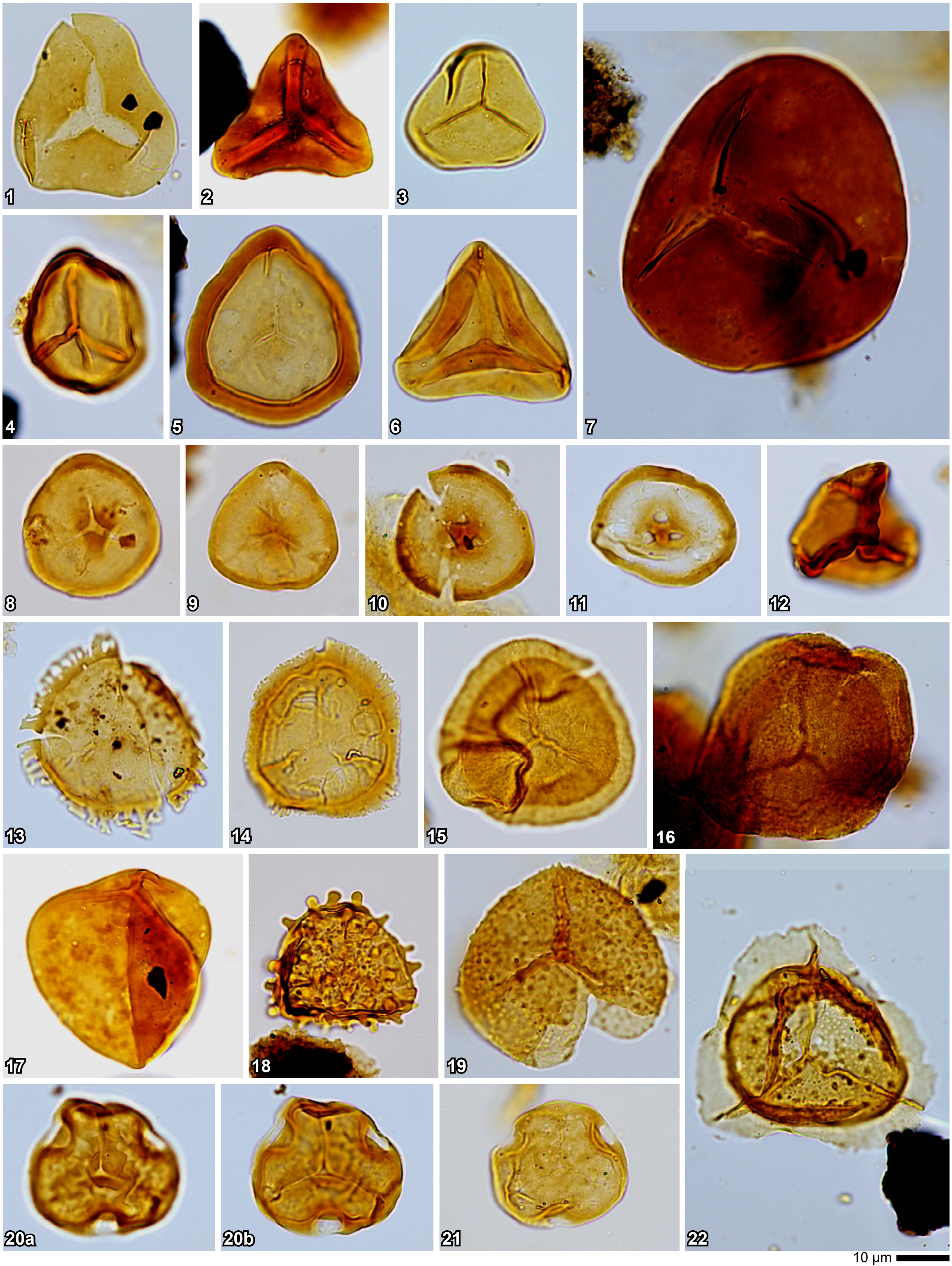


Plate 1

Plate 1. Trilete spores.

1. *Cyathidites minor*. Jerome Olinick No. 16, 5221.92 ft.
2. *Cyathidites* sp. A. Edmond Olinick No. 1, 5935–5965 ft.
3. *Deltoidospora* sp. Jerome Olinick No. 16, 5129.5 ft.
4. *Deltoidospora* sp. A. Jerome Olinick No. 16, 5111.67 ft.
5. *Cingulatisporites* sp. A. Edmond Olinick No. 1, 6161–6191 ft.
6. *Gleicheniidites senonicus*. Jerome Olinick No. 16, 5111.67 ft.
7. *Deltoidospora* sp. Jerome Olinick No. 16, 5151.33 ft.
8. *Stereisporites* sp. Edmond Olinick No. 1, 4949–4979 ft.
9. *Stereisporites* sp. Jerome Olinick No. 16, 5951 ft.
10. *Stereisporites* sp. A. Edmond Olinick No. 1, 5646–5676 ft.
11. *Stereisporites* sp. A. Edmond Olinick No. 1, 5845–5874 ft.
12. *Undulatisporites elsikii*. Edmond Olinick No. 1, 5395–5425 ft.
13. *Stereisporites buchenauensis*. Jerome Olinick No. 16, 5111.67 ft.
14. *Stereisporites buchenauensis*. Jerome Olinick No. 16, 5096.17 ft.
15. *Selaginella perinata*. Edmond Olinick No. 1, 5395–5425 ft.
16. *Selaginella perinata*. Jerome Olinick No. 16, 5135.42 ft.
17. *Triplanosporites* sp. Moczygemba VT No. 11, 4865.25 ft.
18. *Clavatisporites* sp. A. Moczygemba VT No. 11, 4874 ft.
19. *Baculatisporites* sp. Jerome Olinick No. 16, 5129.50 ft.

20a, 20b. *Kuylisporites hamulatis*. Edmond Olinick No. 1, 5845–5874 ft.

21. *Kuylisporites waterbolkii*. Jerome Olinick No. 16, 5102 ft.
22. *Aequitriradites* aff. *spinulosus*. Jerome Olinick No. 16, 5991.42 ft.

Scale bar=10 µm.

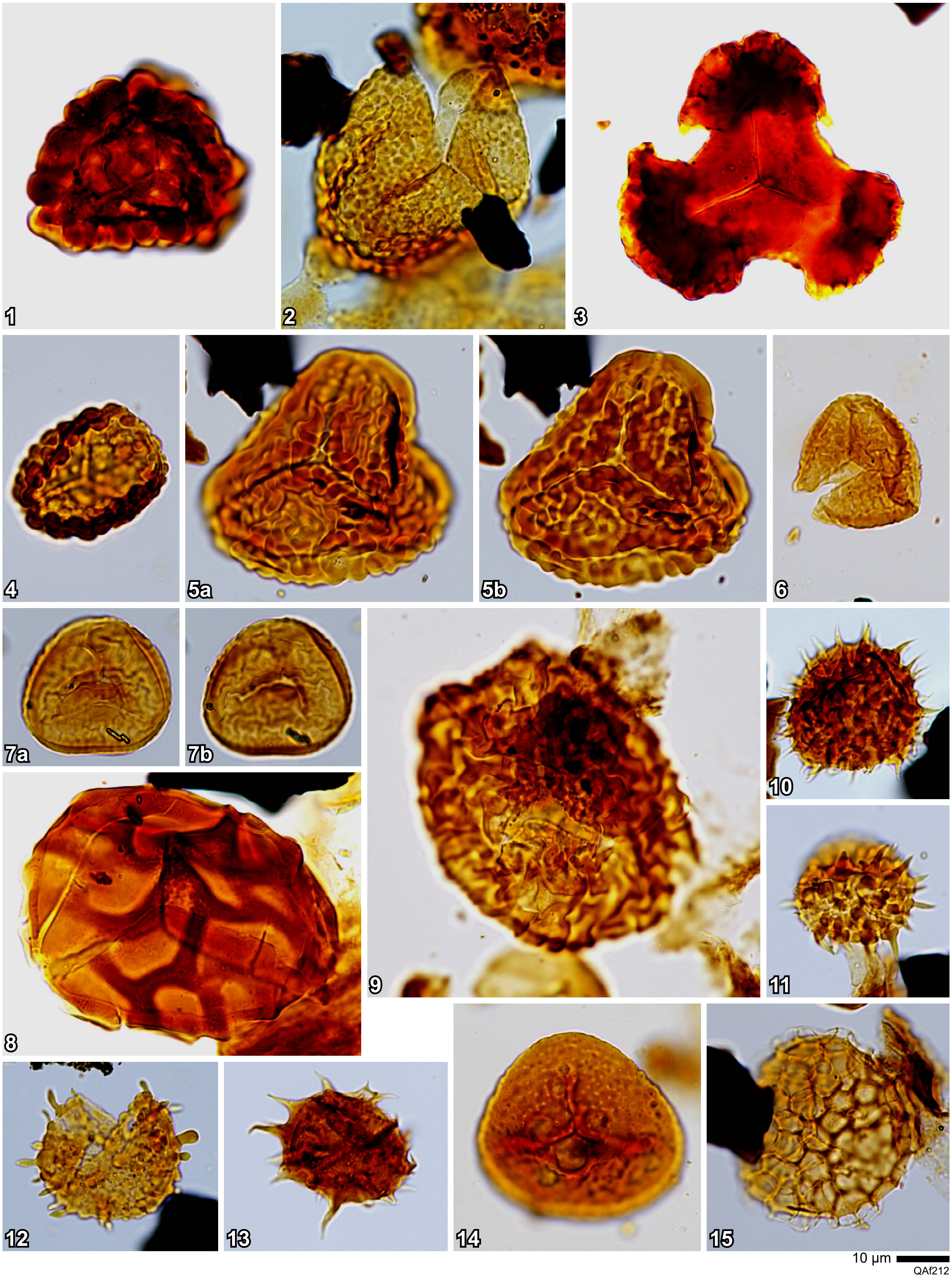


Plate 2

Plate 2. Trilete spores.

1. *Verrucingulatisporis* sp. A. Jerome Olinick No. 16, 5308 ft.
2. *Verrucosisporites* sp. Jerome Olinick No. 16, 5129.50 ft.
3. *Tripartites incisotrilobus*. Edmond Olinick No. 1, 6161–6191 ft.
4. *Verrucosisporites* sp. Edmond Olinick No. 1, 5845–5874 ft.

5a, 5b. *Polypodiaceoisporites gracillimus granoverrucatus*. Jerome Olinick No. 16, 5102 ft.

6. *Hamulatisporis hamulatis*. Jerome Olinick No. 16, 5951 ft.

7a, 7b. *Hamulatisporis hamulatis*. Edmond Olinick No. 1, 5845–5874 ft.

8. *Camarozonosporites grootii*. Jerome Olinick No. 16, 5106.50 ft.
9. *Hamulatisporis amplus*. Moczygemba VT No. 11, 4919.83 ft.
10. *Echinatisporis* sp. Jerome Olinick No. 16, 5096.17 ft.
11. *Echinatisporis* sp. Edmond Olinick No. 1, 5845–5874 ft.
12. *Echinatisporis* sp. Jerome Olinick No. 16, 5151.33 ft.
13. *Echinatisporis* sp. Jerome Olinick No. 16, 5111.67 ft.
14. *Punctatriletes* sp. B. Moczygemba VT No. 11, 4935.17 ft.
15. *Retitriletes globosus*. Jerome Olinick No. 16, 5102 ft.

Scale bar=10 µm.

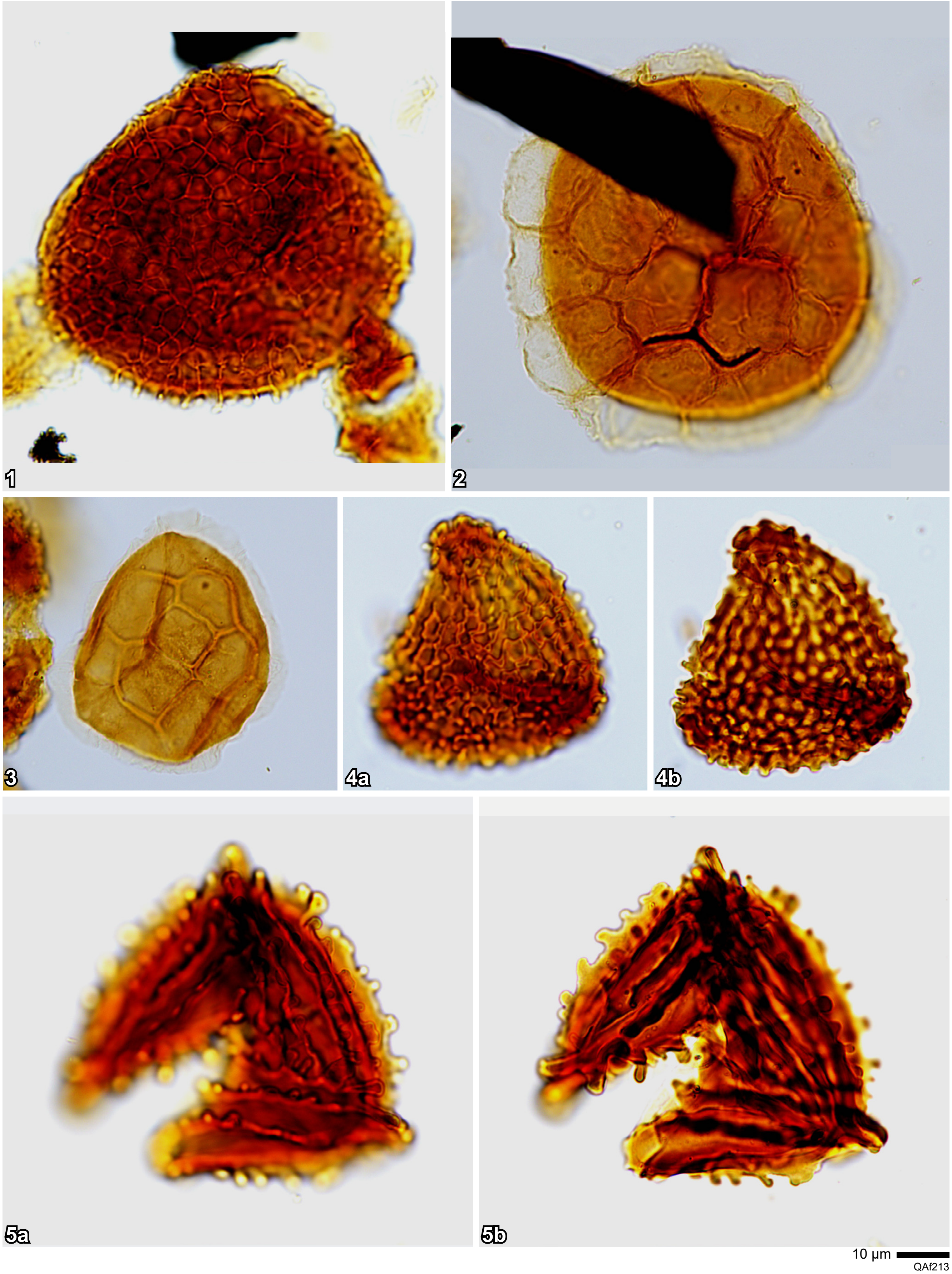


Plate 3

Plate 3. Trilete spores.

1. *Retitriletes*? sp. C. Jerome Olinick No. 16, 5129.50 ft.
2. *Zlivisporis* sp. Edmond Olinick No. 1, 5874 ft.
3. *Zlivisporis* sp. Edmond Olinick No. 1, 5676–5706 ft.

4a, 4b. *Microreticulatisporites* sp. Edmond Olinick No. 1, 5845–5874 ft.

5a, 5b. *Nodosisporites crenimurus*. Jerome Olinick No. 16, 5124.58 ft.

Scale bar=10 µm.

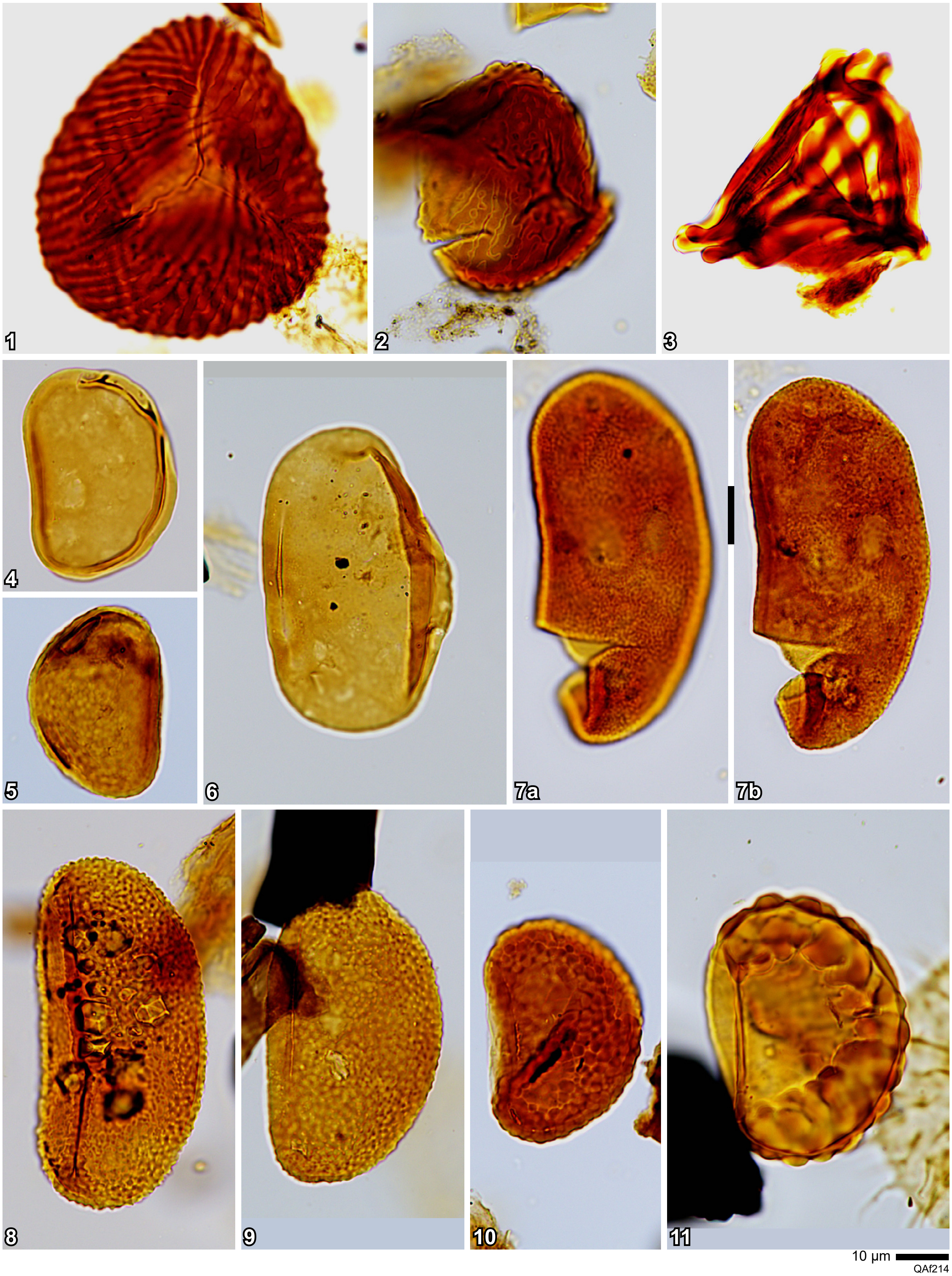


Plate 4

Plate 4. Trilete and monolete spores.

1. *Cicatricosisporites dorogensis*. Edmond Olinick No. 1, 5099–5129 ft.
2. *Cicatricosisporites paradorogensis*. Moczygemba VT No. 11, 4622 ft.
3. *Appendicisporites* sp. Jerome Olinick No. 16, 5106.50 ft.
4. *Laevigatosporites haardtii*. Edmond Olinick No. 1, 4949–4979 ft.
5. *Reticuloidosporites pseudomurii*. Jerome Olinick No. 16, 5298 ft.
6. *Laevigatosporites major*. Jerome Olinick No. 16, 5096.17 ft.

7a, 7b. *Microfoveolatosporis pseudodentatus*. Edmond Olinick No. 1, 4979–5009 ft.

8. *Reticuloidosporites* sp. A. Moczygemba VT No. 11, 4874 ft.
9. *Reticuloidosporites* sp. A. Jerome Olinick No. 16, 5106.50 ft.
10. *Polypodiisporonites favus*. Jerome Olinick No. 16, 5298 ft.
11. *Polypodiisporonites alienus*. Edmond Olinick No. 1, 5646–5676 ft.

Scale bar=10 µm.

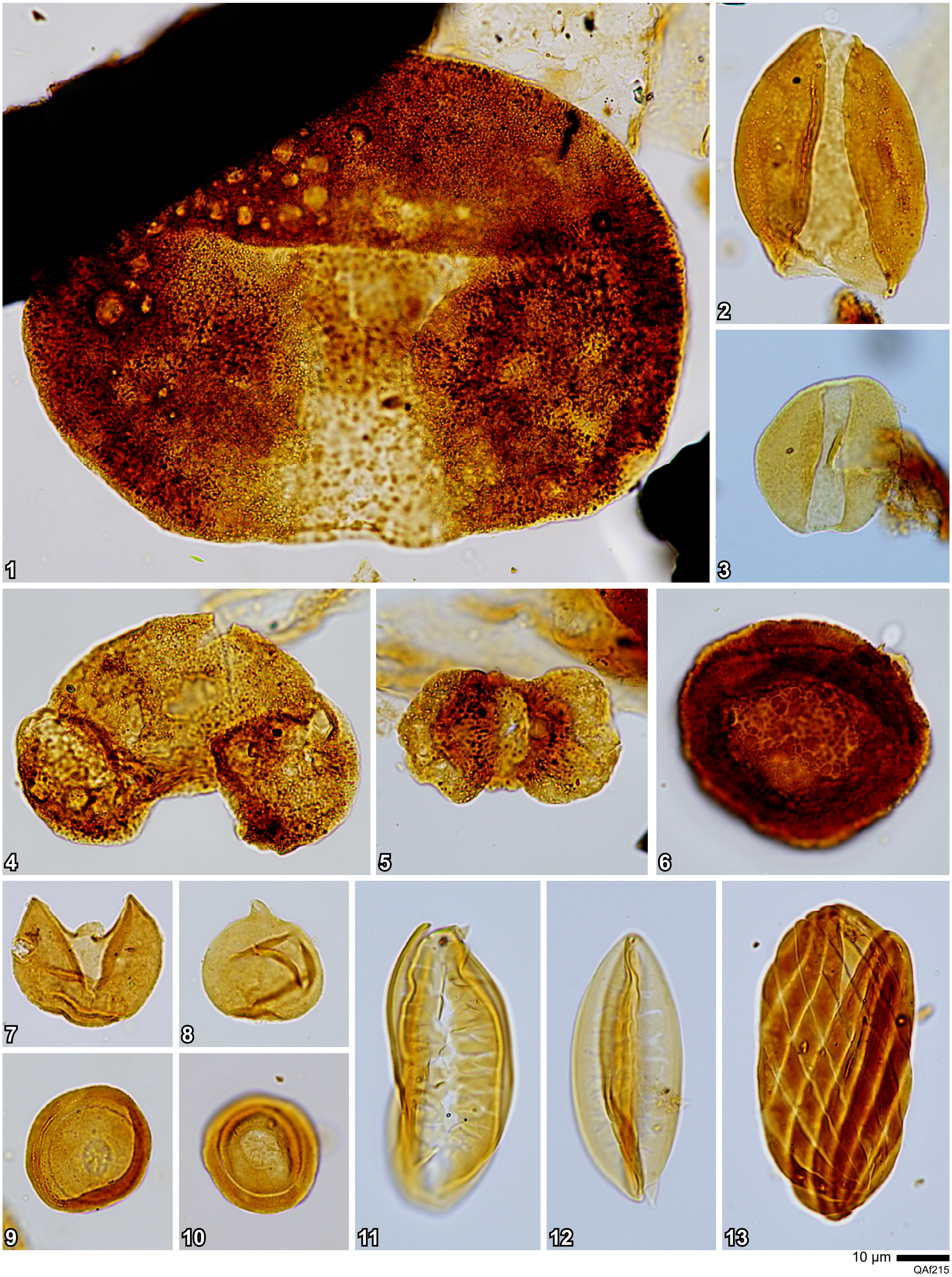


Plate 5

Plate 5. Gymnosperm pollen.

1. *Picea* sp. Moczygemba VT No. 11, 4907.25 ft.
2. *Cycadopites giganteus*. Edmond Olinick No. 1, 5845–5874 ft.
3. *Cycadopites follicularis*. Edmond Olinick No. 1, 6161–6191 ft.
4. Class Pinopsida. Jerome Olinick No. 16, 5124.58 ft.
5. *Podocarpus*? sp. Jerome Olinick No. 16, 5106.50 ft.
6. *Tsuga* sp. Jerome Olinick No. 16, 5106.50 ft.
7. *Inaperturopollenites hiatipites*. Edmond Olinick No. 1, 4979–5009 ft.
8. *Sequiapollenites* sp. Edmond Olinick No. 1, 5425–5455 ft.
9. *Classopollis classoides*. Jerome Olinick No. 16, 5102 ft.
10. *Classopollis classoides*. Moczygemba VT No. 11, 4903.67 ft.
11. *Ephedripites eocenipites*. Edmond Olinick No. 1, 5676–5706 ft.
12. *Ephedripites eocenipites*. Edmond Olinick No. 1, 5995–6025 ft.
13. *Gnetaceaepollenites jansonii*. Jerome Olinick No. 16, 5966 ft.

Scale bar=10 µm.

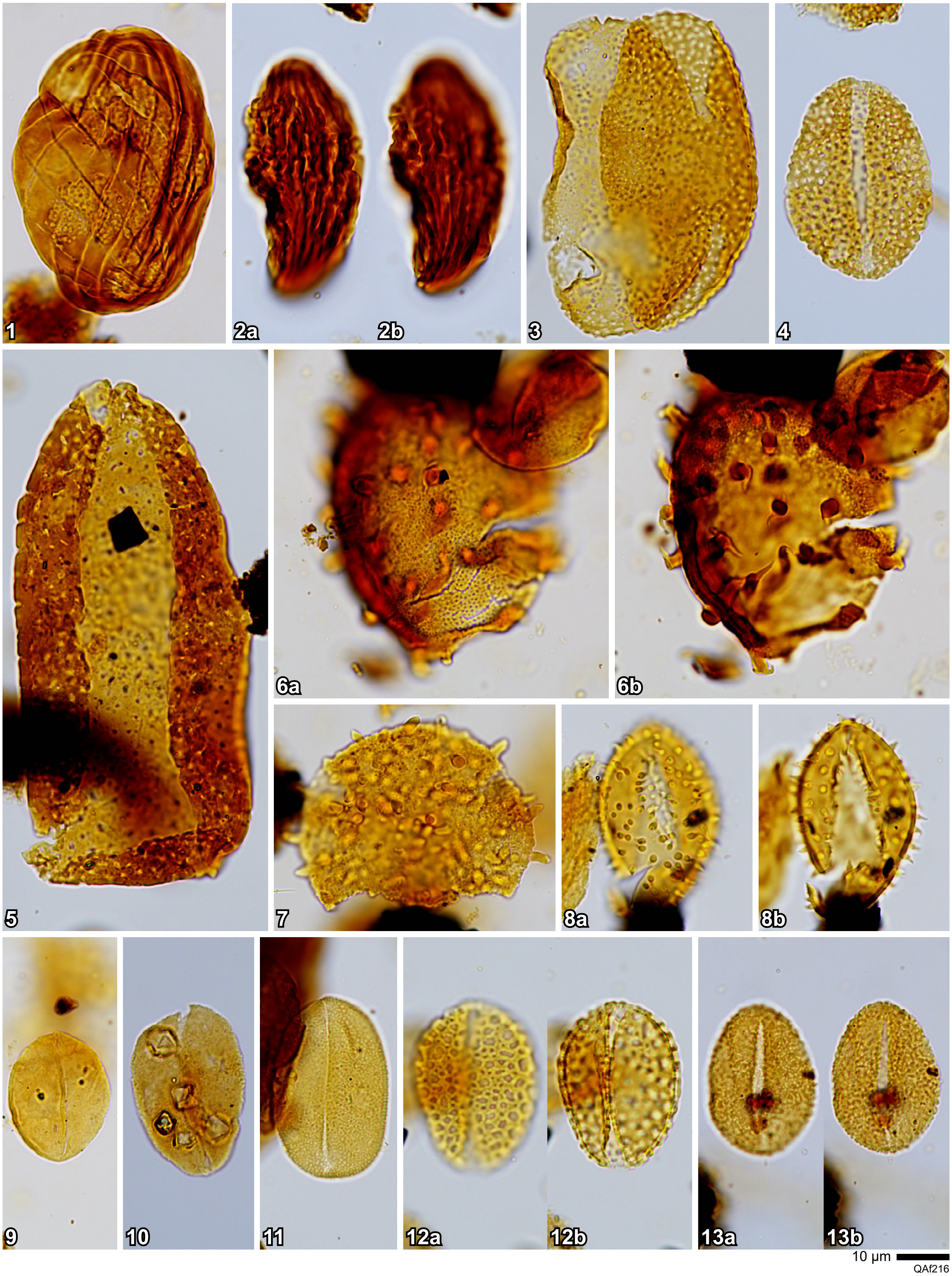
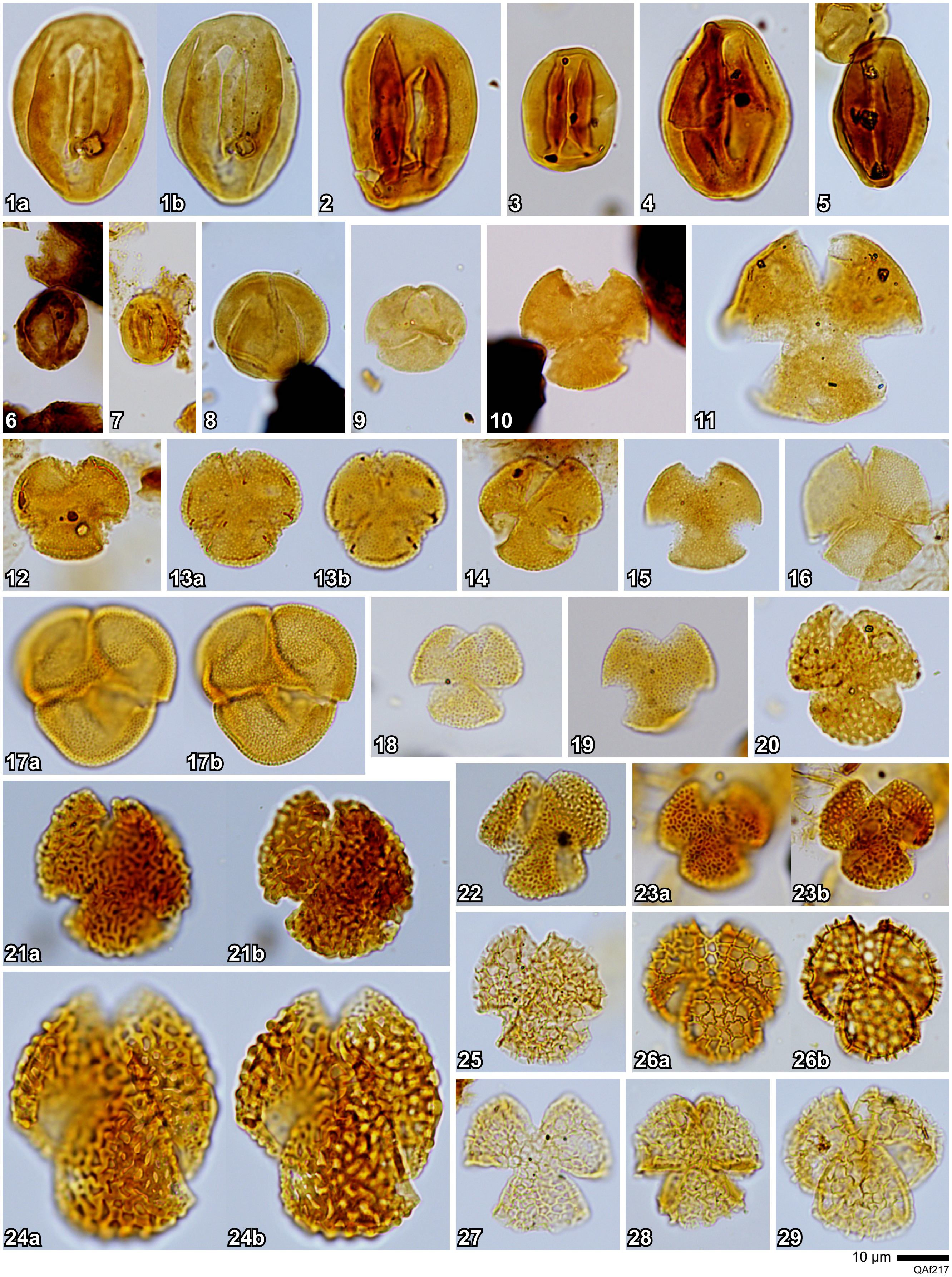


Plate 6

Plate 6. Gymnosperm pollen and monocolpate angiosperm pollen.

1. *Gnetaceaepollenites jansonii*. Moczygemba VT No. 11, 6047 ft.
2a, 2b. *Gnetaceaepollenites* sp. B. Jerome Olinick No. 16, 5151.33 ft.
3. *Longapertites* aff. *vaneendenburgi*. Edmond Olinick No. 1, 5395–5425 ft.
4. *Liliacidites* sp. Edmond Olinick No. 1, 5995–6025 ft.
5. *Proxapertites magnus*. Edmond Olinick No. 1, 5545–5575 ft.
6a, 6b. *Spinizonocolpites* aff. *baculatus*. Moczygemba VT No. 11, 4964.67 ft.
7. *Spinizonocolpites breviechinatus*. Moczygemba VT No. 11, 4935.17 ft.
8a, 8b. *Nupharipollis* sp. Edmond Olinick No. 1, 5395–5425 ft.
9. *Arecipites* sp. (punctate or scabrate). Moczygemba VT No. 11, 4935.17 ft.
10. *Arecipites* sp. (punctate or scabrate). Jerome Olinick No. 16, 5100.50 ft.
11. *Arecipites tenuiexinous*. Edmond Olinick No. 1, 5646–5676 ft.
12a, 12b. *Liliacidites* sp. Edmond Olinick No. 1, 5935–5965 ft.
13a, 13b. *Arecipites pertusus*. Edmond Olinick No. 1, 4979–5009 ft.

Scale bar=10 µm.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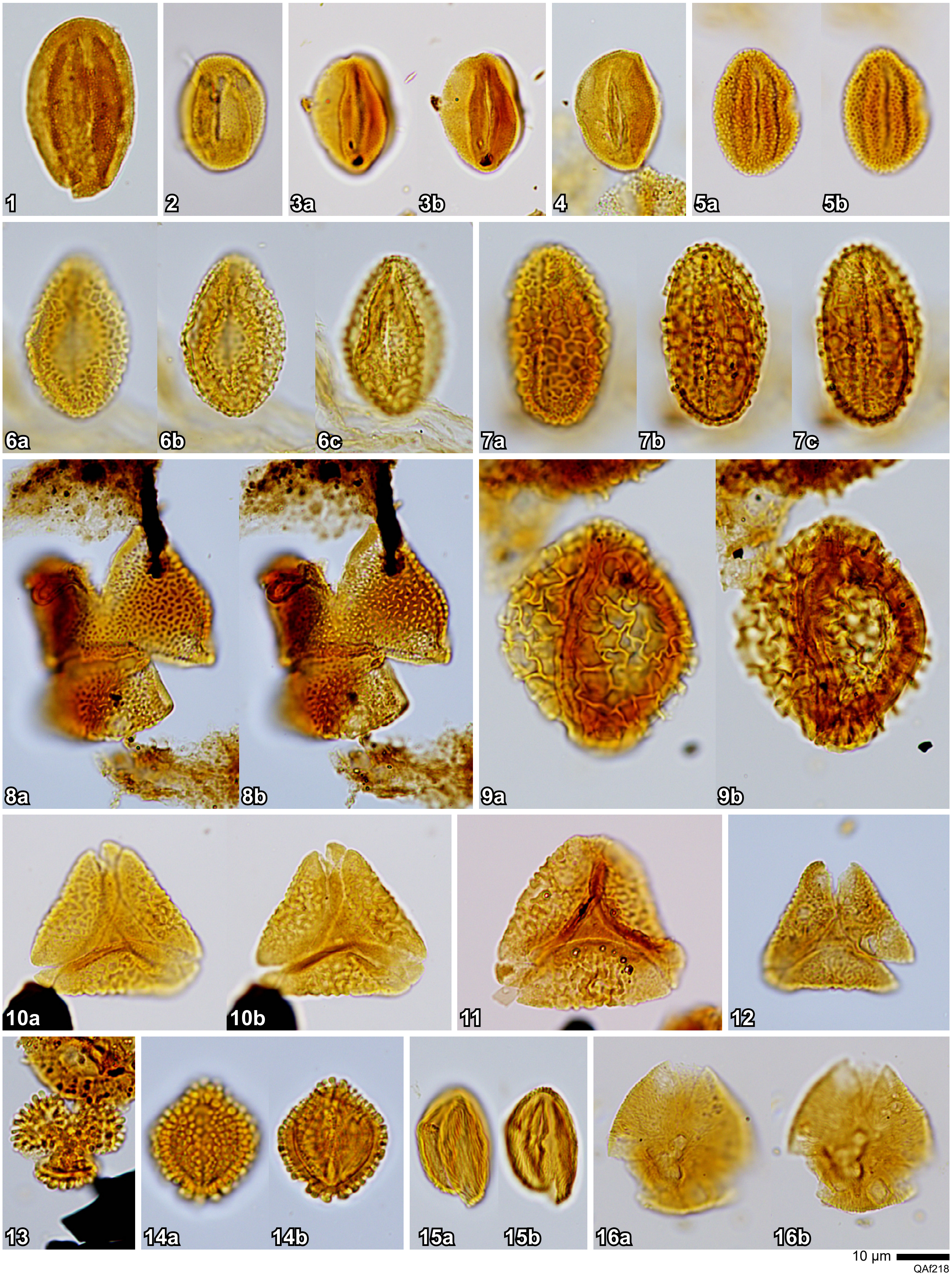
10 µm
QAf217

Plate 7

Plate 7. Tricolpate angiosperm pollen.

1a, 1b. *Eucommia*? sp. Jerome Olinick No. 16, 5287.58 ft.
2. *Eucommia*? sp. Edmond Olinick No. 1, 5515–5545 ft.
3. *Eucommia*? sp. Moczygemba VT No. 11, 4613.50 ft.
4. *Psilatricolpites* sp. (prolate). Edmond Olinick No. 1, 5845–5874 ft.
5. *Psilatricolpites* sp. (prolate). Moczygemba VT No. 11, 4940.75 ft.
6. *Cupuliferoidaepollenites* sp. Lawrence Keseling No. 1, 11020.42 ft.
7. *Cupuliferoidaepollenites* sp. Moczygemba VT No. 11, 4953.92 ft.
8. *Scabratricolpites* sp. (non-prolate). Moczygemba VT No. 11, 4945.83 ft.
9. *Scabratricolpites* sp. (non-prolate). Jerome Olinick No. 16, 5966 ft.
10. *Scabratricolpites* sp. (non-prolate). Jerome Olinick No. 16, 5100.50 ft.
11. *Scabratricolpites* sp. (non-prolate). Jerome Olinick No. 16, 5111.67 ft.
12. *Tricolpites asper*. Edmond Olinick No. 1, 5099–5129 ft.
13a, 13b. *Tricolpites asper*. Jerome Olinick No. 16, 5129.50 ft.
14. *Tricolpites hians*. Edmond Olinick No. 1, 5158–5188 ft.
15. *Tricolpites hians*. Edmond Olinick No. 1, 5845–5874.
16. *Tricolpites hians*. Edmond Olinick No. 1, 5995–6025 ft.
17a, 17b. *Tricolpites reticulatus*. Edmond Olinick No. 1, 5995–6025 ft.
18. *Tricolpites hians*. Jerome Olinick No. 16, 5106.50 ft.
19. *Tricolpites hians* Moczygemba VT No. 11, 4610 ft.
20. *Retitrescolpites* sp. Jerome Olinick No. 16, 5966 ft.
21a, 21b. *Retitrescolpites* sp. Jerome Olinick No. 16, 5151.33 ft.
22. *Retitrescolpites* sp. Edmond Olinick No. 1, 5845–5874 ft.
23a, 23b. *Retitrescolpites* sp. Moczygemba VT No. 11, 4613.50 ft.
24a, 24b. *Retitrescolpites* sp. Edmond Olinick No. 1, 5995–6025 ft.
25. *Retitrescolpites anguloluminosus*. Edmond Olinick No. 1, 5845–5874 ft.
26a. 26b. *Retitrescolpites anguloluminosus*. Jerome Olinick No. 16, 5301 ft.
27. *Retitrescolpites anguloluminosus*. Jerome Olinick No. 16, 5111.67 ft.
28. *Retitrescolpites anguloluminosus*. Jerome Olinick No. 16, 5135.42 ft.
29. *Retitrescolpites anguloluminosus*. Edmond Olinick No. 1, 5515–5545 ft.
Scale bar=10 μm.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10b
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14a
14b
15a
15b
16a
16b
10 µm
QAf218

Plate 8

Plate 8. Tricolpate angiosperm pollen.

1. *Fraxinoipollenites* sp. (micro-reticulate). Jerome Olinick No. 16, 5119 ft.
2. *Fraxinoipollenites* sp. (micro-reticulate). Moczygemba VT No. 11, 4622 ft.

3a, 3b. *Fraxinoipollenites* sp. (micro-reticulate). Moczygemba VT No. 11, 4945.83 ft.

4. *Fraxinoipollenites* sp. (micro-reticulate). Edmond Olinick No. 1, 5039–5069 ft.

5a, 5b. *Retitricolpites* sp. A. Moczygemba VT No. 11, 4907.25 ft.

6a, 6b, 6c. *Retitricolpites* sp. B. Edmond Olinick No. 1, 5646–5676 ft.

7a, 7b, 7c. *Retitricolpites* sp. C. Edmond Olinick No. 1, 5425–5455 ft.

8a, 8b. *Rousea* aff. *crassimurina*. Edmond Olinick No. 1, 5515–5545 ft.

9a, 9b. *Myocolpopollenites reticulatus*. Edmond Olinick No. 1, 4949–4979 ft.

10a, 10b. *Insulapollenites rugulatus*. Moczygemba VT No. 11, 4613.50 ft.

11. *Insulapollenites rugulatus*. Jerome Olinick No. 16, 5100.50 ft.
12. *Insulapollenites rugulatus*. Edmond Olinick No. 1, 5995–6025 ft.
13. *Clavatricolpites* sp. B. Edmond Olinick No. 1, 5845–5874 ft.

14a, 14b. *Clavatricolpites* sp. B. Edmond Olinick No. 1, 5995–6025 ft.

15a, 15b. *Striatopollis grahamii*. Moczygemba VT No. 11, 4622 ft.

16a, 16b. *Striatricolpites* sp. A. Moczygemba VT No. 11, 4632.33 ft.

Scale bar=10 µm.

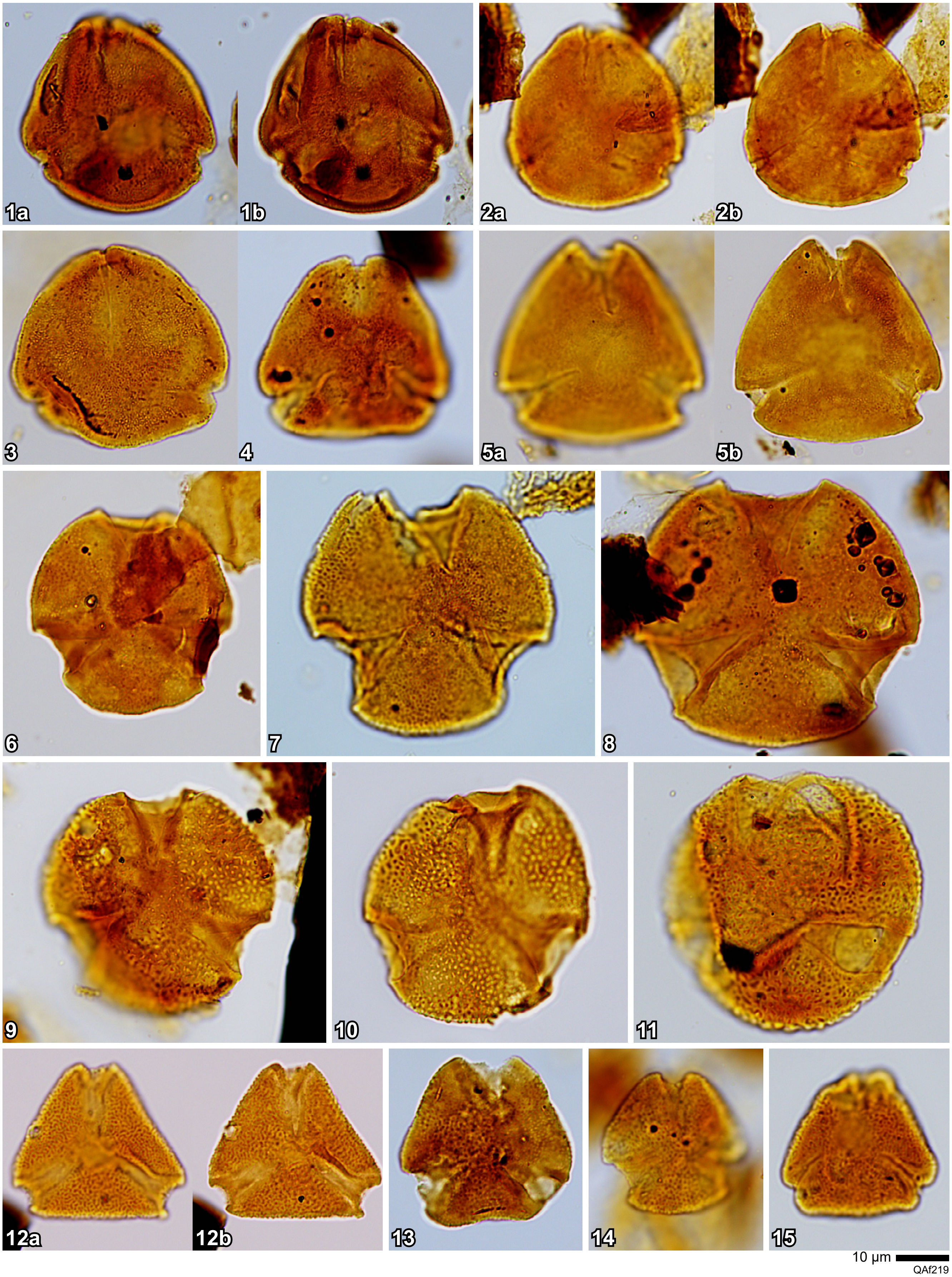
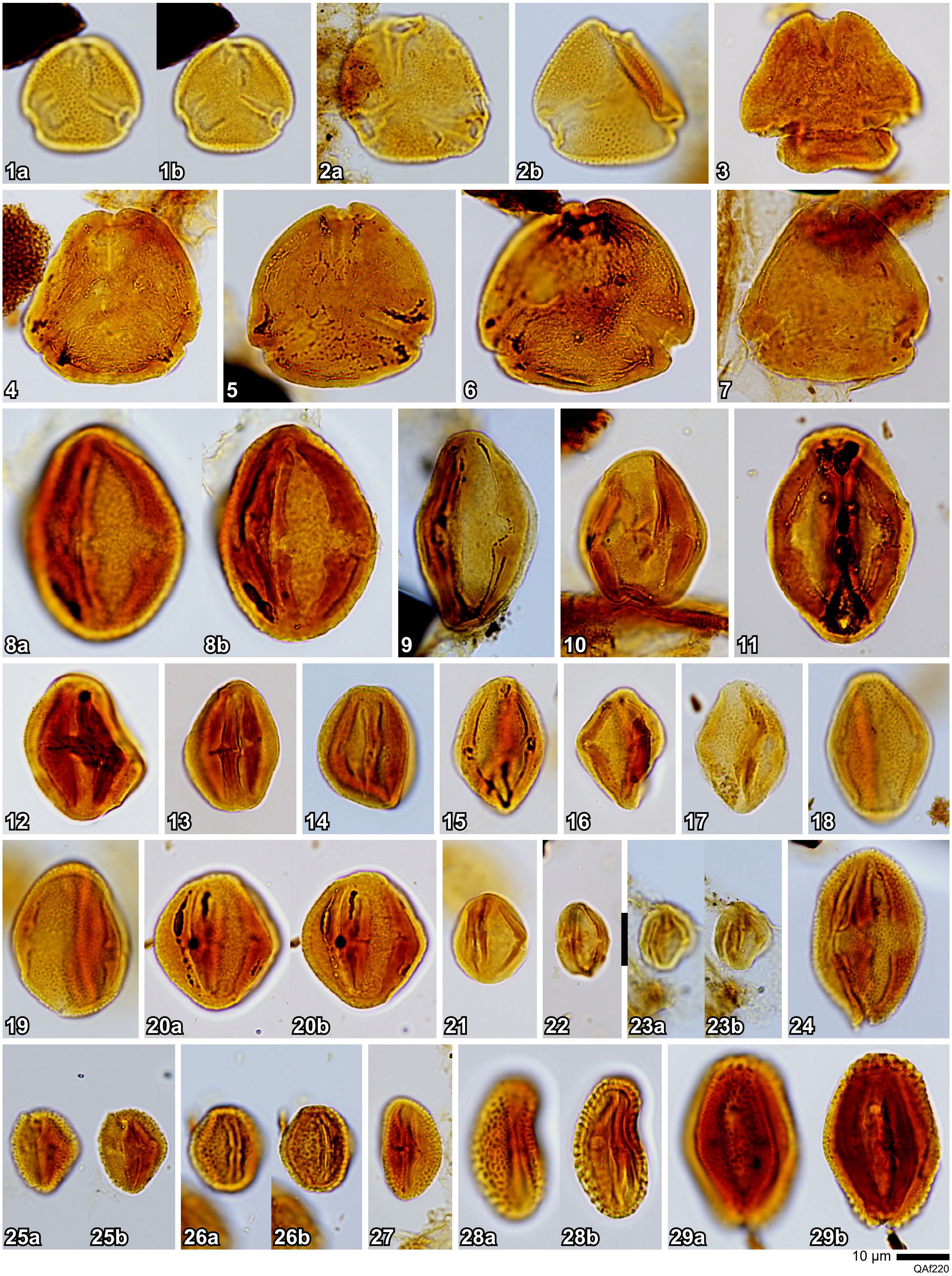


Plate 9

Plate 9. Tricolporate angiosperm pollen.

1a, 1b. *Nyssapollenites* sp. Jerome Olinick No. 16, 5151.33 ft
2a, 2b. *Nyssapollenites* sp. Jerome Olinick No. 16, 5199.33 ft.
3. *Nyssapollenites* sp. Moczygemba VT No. 11, 4903.67 ft.
4. *Nyssapollenites* sp. Jerome Olinick No. 16, 5111.67 ft.
5a, 5b. *Nyssapollenites* sp. Moczygemba VT No. 11, 4903.67 ft.
6. *Lanagiopollis cribellata*. Edmond Olinick No. 1, 4949–4979 ft.
7. *Lanagiopollis cribellata*. Jerome Olinick No. 16, 5129.50 ft.
8. *Lanagiopollis cribellata*. Jerome Olinick No. 16, 5966 ft.
9. *Lanagiopollis lihoka*. Moczygemba VT No. 11, 4912 ft.
10. *Lanagiopollis lihoka*. Edmond Olinick No. 1, 4979–5009 ft.
11. *Lanagiopollis lihoka*. Edmond Olinick No. 1, 5335–5365 ft.
12a, 12b. *Lanagiopollis* sp. Jerome Olinick No. 16, 5100.50 ft.
13. *Lanagiopollis* sp. Edmond Olinick No. 1, 6161–6191 ft.
14. *Lanagiopollis* sp. Jerome Olinick No. 16, 5308 ft.
15. *Lanagiopollis* sp. Jerome Olinick No. 16, 5119 ft.
Scale bar=10 µm.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23a
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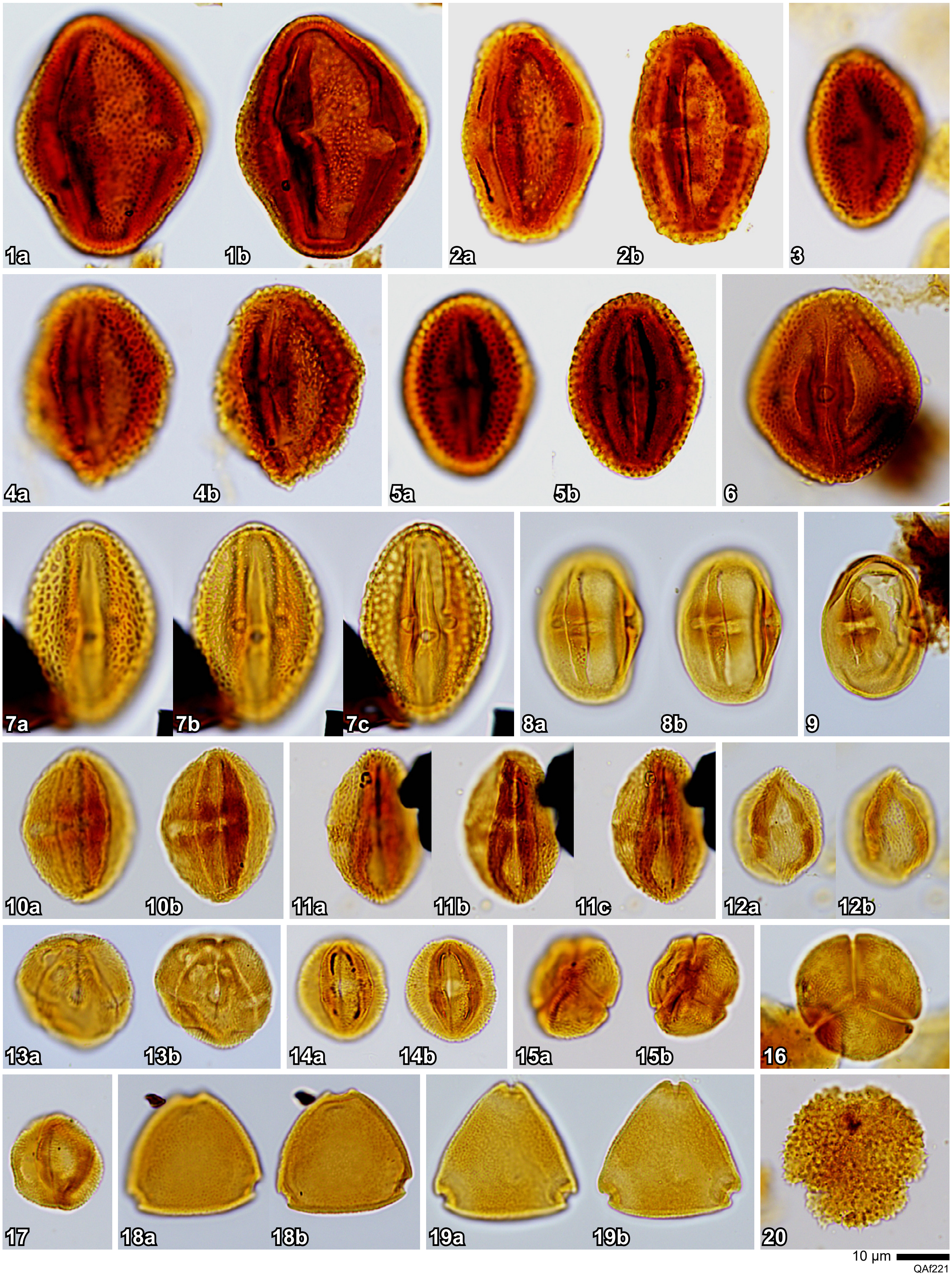
25a
25b
26a
26b
27
28a
28b
29a
29b
10 µm
QAf220

Plate 10

Plate 10. Tricolporate angiosperm pollen.

1a, 1b. *Nyssapollenites pulvinus*. Edmond Olinick No. 1, 5039–5069 ft.
2a, 2b. *Nyssapollenites pulvinus*. Jerome Olinick No. 16, 5301 ft.
3. *Holkopollenites chemardensis*. Moczygemba VT No. 11, 4940.75 ft.
4. *Holkopollenites* sp. A. Moczygemba VT No. 11, 4884 ft.
5. *Holkopollenites* sp. A. Edmond Olinick No. 1, 4949–4979 ft.
6. *Holkopollenites* sp. A. Edmond Olinick No. 1, 4979–5009 ft.
7. *Holkopollenites* sp. A. Moczygemba VT No. 11, 4888 ft.
8a, 8b. *Punctatricolporites* sp. (prolate). Edmond Olinick No. 1, 5935–5965 ft.
9. *Scabratricolporites* sp. Moczygemba VT No. 11, 4940.75 ft.
10. *Scabratricolporites* sp. Moczygemba VT No. 11, 4964.67 ft.
11. *Scabratricolporites* sp. Moczygemba VT No. 11, 4613.50 ft.
12. *Scabratricolporites* sp. Moczygemba VT No. 11, 4912 ft.
13. *Scabratricolporites* sp. Moczygemba VT No. 11, 4945.83 ft.
14. *Scabratricolporites* sp. Jerome Olinick No. 16, 5287.58 ft.
15. *Rhoipites angustus* type. Moczygemba VT No. 11, 4897.67 ft.
16. *Rhoipites angustus* type. Moczygemba VT No. 11, 4940.75 ft.
17. *Rhoipites angustus* type. Edmond Olinick No. 1, 5646–5676 ft.
18. *Rhoipites angustus* type. Edmond Olinick No. 1, 5676–5706 ft.
19. *Rhoipites angustus* type. Edmond Olinick No. 1, 5545–5575 ft.
20a, 20b. *Rhoipites angustus* type. Moczygemba VT No. 11, 4919.83 ft.
21. *Cupuliferoipollenites* sp. Moczygemba VT No. 11, 4622 ft.
22. *Cupuliferoipollenites* sp. Moczygemba VT No. 11, 4892.50 ft.
23a, 23b. *Cupuliferoipollenites* sp. Moczygemba VT No. 11, 4622 ft.
24. *Retitricolporites* sp. Jerome Olinick No. 16, 5966 ft.
25a, 25b. *Retitricolporites* sp. Moczygemba VT No. 11, 4622 ft.
26a, 26b. *Retitricolporites* sp. Jerome Olinick No. 16, 5990 ft.
27. *Retitricolporites* sp. Moczygemba VT No. 11, 4949.50 ft.
28a, 28b. *Retitricolporites* sp. Edmond Olinick No. 1, 5099–5129 ft.
29a, 29b. *Rhoipites cryptoporus*. Moczygemba VT No. 11, 4622 ft.
Scale bar=10 µm.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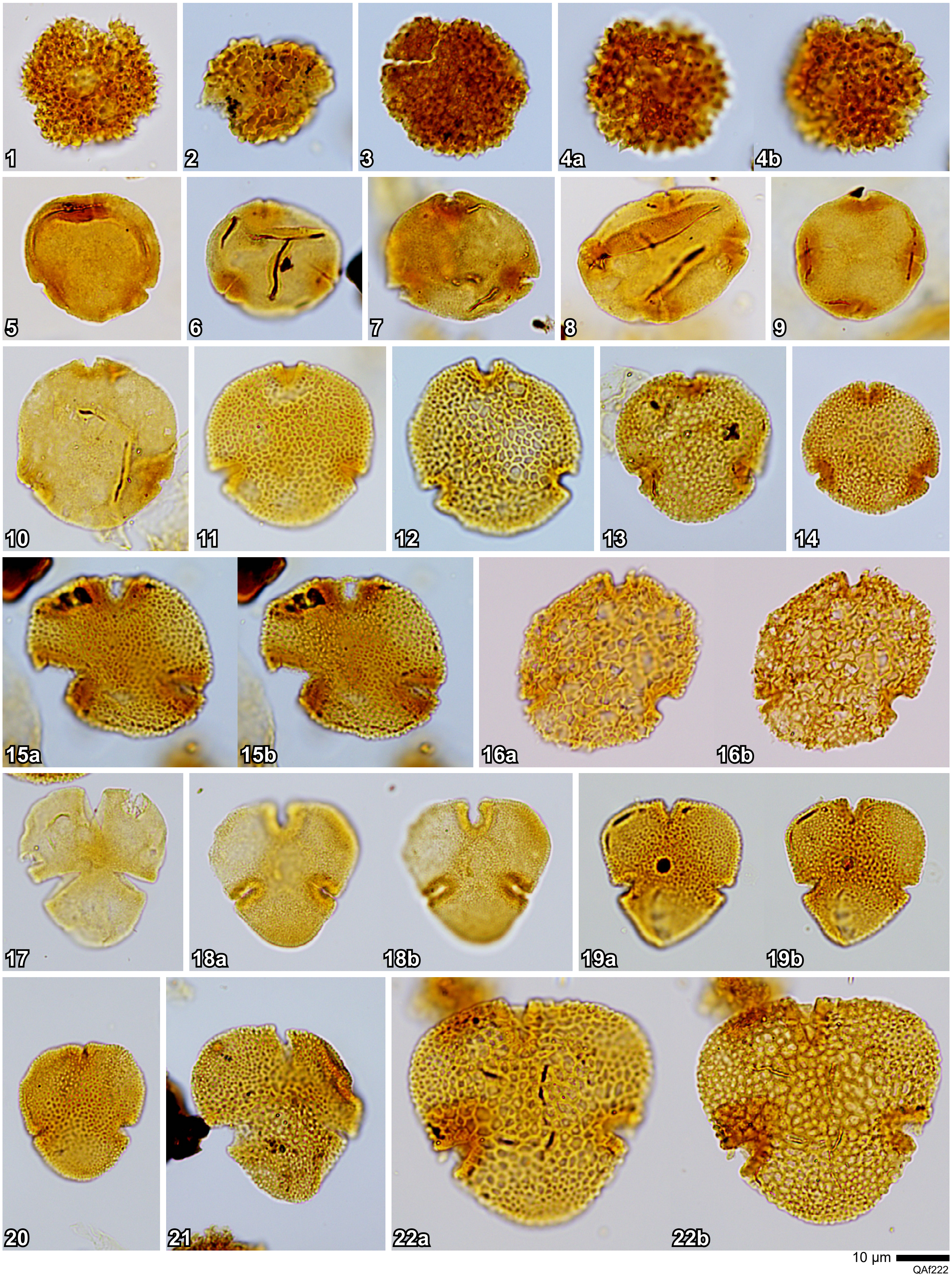
15b
16
17
18a
18b
19a
19b
20
10 µm
QAf221

Plate 11

Plate 11. Tricolporate angiosperm pollen.

1a, 1b. *Rhoipites cryptoporus*. Edmond Olinick No. 1, 5335–5365 ft.
2a, 2b. *Rhoipites cryptoporus*. Moczygemba VT No. 11, 4907.25 ft.
3. *Rhoipites cryptoporus*. Moczygemba VT No. 11, 4865.25 ft.
4a, 4b. *Rhoipites cryptoporus*. Edmond Olinick No. 1, 4949–4979 ft.
5a, 5b. *Rhoipites cryptoporus*. Jerome Olinick No. 16, 5124.58 ft.
6. *Rhoipites cryptoporus*. Moczygemba VT No. 11, 4945.83 ft.
7a, 7b, 7c. *Rhoipites* aff. *latus*. Edmond Olinick No. 1, 4979–5009 ft.
8a, 8b. *Siltaria scabriextima*. Edmond Olinick No. 1, 6161–6191 ft.
9. *Siltaria scabriextima*. Edmond Olinick No. 1, 5395–5425 ft.
10a, 10b. *Ailanthipites berryi*. Jerome Olinick No. 16, 5096.17 ft.
11a, 11b, 11c. *Ailanthipites berryi*. Moczygemba VT No. 11, 6051.67 ft.
12a, 12b. *Ailanthipites berryi*. Moczygemba VT No. 11, 4903.67 ft.
13a, 13b. *Ailanthipites nonprolatus*. Edmond Olinick No. 1, 5845–5874 ft.
14a, 14b. *Aesculiidites circumstriatus*. Moczygemba VT No. 11, 4912 ft.
15a, 15b. *Aesculiidites circumstriatus*. Moczygemba VT No. 11, 4655.33 ft.
16. *Aesculiidites circumstriatus*. Edmond Olinick No. 1, 5935–5965 ft.
17. *Aesculiidites circumstriatus*. Edmond Olinick No. 1, 5646–5676 ft.
18a, 18b. *Symplocos*? *virginiensis* group. Edmond Olinick No. 1, 5676–5706 ft.
19a, 19b. *Symplocos*? *virginiensis* group. Edmond Olinick No. 1, 5039–5069 ft.
20. *Spinaepollis spinosa*. Moczygemba VT No. 11, 4892.50 ft.
Scale bar=10 µm.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18a
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19a
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21
22a
22b
10 µm
QAf222

Plate 12

Plate 12. Tricolporate angiosperm pollen.

1. *Spinaepollis spinosa*. Moczygemba VT No. 11, 4919.83 ft.
2. *Spinaepollis spinosa*. Jerome Olinick No. 16, 5966 ft.
3. *Spinaepollis spinosa*. Jerome Olinick No. 16, 5111.67 ft.

4a, 4b. *Spinaepollis spinosa*. Edmond Olinick No. 16, 5995–6025 ft.

5. *Intratriporopollenites vescipites*. Moczygemba VT No. 11, 6072.83 ft.
6. *Intratriporopollenites vescipites*. Edmond Olinick No. 1, 5845–5874 ft.
7. *Intratriporopollenites vescipites*. Jerome Olinick No. 16, 5135.42 ft.
8. *Intratriporopollenites vescipites*. Moczygemba VT No. 11, 4907.25 ft.
9. *Intratriporopollenites vescipites*. Jerome Olinick No. 16, 5308 ft.
10. *Intratriporopollenites vescipites*. Moczygemba VT No. 11, 4884 ft.
11. *Bombacacidites reticulatus*. Edmond Olinick No. 1, 5935–5965 ft.
12. *Bombacacidites reticulatus*. Jerome Olinick No. 16, 5129.50 ft.
13. *Bombacacidites reticulatus*. Jerome Olinick No. 16, 5308 ft.
14. *Bombacacidites reticulatus*. Jerome Olinick No. 16, 5298 ft.

15a, 15b. *Bombacacidites* sp. C. Jerome Olinick No. 16, 5990 ft.

16a, 16b. *Bombacacidites* sp. C. Jerome Olinick No. 16, 5100.50 ft.

17. *Bombacacidites*? aff. *nanobrochatus*. Jerome Olinick No. 16, 5106.50 ft.

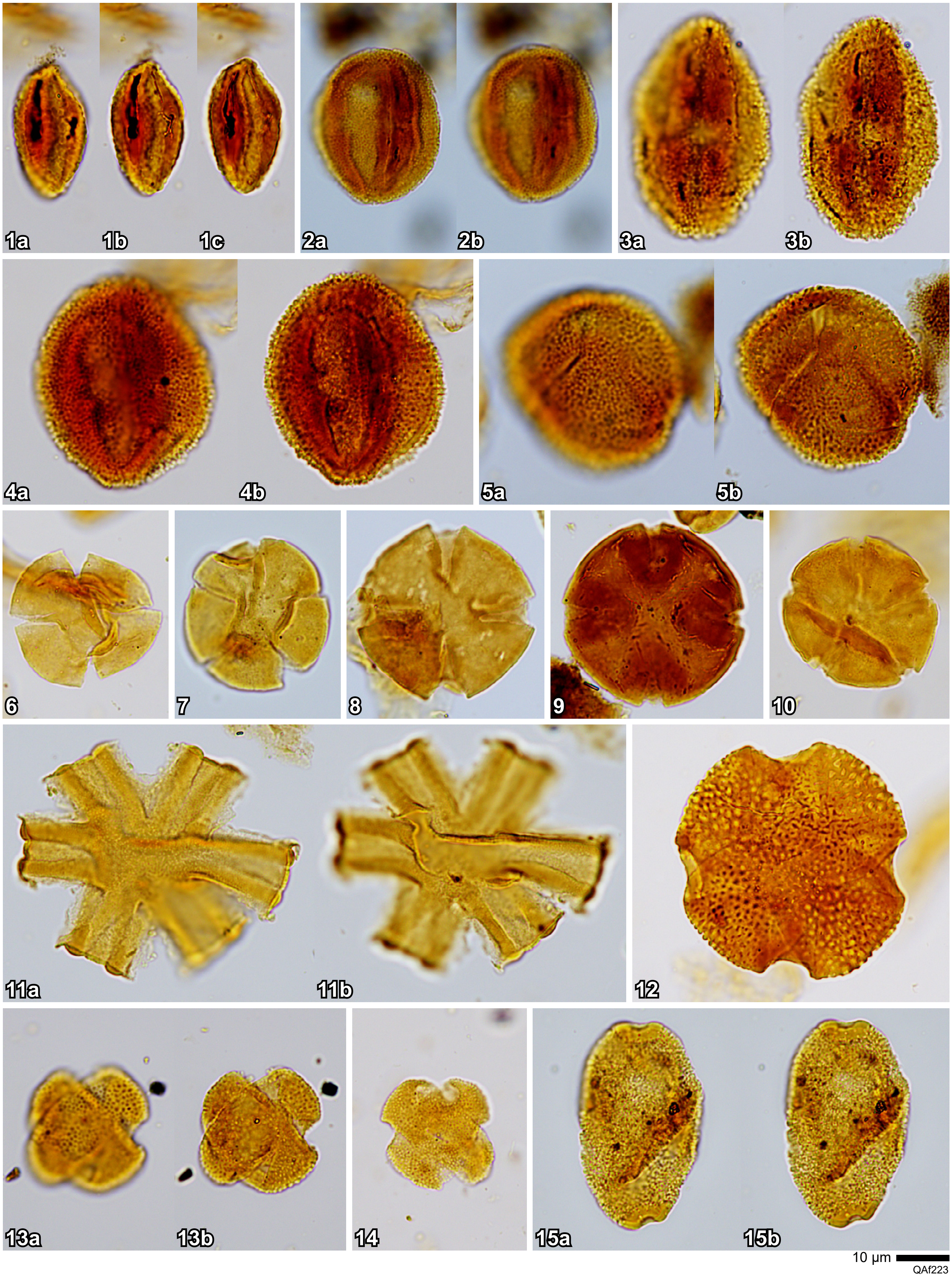
18a, 18b. *Bombacacidites nanobrochatus*. Edmond Olinick No. 1, 5099–5129 ft.

19a, 19b. *Bombacacidites bombaxoides*. Edmond Olinick No. 1, 5335–5365 ft.

20. *Bombacacidites bombaxoides*. Edmond Olinick No. 1, 4949–4979 ft.
21. *Bombacacidites nacimientoensis*. Jerome Olinick No. 16, 5135.42 ft.

22a, 22b. *Bombacacidites nacimientoensis*. Moczygemba VT No. 11, 4655.33 ft.

Scale bar=10 µm.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11a
11b
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13a
13b
14
15a
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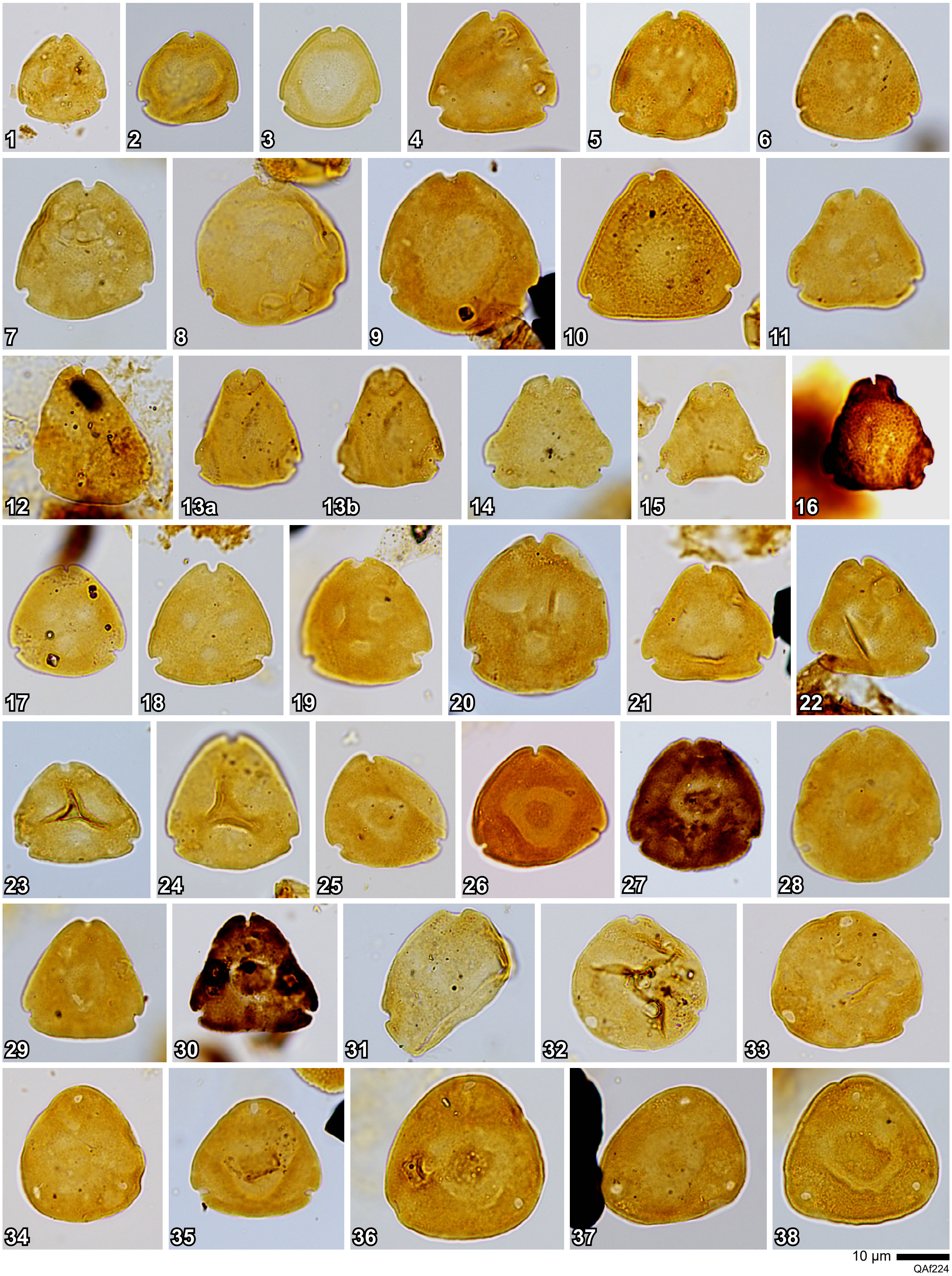
10 µm
QAf223

Plate 13

Plate 13. Tricolporate, stephanocolpate, stephanocolporate, and diporate angiosperm pollen.

1a, 1b, 1c. *Verrutricolporites* sp. A. Moczygemba VT No. 11, 4907.25 ft.
2a, 2b. *Favitricolporites baculoferus*. Jerome Olinick No. 16, 5096.17 ft.
3a, 3b. *Favitricolporites baculoferus*. Edmond Olinick No. 16, 4979–5009 ft.
4a, 4b. *Favitricolporites baculoferus*. Edmond Olinick No. 1, 4949–4979 ft.
5a, 5b. *Favitricolporites baculoferus*. Jerome Olinick No. 16, 5135.42 ft.
6. *Scabrastephanocolpites* sp. Moczygemba VT No. 11, 6047 ft.
7. *Scabrastephanocolpites* sp. Edmond Olinick No. 1, 5425–5455 ft.
8. *Quadrapollenites vagus*. Edmond Olinick No. 1, 5676–5706 ft.
9. *Quadrapollenites vagus*. Jerome Olinick No. 16, 5106.50 ft.
10. *Quadrapollenites vagus*. Moczygemba VT No. 11, 4940.75 ft.
11a, 11b. *Stephanocolpites* sp. A. Edmond Olinick No. 1, 4949–4979 ft.
12. aff. *Lanagiopollis lihoka* (4-colporate). Moczygemba VT No. 11, 4907.25 ft.
13a, 13b. *Retistephanocolpites* sp. A. Moczygemba VT No. 11, 4632.33 ft.
14. *Retistephanocolpites* sp. A. Moczygemba VT No. 11, 4907.25 ft.
15a, 15b. *Retidiporites* sp. A. Edmond Olinick No. 1, 5039–5069 ft.
Scale bar=10 µm.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34
35
36
37
38
10 µm
QAf224

Plate 14

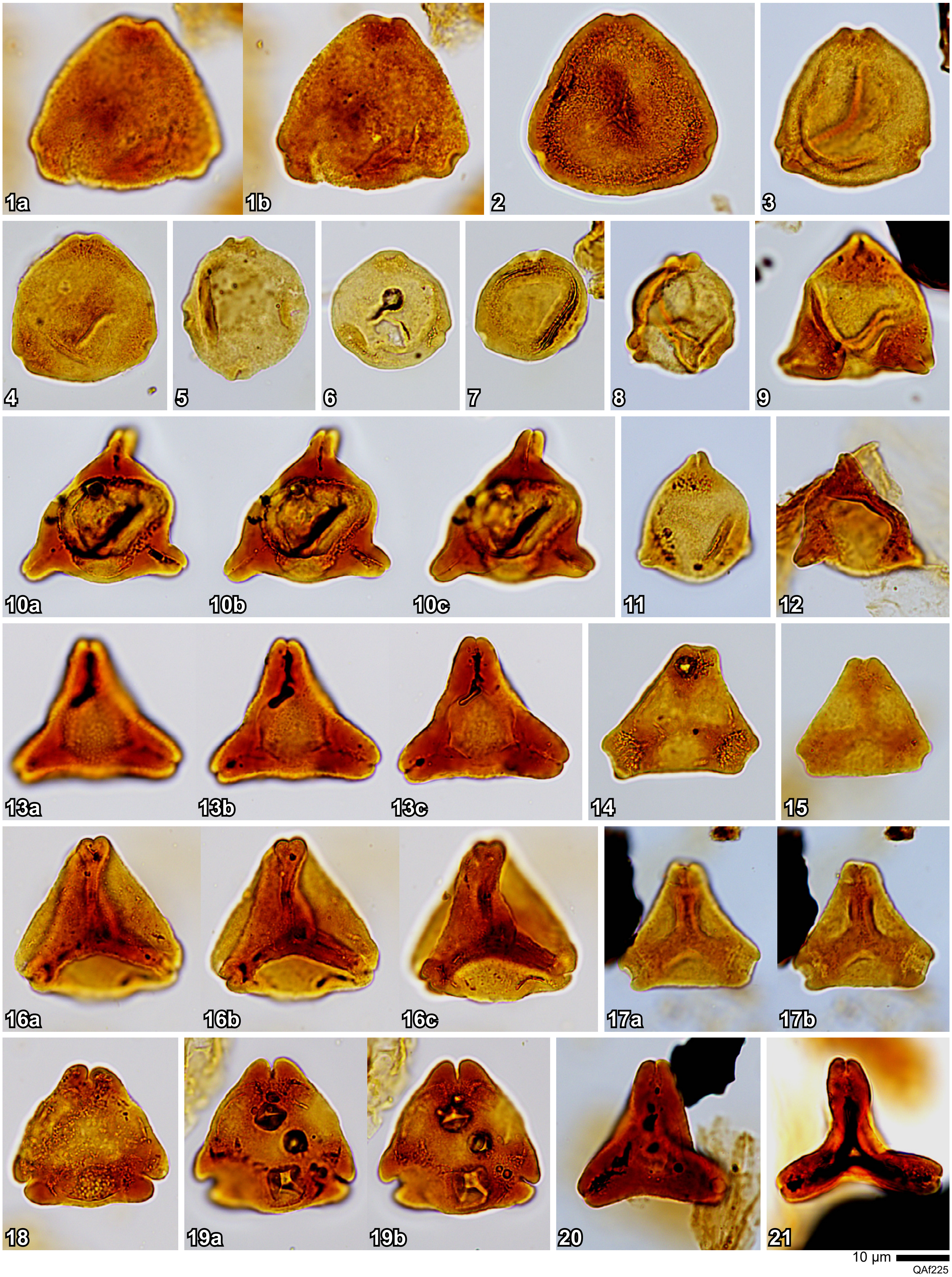
Plate 14. Triporate angiosperm pollen.

1. *Momipites tenuipolus*. Moczygemba VT No. 11, 4976.33 ft.
2. *Momipites tenuipolus*. Moczygemba VT No. 11, 4643 ft.
3. *Momipites tenuipolus*. Edmond Olinick No. 1, 5039–5069 ft.
4. *Momipites coryloides* (20–27 µm). Moczygemba VT No. 11, 4610 ft.
5. *Momipites coryloides* (20–27 µm). Edmond Olinick No. 1, 6161–6191 ft.
6. *Momipites coryloides* (20–27 µm). Edmond Olinick No. 1, 5845–5874 ft.
7. *Momipites coryloides* (20–27 µm). Edmond Olinick No. 1, 5039–5069 ft.
8. *Momipites coryloides* (>27 µm). Moczygemba VT No. 11, 4613.50 ft.
9. *Momipites coryloides* (>27 µm). Jerome Olinick No. 16, 5966 ft.
10. *Momipites waltmanensis*. Moczygemba VT No. 11, 4655.33 ft.
11. *Momipites waltmanensis*. Edmond Olinick No. 1, 5099–5129 ft.
12. *Momipites inaequalis*. Jerome Olinick No. 16, 5096.17 ft.

13a, 13b. *Momipites* cf. *inaequalis*. Moczygemba VT No. 11, 4613.50 ft.

14. *Momipites dilatus*. Jerome Olinick No. 16, 5292.42 ft.
15. *Momipites dilatus*. Moczygemba VT No. 11, 4935.17 ft.
16. *Momipites dilatus*. Lawrence Keseling No. 1, 10888 ft.
17. *Momipites rotundus*. Moczygemba VT No. 11, 4935.17 ft.
18. *Momipites rotundus*. Jerome Olinick No. 16, 5199.33 ft.
19. *Momipites rotundus*. Moczygemba VT No. 11, 4622 ft.
20. *Momipites rotundus*. Edmond Olinick No. 1, 5515–5545 ft.
21. *Momipites triorbicularis*. Moczygemba VT No. 11, 4919.83 ft.
22. *Momipites triorbicularis*. Edmond Olinick No. 1, 5515–5545 ft.
23. *Momipites triradiatus* type. Jerome Olinick No. 16, 5221.92 ft.
24. *Momipites triradiatus* type. Jerome Olinick No. 16, 5119 ft.
25. *Momipites anellus*. Moczygemba VT No. 11, 6063.83 ft.
26. *Momipites anellus*. Edmond Olinick No. 1, 5676–5706 ft.
27. *Momipites anellus*. Lawrence Keseling No. 1, 11038 ft.
28. *Momipites amplus*. Edmond Olinick No. 1, 5395–5425 ft.
29. *Momipites leffingwellii*. Edmond Olinick No. 1, 6161–6191 ft.
30. *Momipites leffingwelii*. Lawrence Keseling No. 1, 11063.42 ft.
31. *Caryapollenites–Momipites* sp. Moczygemba VT No. 11, 4627.75 ft.
32. *Caryapollenites* aff. *imparalis*. Moczygemba VT No. 11, 4971.75 ft.
33. *Caryapollenites imparalis*. Moczygemba VT No. 11, 4907.25 ft.
34. *Caryapollenites inelegans*. Moczygemba VT No. 11, 4945.83 ft.
35. *Caryapollenites prodromus*. Edmond Olinick No. 1, 5845–5874 ft.
36. *Caryapollenites wodehousei*. Jerome Olnick No. 16, 5119 ft.
37. *Caryapollenites veripites*. Moczygemba VT No. 11, 4610 ft.
38. *Caryapollenites veripites*. Edmond Olinick No. 1, 5455–5485 ft.

Scale bar=10 µm.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16a
16b
16c
17a
17b
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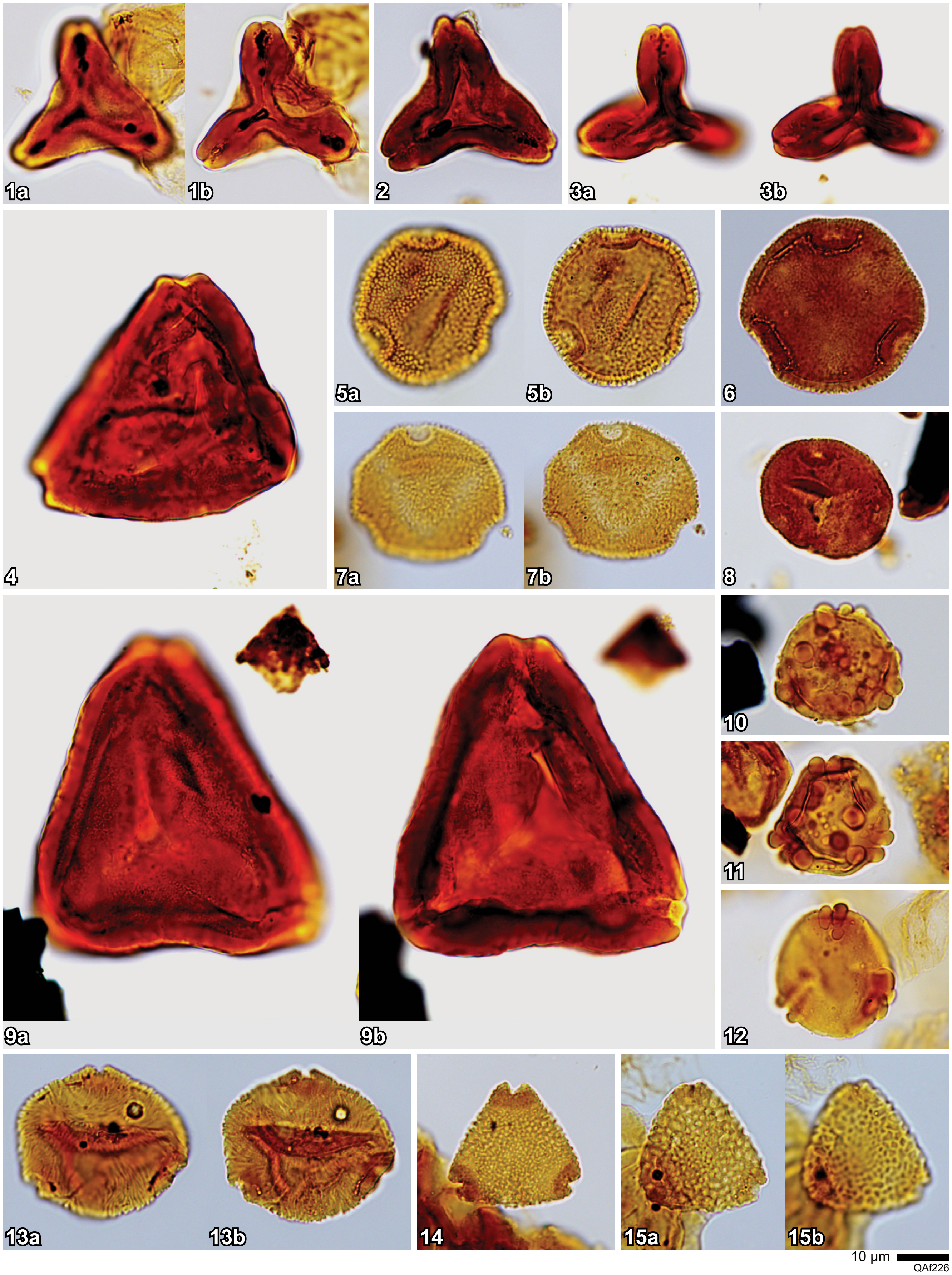
19a
19b
20
21
10 µm
QAf225

Plate 15

Plate 15. Triporate angiosperm pollen.

1a, 1b. Betulaceae–Myricaceae type. Edmond Olinick No. 1, 4949–4979 ft.
2. Betulaceae–Myricaceae type. Moczygemba VT No. 11, 4971.75 ft.
3. Betulaceae–Myricaceae type. Edmond Olinick No. 1, 5676–5706 ft.
4. Betulaceae–Myricaceae type. Moczygemba VT No. 11, 4935.17 ft.
5. Betulaceae–Myricaceae type. Edmond Olinick No. 1, 5039–5069 ft.
6. Betulaceae–Myricaceae type. Moczygemba VT No. 11, 4643 ft.
7. Betulaceae–Myricaceae type. Moczygemba VT No. 11, 4643 ft.
8. *Trivestibulopollenites* sp. Edmond Olinick No. 1, 5995–6025 ft.
9. *Nudopollis terminalis*. Edmond Olinick No. 1, 5158–5188 ft.
10a, 10b, 10c. *Nudopollis terminalis*. Moczygemba VT No. 11, 4971.75 ft.
11. *Nudopollis terminalis*. Edmond Olinick No. 1, 5995–6025 ft.
12. *Nudopollis terminalis*. Edmond Olinick No. 1, 5845–5874 ft.
13a, 13b, 13c. *Nudopollis* aff. *endangulatus*. Moczygemba VT No. 11, 4610 ft.
14. *Plicapollis vacuus*. Jerome Olinick No. 16, 5226 ft.
15. *Plicapollis vacuus*. Edmond Olinick No. 1, 5935–5965 ft.
16a, 16b, 16c. *Pseudoplicapollis limitata*. Moczygemba VT No. 11, 4888 ft.
17a, 17b. *Plicapollis vacuus*. Jerome Olinick No. 16, 5960.33 ft.
18. *Trudopollis plenus*. Moczygemba VT No. 11, 4907.25 ft.
19a, 19b. *Trudopollis plenus*. Moczygemba VT No. 11, 4865.25 ft.
20. *Choanopollenites alabamicus*. Edmond Olinick No. 1, 4979–5009 ft.
21. *Choanopollenites alabamicus*. Edmond Olinick No. 1, 4979–5009 ft.
Scale bar=10 µm.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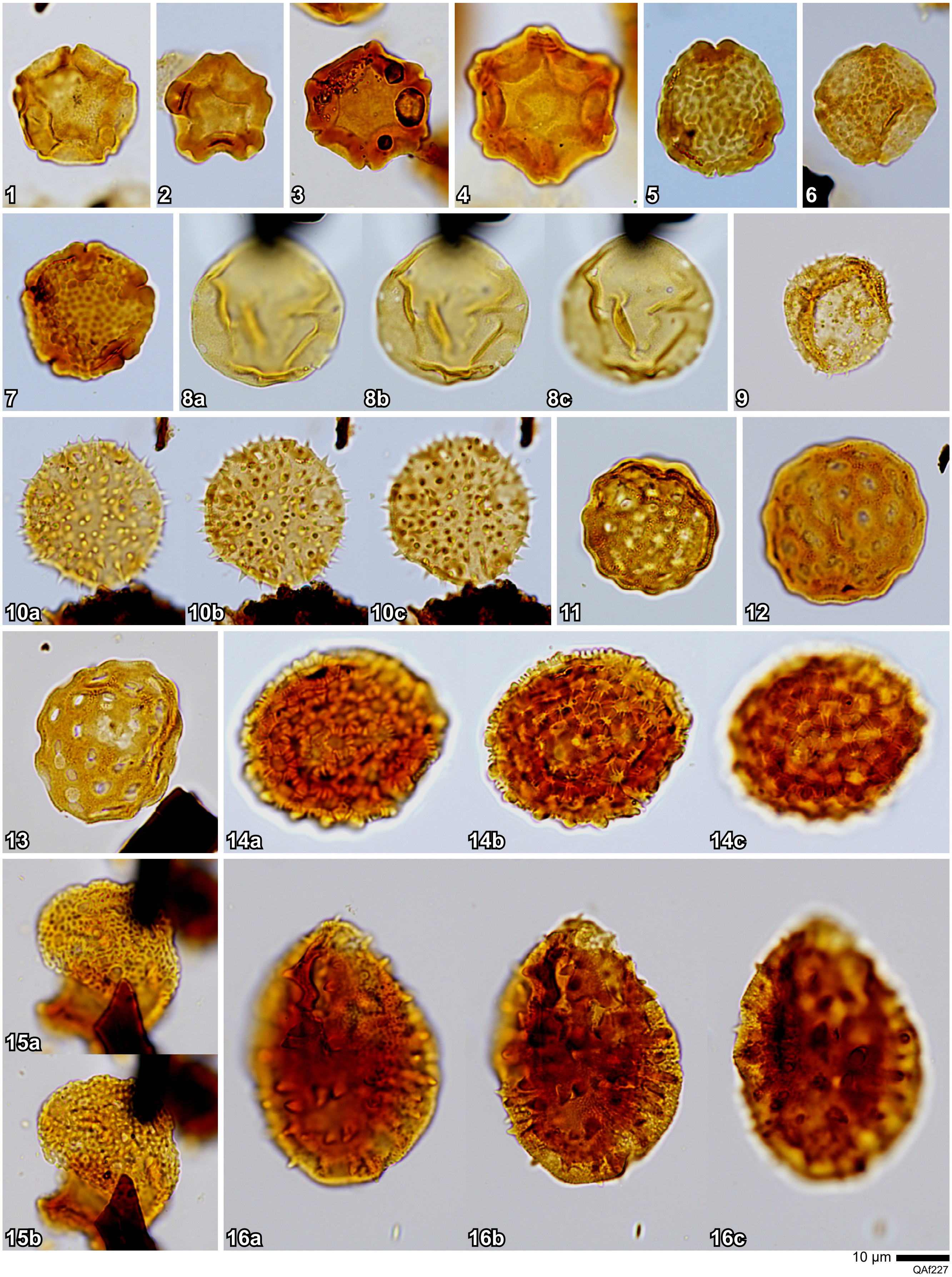
13a
13b
14
15a
15b
10 µm
QAf226

Plate 16

Plate 16. Triporate angiosperm pollen.

1a, 1b. *Choanopollenites alabamicus*. Moczygemba VT No. 11, 4884 ft.
2. *Choanopollenites alabamicus*. Edmond Olinick No. 1, 4979–5009 ft.
3a, 3b. *Choanopollenites alabamicus*. Moczygemba VT No. 11, 4638 ft.
4. *Choanopollenites* aff. *eximius* (small). Jerome Olinick No. 16, 5119 ft.
5a, 5b. *Thomsonipollis magnificus*. Moczygemba VT No. 11, 4643 ft.
6. *Thomsonipollis magnificus*. Jerome Olinick No. 16, 5100.50 ft.
7a, 7b. *Thomsonipollis magnificus*. Jerome Olinick No. 16, 5298 ft.
8. *Thomsonipollis magnificus*. Jerome Olinick No. 16, 5951 ft.
9a, 9b. *Choanopollenites* aff. *eximius* (small). Moczygemba VT No. 11, 4643 ft.
10. *Pistillipollenites mcgregorii*. Jerome Olinick No. 16, 5096.17 ft.
11. *Pistillipollenites mcgregorii*. Moczygemba VT No. 11, 4945.83 ft.
12. *Pistillipollenites mcgregorii*. Moczygemba VT No. 11, 4884 ft.
13a, 13b. *Brosipollis striata*. Edmond Olinick No. 1, 5395–5425 ft.
14. *Tschudypollis retusus*. Jerome Olinick No. 16, 5106.50 ft.
15a, 15b. *Tschudypollis retusus*. Jerome Olinick No. 16, 5135.42 ft.
Scale bar=10 µm.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14c
15a
15b
16a
16b
16c
10 µm
QAf227

Plate 17

Plate 17. Stephanoporate and pantoporate angiosperm pollen.

1. *Alnus verus*. Moczygemba VT No. 11, 4919.83 ft.
2. *Alnus verus*. Jerome Olinick No. 16, 5966 ft.
3. *Alnus verus*. Moczygemba VT No. 11, 6051.67 ft.
4. *Alnus scotica*. Edmond Olinick No. 1, 5545–5575 ft.
5. *Ulmipollenites krempii*. Edmond Olinick No. 1, 6161–6191 ft.
6. *Ulmipollenites krempii*. Jerome Olinick No. 16, 5100.50 ft.
7. *Ulmipollenites krempii*. Edmond Olinick No. 1, 5845–5874 ft.

8a, 8b, 8c. *Juglans nigripites*. Edmond Olinick No. 1, 5935–5965 ft.

9. *Malvacipollis* sp. (Euphorbiaceae type). Moczygemba VT No. 11, 4884 ft.

10a, 10b, 10c. *Malvacipollis* sp. (Euphorbiaceae type). Edmond Olinick No. 1, 5845–5874 ft.

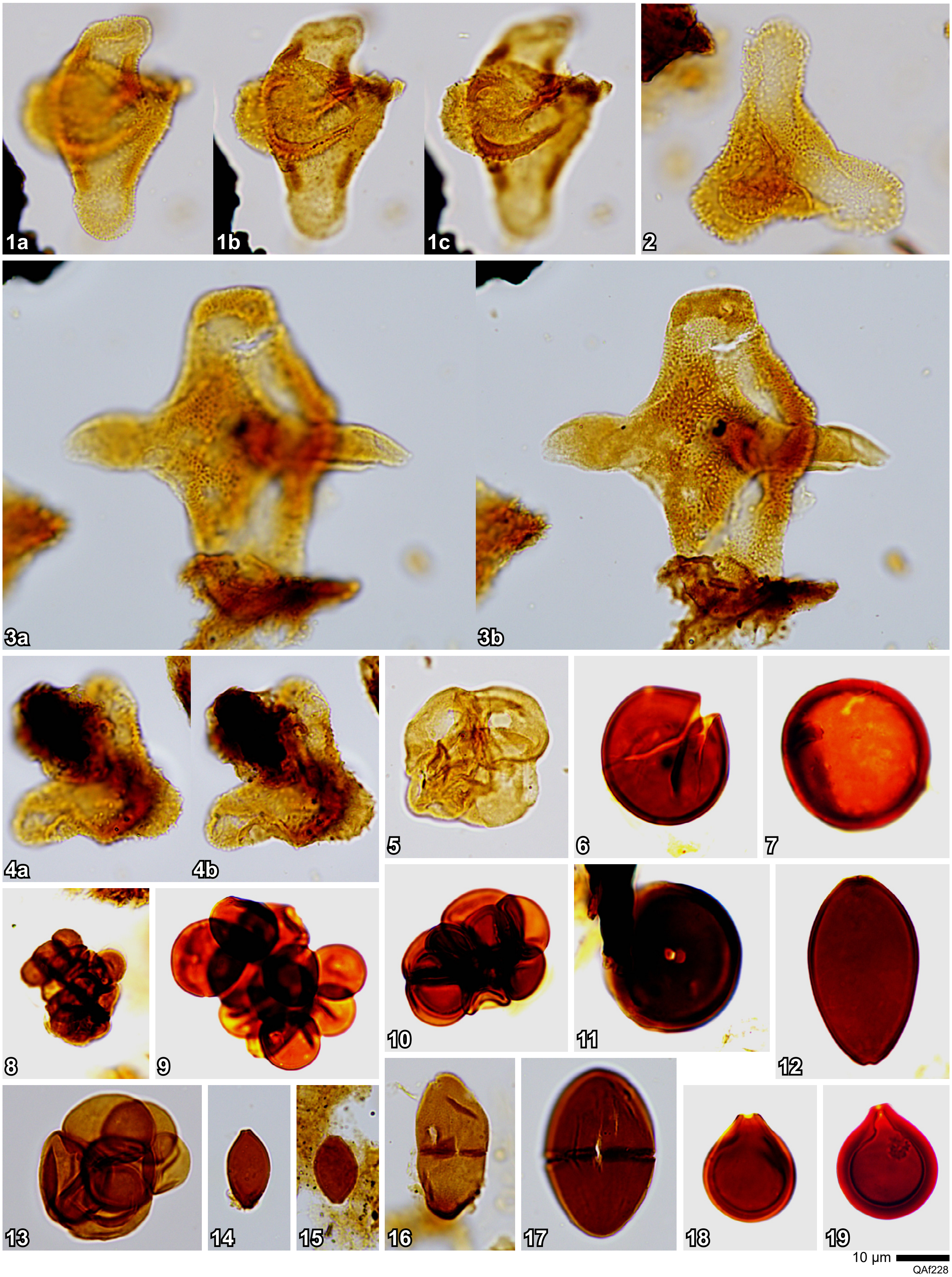
11. *Chenopodipollis* sp. Jerome Olinick No. 16, 5124.58 ft.
12. *Chenopodipollis* sp. Edmond Olinick No. 1, 5335–5365 ft.
13. *Chenopodipollis* sp. Moczygemba VT No. 11, 4940.75 ft.

14a, 14b, 14c. *Erdtmanipollis pachysandroides*. Jerome Olinick No. 16, 5135.42 ft.

15a, 15b. Thymelaeaceae? sp. A. Moczygemba VT No. 11, 4892.50 ft.

16a, 16b, 16c. *Wodehouseia spinata*. Moczygemba VT No. 11, 4610 ft.

Scale bar=10 µm.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19
10 µm
QAf228

Plate 18

Plate 18. Triprojectate angiosperm pollen, jugate angiosperm pollen, and fungi.

1a, 1b, 1c. *Aquilapollenites* aff. *attenuatus*. Moczygemba VT No. 11, 4632.33 ft.
2. *Aquilapollenites* aff. *attenuatus*. Moczygemba VT No. 11, 4892.50 ft.
3a, 3b. *Integricorpus reticulatus*. Jerome Olinick No. 16, 5106.50 ft.
4a, 4b. *Aquilapollenites spinulosus*. Lawrence Keseling No. 1, 8994.17 ft.
5. *Ericipites* sp. Moczygemba VT No. 11, 4940.75 ft.
6. *Inapertisporites* sp. Edmond Olinick No. 1, 4949–4979 ft.
7. *Inapertisporites* sp. Jerome Olinick No. 1, 5124.58 ft.
8. *Microsporonites* sp. Moczygemba VT No. 11, 4925.67 ft.
9. *Microsporonites* sp. Jerome Olinick No. 16, 5951 ft.
10. *Microsporonites* sp. Moczygemba VT No. 11, 4638 ft.
11. *Diporisporites* sp. A. Jerome Olinick No. 16, 5221.92 ft.
12. *Diporisporites* sp. B. Moczygemba VT No. 11, 4888 ft.
13. *Microsporonites* sp. Moczygemba VT No. 11, 4935.17 ft.
14. *Diporisporites hammenii*. Moczygemba VT No. 11, 4870.50 ft.
15. *Diporisporites hammenii*. Moczygemba VT No. 11, 4903.67 ft.
16. *Dicellaesporites* sp. Moczygemba VT No. 11, 4870.50 ft.
17. *Dicellaesporites* sp. Moczygemba VT No. 11, 4949.50 ft.
18. *Monoporisporites* sp. Edmond Olinick No. 1, 5039–5069 ft.
19. *Monoporisporites* sp. Moczygemba VT No. 11, 4627.75 ft.

Scale bar=10 µm.

Plate 19

Plate 19. Fungi.

1. *Dicellaesporites* sp. Jerome Olinick No. 16, 5966 ft.
2. *Dicellaesporites* sp. Jerome Olinick No. 16, 5111.67 ft.
3. *Dicellaesporites* sp. Lawrence Keseling No. 1, 10982.58 ft.
4. *Fusiformisporites crabbii*. Moczygemba VT No. 11, 4874 ft.
5. *Fusiformisporites crabbii*. Moczygemba VT No. 11, 4945.83 ft.
6. *Fusiformisporites crabbii*. Jerome Olinick No. 16, 5106.50 ft.
7. *Dicellaeporisporites* sp. A. Jerome Olinick No. 16, 5966 ft.

8a, 8b. Phragmosporae sp. B. Moczygemba VT No. 11, 4884 ft.

9a, 9b. *Multicellites*? sp. A (echinate). Lawrence Keseling No. 1, 10957.17 ft.

10. Phragmosporae sp. A. Moczygemba VT No. 11, 4655.33 ft.
11. Phragmosporae sp. Jerome Olinick No. 16, 5221.92 ft.
12. Phragmosporae sp. Lawrence Keseling No. 1, 10957.17 ft.
13. Phragmosporae sp. Jerome Olinick No. 16, 5226 ft.
14. Phragmosporae sp. Moczygemba VT No. 11, 4648.33 ft.
15. Phragmosporae sp. Jerome Olinick No. 16, 5298 ft.

16a, 16b. *Pesavis tagluensis*. Jerome Olinick No. 16, 5226 ft.

17. *Pesavis tagluensis*. Jerome Olinick No. 16, 5226 ft.
18. *Pesavis tagluensis*. Moczygemba VT No. 11, 4953.92 ft.

Scale bar=10 µm.

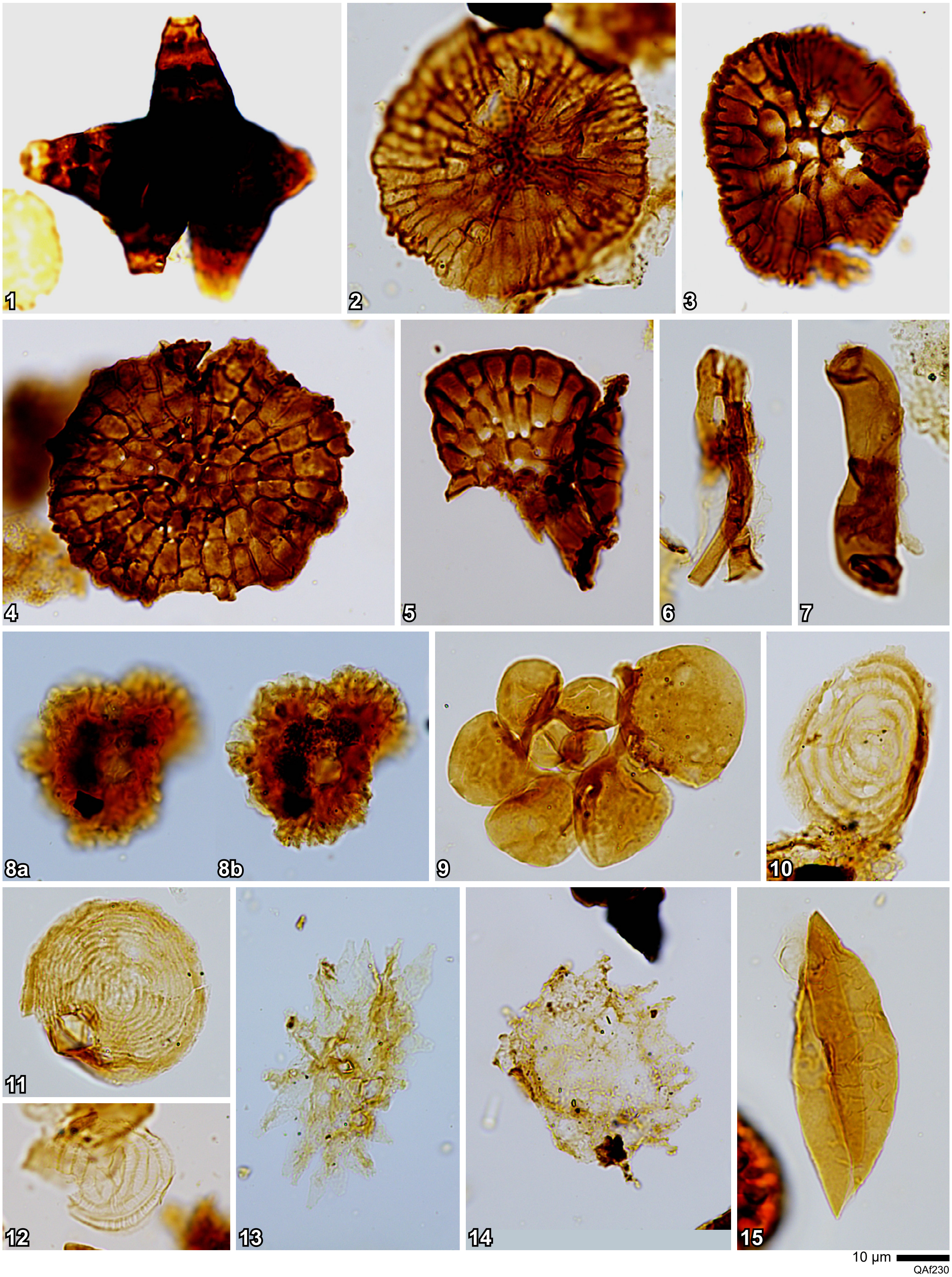

Plate 20

Plate 20. Fungi and algae.

1. Staurosporae sp. Jerome Olinick No. 16, 5124.58 ft.
2. *Phragmothyrites* sp. Jerome Olinick No. 16, 5951 ft.
3. *Phragmothyrites* sp. Lawrence Keseling No. 1, 10964.58 ft.
4. *Callimothallus* sp. Lawrence Keseling No. 1, 10957.17 ft.
5. *Callimothallus* sp. Moczygemba VT No. 11, 4907.25 ft.
6. Fungal hyphae. Jerome Olinick No. 16, 5226 ft.
7. Fungal hyphae. Edmond Olinick No. 1, 5395–5425 ft.

8a, 8b. *Botrococcus braunii*. Jerome Olinick No. 16, 5111.67 ft.

9. Foraminiferal test lining. Jerome Olinick No. 16, 5951 ft.
10. *Pseudoschizaea circula*. Edmond Olinick No. 1, 5545–5575 ft.
11. *Pseudoschizaea circula*. Jerome Olinick No. 16, 5119 ft.
12. *Pseudoschizaea circula*. Moczygemba VT No. 11, 6072.83 ft.
13. *Pediastrum* sp. Jerome Olinick No. 16, 5990 ft.
14. *Pediastrum* sp. Lawrence Keseling No. 1, 9004 ft.
15. *Ovoidites* sp. Jerome Olinick No. 16, 5102 ft.

Scale bar=10 µm.

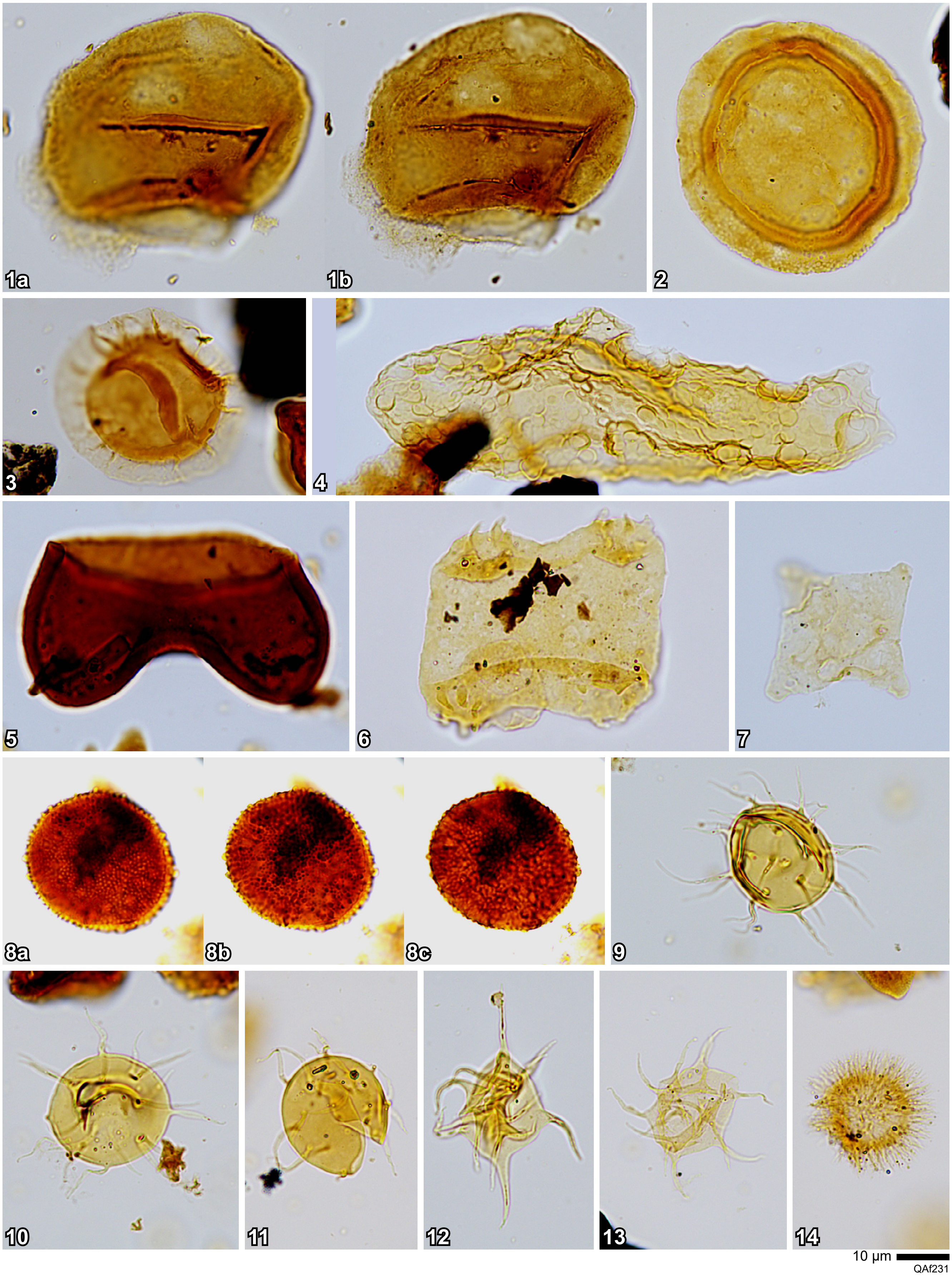

Plate 21

Plate 21. Algae and acritarchs.

1a, 1b. *Catillopsis abdita*?. Moczygemba VT No. 11, 6051.67 ft.
2. *Pterospermopsis*? sp. A. Moczygemba VT No. 11, 6051.67 ft.
3. *Pterospermopsis* sp. Moczygemba VT No. 11, 4613.50 ft.
4. *Stigmozygodites* sp. Jerome Olinick No. 16, 5204.75 ft.
5. *Schizocystia rugosa*. Jerome Olinick No. 16, 5966 ft.
6. *Tetraporina spinifera*. Edmond Olinick No. 1, 4979–5009 ft.
7. *Tetraporina* sp. (psilate). Edmond Olinick No. 1, 5676–5706 ft.
8a, 8b, 8c. *Tasmanites* sp. A. Lawrence Keseling No. 1, 10995.08 ft.
9. *Baltisphaeridium* aff. *distentum*. Edmond Olinick No. 1, 5039–5069 ft.
10. *Baltisphaeridium* aff. *distentum*. Jerome Olinick No. 16, 5951 ft.
11. *Baltisphaeridium* aff. *distentum*. Moczygemba VT No. 11, 6047 ft.
12. *Micrhystridium*? sp. A. Jerome Olinick No. 16, 5951 ft.
13. *Micrhystridium*? sp. A. Moczygemba VT No. 11, 4912 ft.
14. *Comasphaeridium* sp. A. Moczygemba VT No. 11, 4622 ft.

Scale bar=10 µm.