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Paleocene–Eocene palynomorphs from the Chicxulub impact crater, Mexico. Part 2: angiosperm pollen

Vann Smith^{a,b} , Sophie Warny^{a,b}, David M. Jarzen^c, Thomas Demchuk^a, Vivi Vajda^d and Sean P.S. Gulick^e

^aDepartment of Geology and Geophysics, LSU, Baton Rouge, LA, USA; ^bMuseum of Natural Science, LSU, Baton Rouge, LA, USA; ^cCleveland Museum of Natural History, Cleveland, OH, USA; ^dSwedish Museum of Natural History, Stockholm, Sweden; ^eInstitute for Geophysics and Department of Geological Sciences, Jackson School of Geosciences, University of Texas at Austin, TX, USA

ABSTRACT

At the end of the Cretaceous Period, an asteroid collided with the Earth and formed the Chicxulub impact structure on the Yucatán Platform. International Ocean Discovery Program (IODP) Expedition 364 drilled into the peak ring of the Chicxulub impact crater. The post-impact section of the core was sampled for terrestrial palynological analysis, yielding a high-resolution record ranging from the early Paleocene to the earliest Eocene (Ypresian), including a black shale deposited during the Paleocene–Eocene Thermal Maximum (PETM). The IODP 364 core provides the first record of floral recovery following the K–Pg mass extinction from inside the Chicxulub impact crater. The systematic taxonomy of the angiosperm pollen provided here follows a separate publication describing the systematic paleontology of the plant spores and gymnosperm pollen from the IODP 364 core (Smith et al. 2019). The Paleocene section of the core is nearly barren, but with unusually high relative abundances of the angiosperm pollen *Chenopodipollis* sp. A (comparable to the Amaranthaceae), possibly indicating an estuarine pollen source. Pollen recovery is higher in the PETM section, and variable but generally increasing in the later Ypresian section, with excellent preservation in several samples. Estimated absolute ages of several potentially useful regional biostratigraphic events are provided. One new genus (*Scabristephanoporites*) and five new species (*Brosipollis reticulatus*, *Echimonocolpites chicxulubensis*, *Psilastephanocolporites hammenii*, *Scabristephanoporites variabilis*, and *Striatopollis grahamii*) are formally described.

KEYWORDS

Mexico; Paleocene; Eocene; PETM; Cretaceous–Paleogene boundary; angiosperm pollen

1. Introduction

The geologic background for the International Ocean Discovery Program (IODP) 364 core has been described in Smith et al. (2019). Further information about IODP 364 and the Chicxulub impact event can be found in Schulte et al. (2010), Morgan et al. (2016, 2017), Gulick et al. (2017, 2019), and Lowery et al. (2018). The systematic paleontology of the angiosperm pollen presented here provides an essential basis for the interpretation of the terrestrial palynology within the Chicxulub impact crater, and the development of the vegetation in the vicinity of the crater through the Paleocene to early Eocene. The Paleogene palynology of the Yucatán Peninsula is nearly unknown. Apart from Holocene palynological studies (e.g. Correa-Metrio et al. 2011; Aragón-Moreno et al. 2012), the only publications on the palynology of the Yucatán Peninsula are based on Deep Sea Drilling Project (DSDP) Site 94 on the Campeche escarpment, where a late Eocene to early Miocene pollen assemblage was recovered (Barron 2015; Barron et al. 2017). During the Cretaceous, the Yucatán Peninsula was part of the *Aquillapollenites* province (Herngreen et al. 1996; Vajda and Bercovici 2014), characterized by abundant representatives of the morphologically distinctive *Aquillapollenites* pollen group. The K–Pg mass

extinction affected most representatives of this group, and the post-extinction palynological assemblages are thus clearly different compared with the Maastrichtian ones, within both the *Aquillapollenites* province and the *Palmae* province located in the paleo-tropical belt. Geographically proximal Paleogene palynological assemblages have been described from the Eocene and Oligocene of Cuba (Areces-Mallea 1987, 1988, 1990; Graham et al. 2000), the Oligocene of Puerto Rico (Graham and Jarzen 1969), the Eocene of Jamaica (Graham 1993), the Eocene of Panama (Graham 1985), and various Paleocene–Oligocene sections in mainland Mexico (e.g. Biaggi 1978; Martínez-Hernández et al. 1980; Tomasini-Ortiz and Martínez-Hernández 1984; Graham 1999; Martínez-Hernández and Ramírez-Arriaga 1999; Altamira-Areyán 2002; Ramírez-Arriaga et al. 2006; Carrasco-Velázquez et al. 2009; Ramírez-Arriaga, Prámparo, et al. 2014; Ramírez-Arriaga and Reyes-Salas 2014; Ramírez-Arriaga et al. 2017).

2. Methods

The palynological sample processing methods used here are identical to those described in Smith et al. (2019), and essentially follow methods described by Traverse (2007). Slides were scanned until 300 identifiable pollen and spore grains

CONTACT Vann Smith  vannpaleo@gmail.com  Department of Geology and Geophysics, LSU, Baton Rouge, LA, USA.

 Supplemental data for this article can be accessed [here](#).

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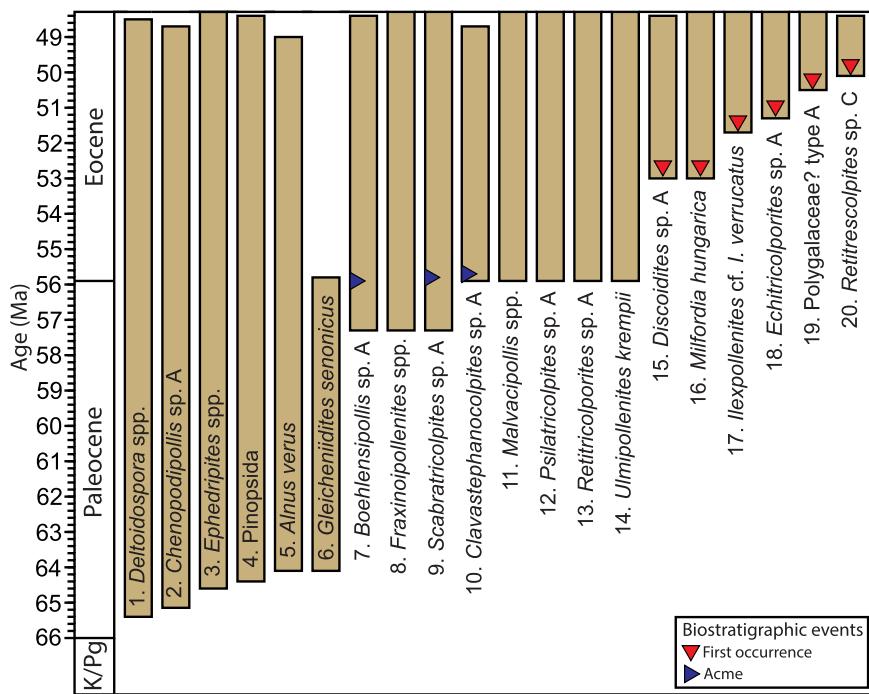


Figure 1. Observed stratigraphic ranges and events for selected taxa recovered from the IODP 364 core, organized by first occurrence datum. Ranges are illustrated for biostratigraphically important taxa (ranges 7, 9–10, 15–20), particularly abundant taxa (ranges 8, 11–14), and taxa with observed ranges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

were counted, or until the slides at a sample depth were fully scanned. For each species, size ranges are given, with a mean size given in parentheses for species with more than 10 measured specimens. Abundance data for all samples are provided in the [Supplementary material](#). Absolute age estimates for biostratigraphic events are constrained by foraminiferal and nannofossil biostratigraphy. The age model is provided as [Supplementary material](#), modified from Gulick et al. (2017) (Chris Lowery, personal communication, 2019), following the Gradstein et al. (2012) time scale. The bottom and top of the Paleocene–Eocene Thermal Maximum (PETM) are given age estimates of 55.93 Ma and 55.71 Ma, respectively (Westerhold et al. 2017; Hollis et al. 2019). Potentially useful biostratigraphic events are given an age range based on age estimates of the nearest biostratigraphic events, with an estimated age in parentheses based on linear interpolation, assuming a constant sedimentation rate. Age estimates are also provided for each sample depth along with the quantitative counts, using the age model and linear interpolation (linear extrapolation for the top sample depth). Observed ranges of common and biostratigraphically useful taxa are illustrated in Figure 1.

3. Morphology, systematic nomenclature, and paleoecological interpretation

As in Smith et al. (2019), morphological terminology generally follows Punt et al. (2007); however, in this study, the term 'striae' will refer to the elevated sculptural elements in striate sculpture, following Hesse et al. (2009). Botanical affinities are based on reviews of the scientific literature or by comparison

with modern pollen from the Center for Excellence in Palynology (CENEX) research collection at Louisiana State University (LSU). Paleoecological interpretations are generally based on the modern ecologies of plants which produce pollen similar to the observed fossil pollen, or based on previous paleoecological interpretations in the literature, particularly those of Ramírez-Arriaga, Prámparo et al. (2014). The paleoecologies of Paleocene and lower Eocene ancestors of modern plants may be different than those of their modern descendants (e.g. Frederiksen 1985), so the paleoecological interpretations provided here are considered tentative.

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

Paleogene of North America (including Mexico) and South America. This information is only given for taxa with reasonably well-established paleogeographic ranges in the literature. Paleogeographic distribution was determined using the database of Palynodata Inc. and White (2008), Graham (2010), and a review of the literature.

Pollen are generally identified using form genera, in many cases using informal species names (sp. A, sp. B, etc.). Several genera named in this study were first proposed (originally as subgenera) by van der Hammen (1954, 1956) in an attempt to create a standardized system of classification based on pollen morphology. Because he chose modern pollen as his type species for these form genera, technically his form genera are all junior synonyms of whatever natural genus the modern pollen belonged to (Jansonius and Hills 1976; Potonié 1960). This is an unfortunate technicality, because the reasoning was sound; by choosing modern species as the type species of form genera, access to the 'type material' only requires access to pollen or spores of the modern species. Despite the questionable validity of some of van der Hammen's genera, his form generic names are quite useful for classifying pollen of unknown botanical affinity using morphology. For some of these genera, new type species of fossil pollen were later chosen, validating the generic name (e.g. van der Hammen and Wymstra 1964). Hoorn (1993) has argued that invalidly published form genera can be later validated by designating a new holotype and type species.

The following systematic paleontology section has been condensed and abbreviated for publication, with a focus on new species, abundant taxa, or otherwise notable taxa. A comprehensive systematic paleontology, with full descriptions for all species, is provided in the [Supplementary material](#). Light microscopy (LM) images are provided in [Plates 1–13](#), organized by aperture class and exine sculpture, and scanning electron microscopy (SEM) images are provided in [Plates 14–15](#). [Plate 14](#) also includes some SEM images of spore and gymnosperm pollen taxa previously described in Smith et al. (2019), namely *Raistrickia* sp. A ([Plate 14](#), figure 1), *Gnetaceaepollenites* sp. A ([Plate 14](#), figure 2), and Class Pinopsida ([Plate 14](#), figure 3). LM images with a dark gray or blue background are phase contrast images. Depending on the specimen, phase contrast images sometimes provided a better visualization of morphological features, particularly more transparent specimens and specimens with finely reticulate sculpture. In other cases, standard bright-field microscopy provided better results. Often, the same specimen is imaged using both methods (e.g. [Plate 1](#), figures 3a,b). LM was conducted using an Olympus BX41 microscope at 600 \times and 1000 \times magnification. Electron microscopy was conducted using an FEI Quanta 3D DualBeam FEG FIB-SEM microscope located in the Shared Instrumentation Facility at LSU. A list of all described angiosperm pollen taxa, along with their aperture class, botanical affinity, and paleoecology, is provided in the [Supplementary material](#). Occurrence information is given both in terms of total specimens observed and in terms of relative abundance compared to the total identified pollen and plant spores in all samples from the IODP 364 core (16,246 specimens).

4. Systematic paleontology

4.1. Inaperturate pollen

Genus *Retipollenites* González Guzmán 1967

Retipollenites? sp. A

[Plate 1](#), figure 1; [Plate 14](#), figure 4

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

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

Botanical affinity. Probably eudicots, lower affinity unknown.

4.2. Monocolpate and trichotomocolpate pollen

Genus *Echimonocolpites* van der Hammen & Garcia 1966

Echimonocolpites chicxulubensis sp. nov.

[Plate 2](#), figures 9–11

Holotype. [Plate 2](#), figure 9 (523.92 mbsf (meters below sea-floor), slide 1, EFS M13/1).

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

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

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

Description. Monocolpate, occasionally longicolpate to ambiguously zonocolpate, echinate to baculate, length 30 (35) 48 μ m, width 16 (23) 33 μ m. Exine ca. 0.5–1.0 μ m thick, not visibly columellate. Shape elliptical to circular in equatorial view. The colpus may extend to the edge of the grain (e.g. [Plate 2](#), figure 9), but in some specimens (e.g. [Plate 2](#), figures 10–11) the colpus appears to partially or entirely encircle the grain, and could be interpreted as longicolpate or even zonocolpate. Commonly, the pollen grain is folded, and the morphology of the colpus is difficult to determine with certainty. Exine covered in scattered spines, otherwise psilate to scabrate, possibly indistinctly punctate. Spines broadly conical to slender, sometimes with expanded bases, occasionally baculate, 0.5–3 μ m long. The spines are not deep-rooted, and do not indent the underlying exine as in *Mauritiidites* van Hoeken-Klinkenburg 1964.

Discussion. The colpus in *Echimonocolpites chicxulubensis* sp. nov. is quite variable, and in some specimens the colpus appears to nearly completely encircle the grain (i.e. zonocolpate). These possibly zonocolpate specimens have not been assigned to *Spinizonocolpites* Muller 1968 emend. Muller et al. 1987, first because they are otherwise similar to clearly monocolpate specimens of *Echimonocolpites chicxulubensis* sp. nov., and second because this would incorrectly imply that *Echimonocolpites chicxulubensis* sp. nov. has a botanical affinity with the modern mangrove palm *Nypa* van Wurmb (Arecaceae).

Botanical affinity. Probably Arecaceae. Echinate, monocolpate pollen is produced by many species in the family. In

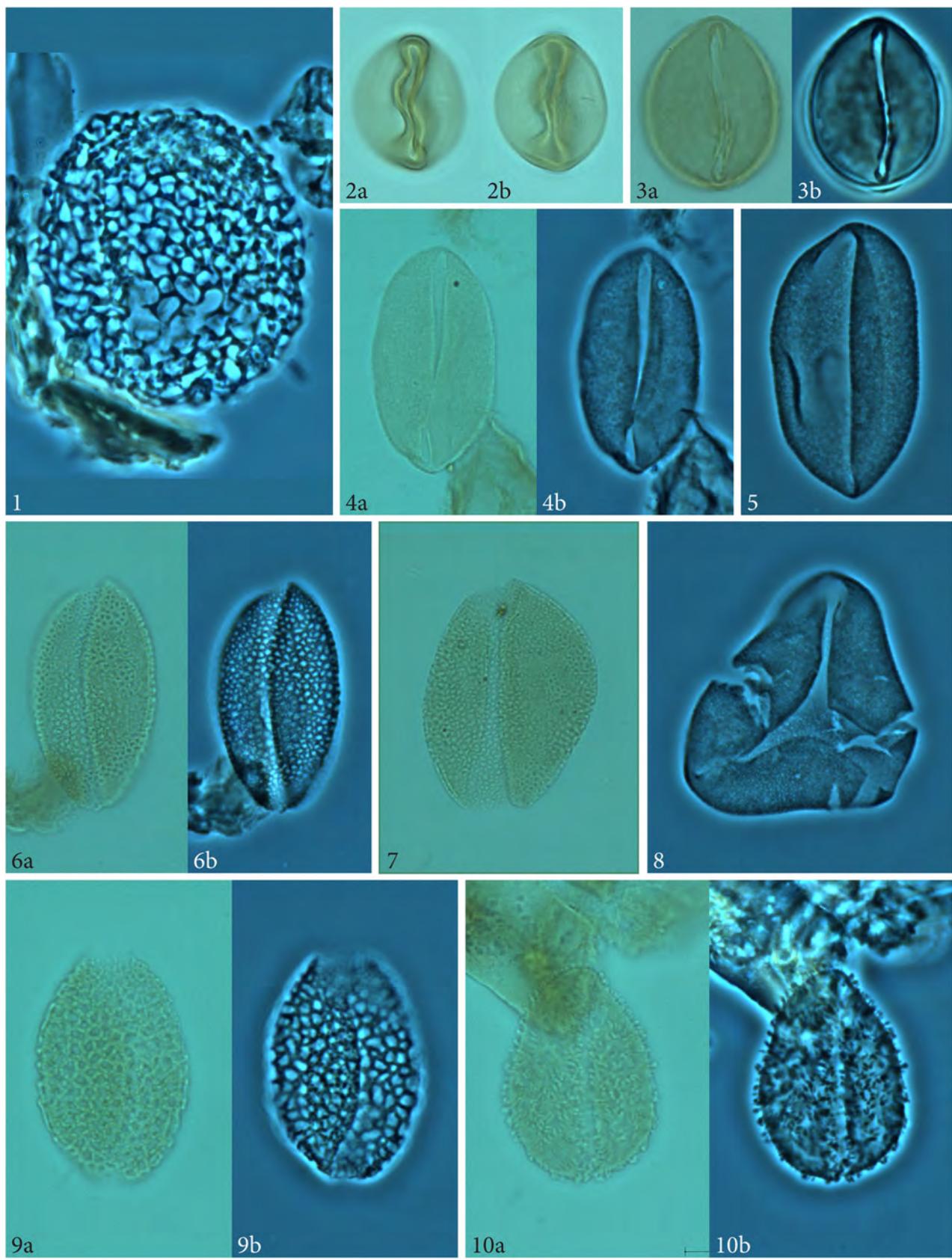


Plate 1. Inaperturate, monocolpate, and trichotomocolpate pollen from IODP (International Ocean Discovery Program) 364. 1. *Retipollenites*? sp. A, 559.91 mbsf (meters below seafloor), slide 1, EFS England Finder Slide M31/2. 2. *Monocolpopollenites* cf. *M. tranquilloides*, 539.43 mbsf, slide 1, EFS Q18/1. 3. *Monocolpopollenites tranquillus*, 572.75 mbsf, slide 1, EFS L38/1. 4. *Arecipites tenuixinous*, 539.43 mbsf, slide 1, EFS 043/1. 5. *Arecipites tenuixinous*, 520.79 mbsf, slide 1, EFS V30/2. 6. *Liliacidites variegatus*, 534.85 mbsf, slide 1, EFS P34/1. 7. *Liliacidites variegatus*, 569.50 mbsf, slide 1, EFS S39/1. 8. *Liliacidites* sp. B, 555.07 mbsf, slide 1, EFS G28/4. 9. *Liliacidites* sp. A, 553.54 mbsf, slide 1, EFS T39/1. 10. *Clavamonocolpites* sp. A, 516.00 mbsf, slide 1, EFS U15/0. Scale bar = 10 μ m.

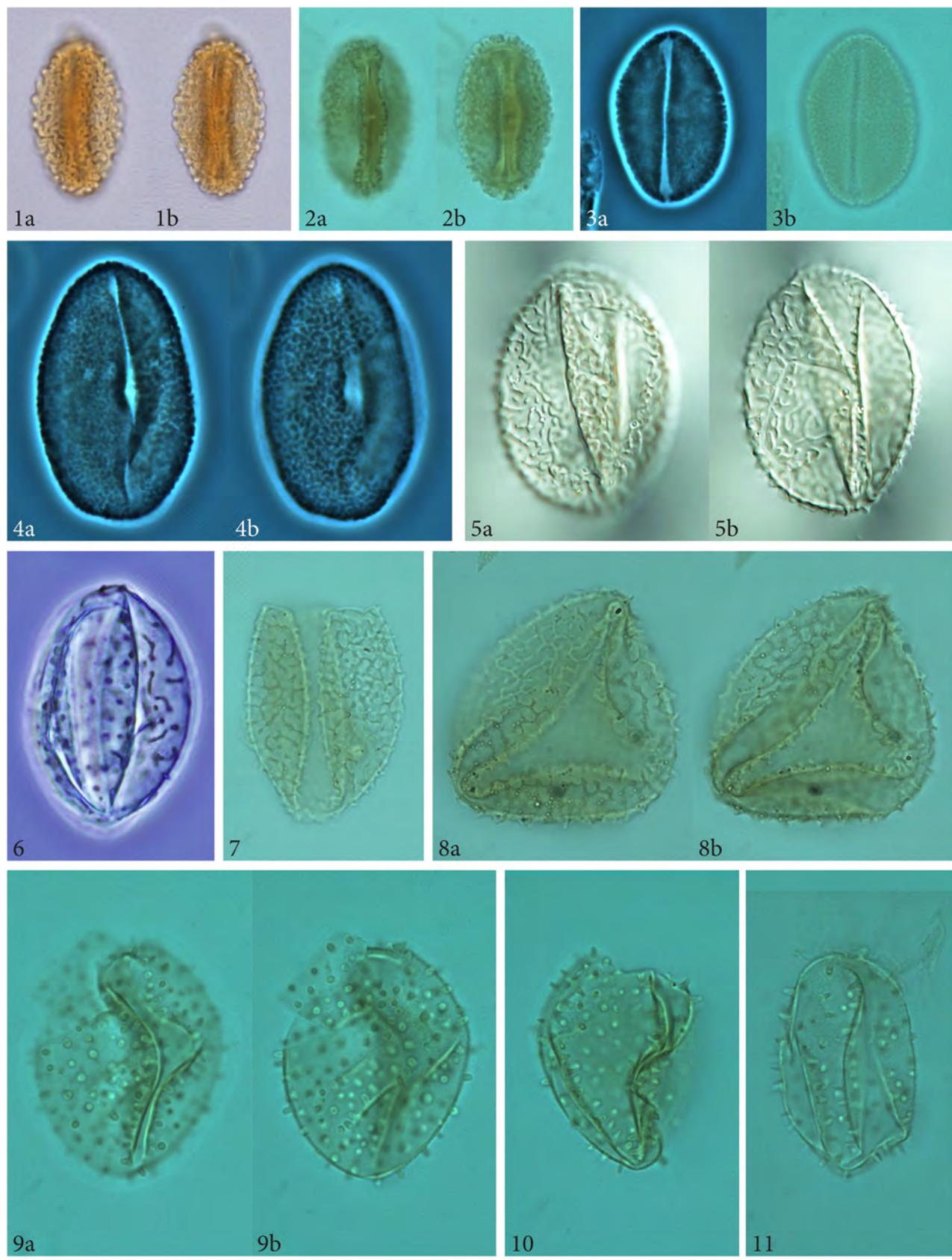


Plate 2. Monocolpate and trichotomocolpate pollen from IODP (International Ocean Discovery Program) 364. 1. *Rugumonocolpites* sp. A, 577.73 mbsf (meters below seafloor), slide 2, EFS England Finder Slide Q24/3. 2. *Rugumonocolpites* sp. A, 523.92 mbsf, slide 1, EFS Q36/1. 3. *Rugumonocolpites* sp. B, 527.08 mbsf, slide 1, U16/1. 4. *Rugumonocolpites* sp. B, 607.22 mbsf, slide 2, EFS S46/0. 5. *Rugumonocolpites* sp. C, 505.88 mbsf, slide 1, EFS Q33/1. 6. *Rugumonocolpites* sp. C, 520.79 mbsf, slide 1, EFS L18/0. 7. *Rugumonocolpites* sp. C, 505.88 mbsf, slide 2, EFS P30/1. 8. *Rugumonocolpites* sp. C, 505.88 mbsf, slide 1, EFS N17/0. 9. *Echimonocolpites chickulubensis*, sp. nov. (holotype), 523.92 mbsf, slide 1, EFS N18/0. 10. *Echimonocolpites chickulubensis*, sp. nov., 563.29 mbsf, slide 1, EFS N41/0. 11. *Echimonocolpites chickulubensis*, sp. nov., 561.48 mbsf, slide 1, EFS U30/2. Scale bar = 10 μ m.

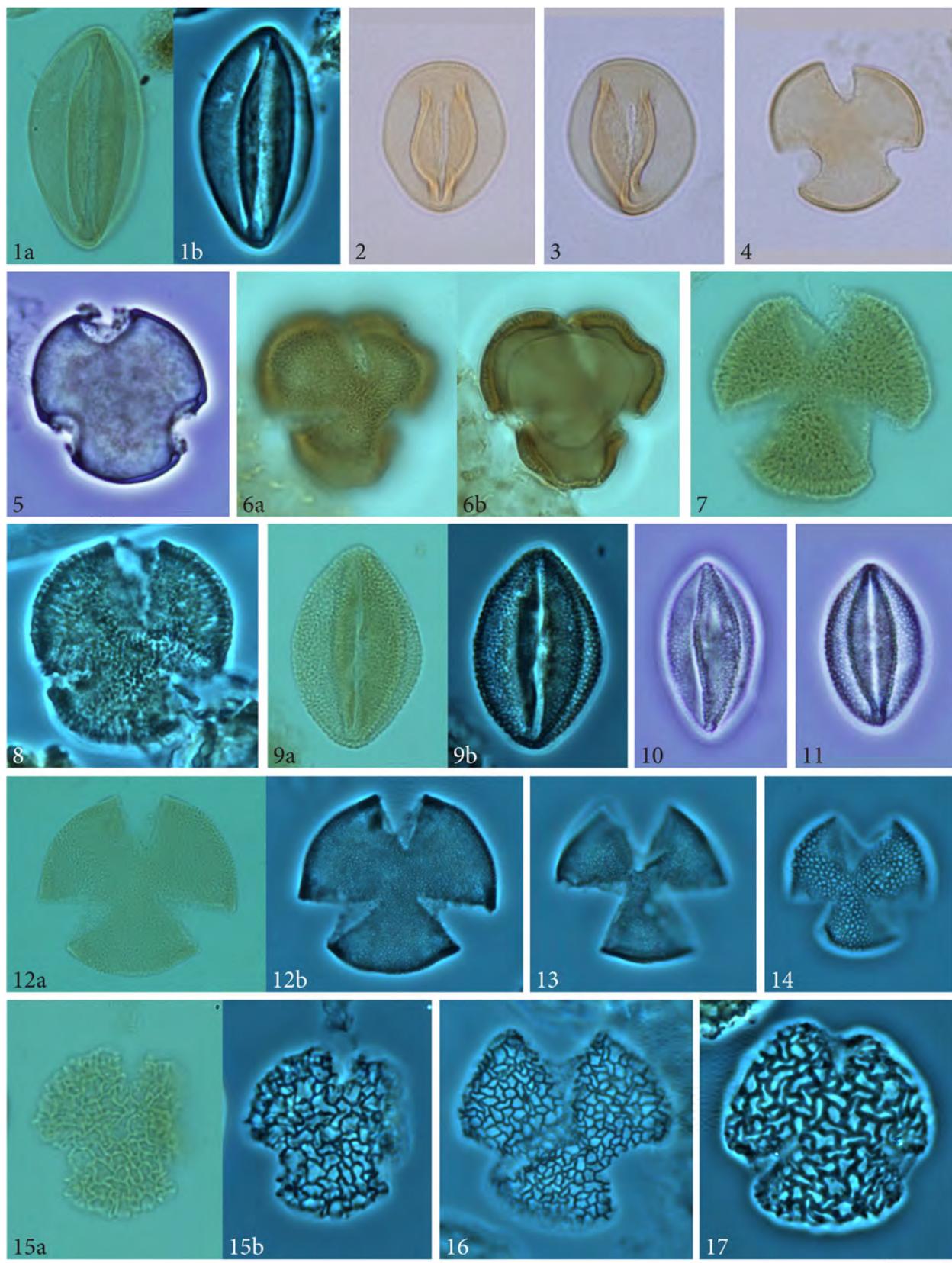


Plate 3. Tricolpate pollen from IODP (International Ocean Discovery Program) 364. 1. *Cupuliferoidaepollenites* sp., 569.50 mbsf (meters below seafloor), slide 1, EFS England Finder Slide L34/1. 2. *Eucommia?* sp. A, 519.31 mbsf, slide 1, EFS U19/0. 3. *Eucommia?* sp. A, 525.48 mbsf, slide 1, EFS H31/1. 4. *Psilatricolpites* sp. A, 577.73 mbsf, slide 2, EFS V26/0. 5. *Psilatricolpites* sp. A, 520.79 mbsf, slide 1, EFS R35/1. 6. *Scabratricolpites* sp. B, 606.61 mbsf, slide 2, EFS R34/2. 7. *Scabratricolpites* sp. A, 540.89 mbsf, slide 1, EFS S31/1. 8. *Scabratricolpites* sp. A, 548.96 mbsf, slide 1, EFS P43/0. 9. *Fraxinoipollenites* sp., 520.79 mbsf, slide 1, EFS S39/1. 10. *Fraxinoipollenites* sp., 509.17 mbsf, slide 2, EFS G29/0. 11. *Fraxinoipollenites* sp. 509.17 mbsf, slide 2, EFS K22/1. 12. *Tricolpites hians*, 564.86 mbsf, slide 1, EFS P37/1. 13. *Tricolpites hians*, 564.86 mbsf, slide 1, EFS P39/1. 14. *Tricolpites* sp. A, 531.75 mbsf, slide 1, EFS U44/1. 15. *Retitrescolpites anguloluminosus*, 520.79 mbsf, slide 1, EFS R27/2. 16. *Retitrescolpites anguloluminosus*, 547.42 mbsf, slide 2, EFS L27/2. 17. *Retitrescolpites* sp. A, 530.24 mbsf, slide 2, EFS Q13/1. Scale bar = 10 μ m.

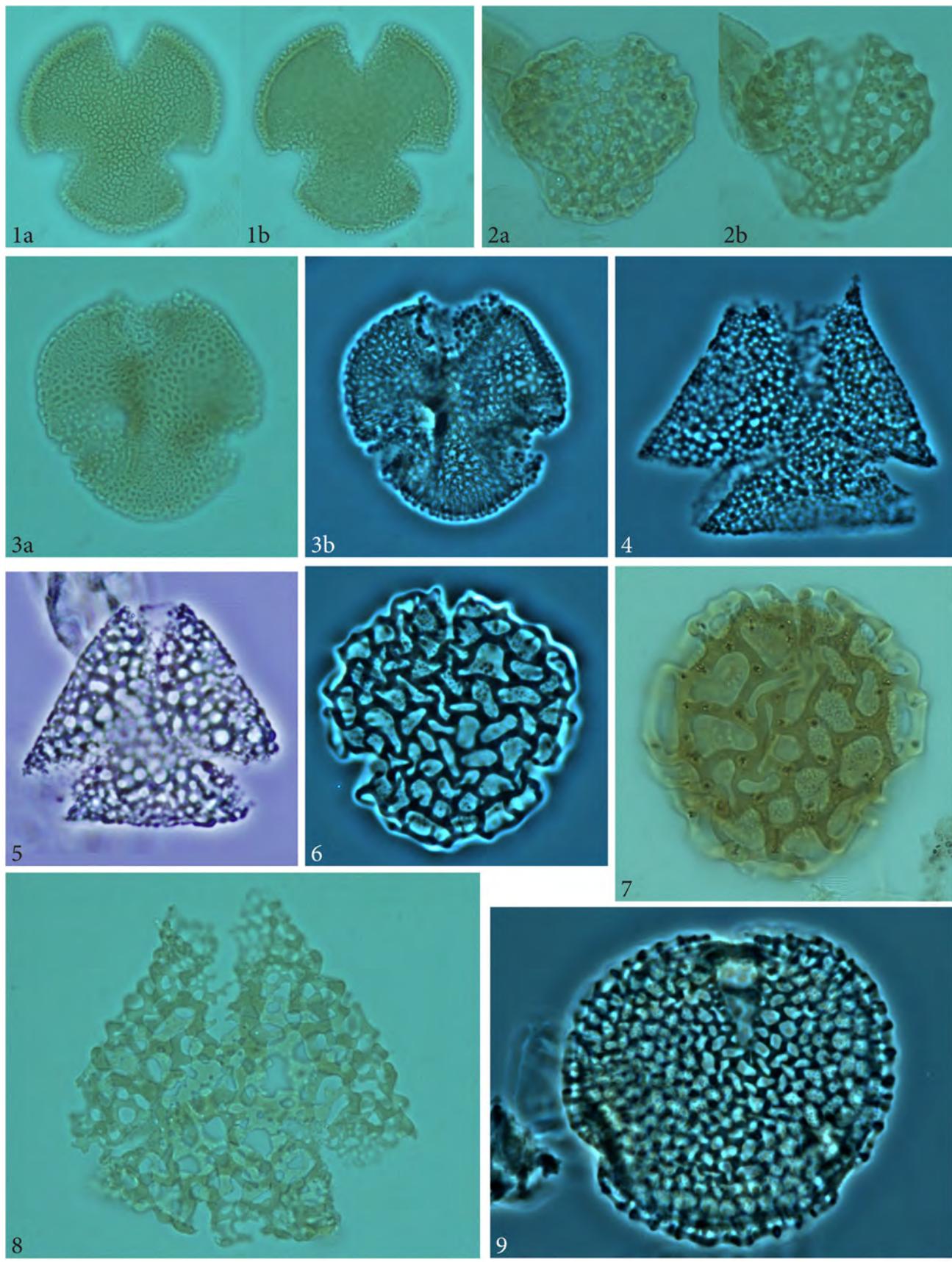


Plate 4. Tricolpate pollen from IODP (International Ocean Discovery Program) 364. 1. *Retitrescolpites* sp. A, 558.26 mbsf (meters below seafloor), slide 1, EFS England Finder Slide R13/1. 2. *Retitrescolpites* sp. A, 561.48 mbsf, slide 1, EFS S40/1. 3. *Retitrescolpites* sp. B, 561.00 mbsf, slide 1, EFS U12/1. 4. *Retitrescolpites* sp. C, 561.48 mbsf, slide 1, EFS Q21/2. 5. *Retitrescolpites* sp. C, 520.79 mbsf, slide 2, EFS O31/0. 6. *Spirosyncolpites spiralis*, 561.48 mbsf, slide 1, EFS V10/1. 7. *Spirosyncolpites spiralis*, 582.78 mbsf, slide 1, EFS T29/0. 8. *Retitrescolpites* sp. C, 516.00 mbsf, slide 1, EFS Q32/1. 9. *Spirosyncolpites spiralis*, 510.90 mbsf, slide 1, EFS O28/2. Scale bar = 10 μ m.

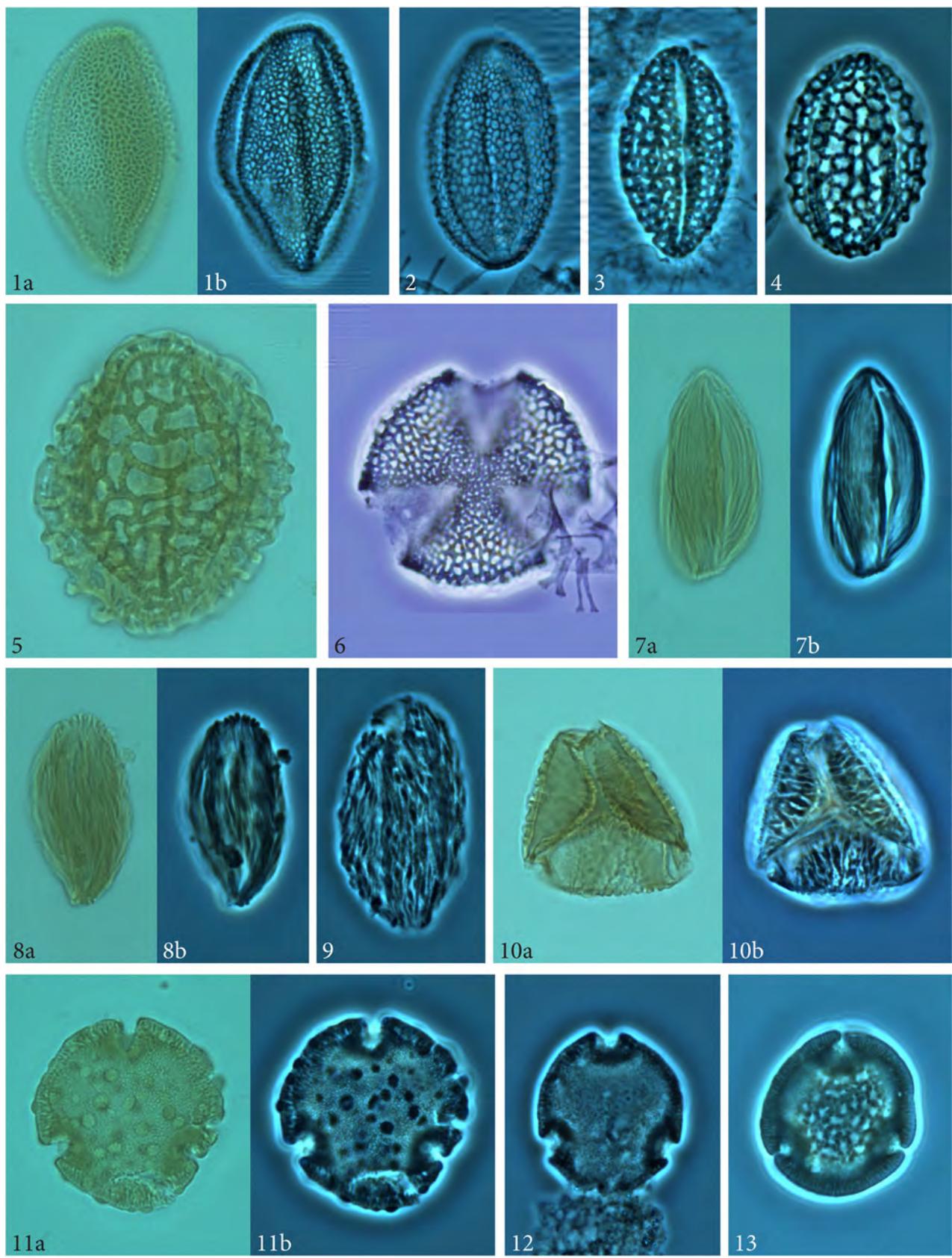


Plate 5. Tricolpate pollen from IODP (International Ocean Discovery Program) 364. 1. *Retitricolpites* sp. A, 555.07 mbsf (meters below seafloor), slide 1, EFS England Finder Slide R38/1. 2. *Retitricolpites* sp. A, 536.39 mbsf, slide 1, EFS T45/1. 3. *Retitricolpites* sp. B, 536.39 mbsf, slide 1, EFS Q20/0. 4. *Retitricolpites* sp. B, 505.88 mbsf, slide 2, EFS Q31/1. 5. *Retitricolpites* sp. C, 523.92 mbsf, slide 1, EFS P22/2. 6. *Roused* sp. A, 520.79 mbsf, slide 1, EFS K19/0. 7. *Striatopollis grahamii*, sp. nov., 551.98 mbsf, slide 1, EFS T37/1. 8. *Striatopollis grahamii*, sp. nov. (holotype), 520.79 mbsf, slide 1, EFS S39/1. 9. *Striatopollis grahamii*, sp. nov., 520.79 mbsf, slide 1, EFS W23/2. 10. *Insulapollenites* aff. *I. rugulatus*, 606.61 mbsf, slide 1, EFS W42/1. 11. *Discoidites* sp. A, 520.79 mbsf, slide 1, EFS R 46/0. 12. *Discoidites* sp. A, 597.10 mbsf, slide 2, EFS U30/2. 13. *Discoidites* sp. A, 533.27 mbsf, slide 1, EFS Q28/1. Scale bar = 10 µm.

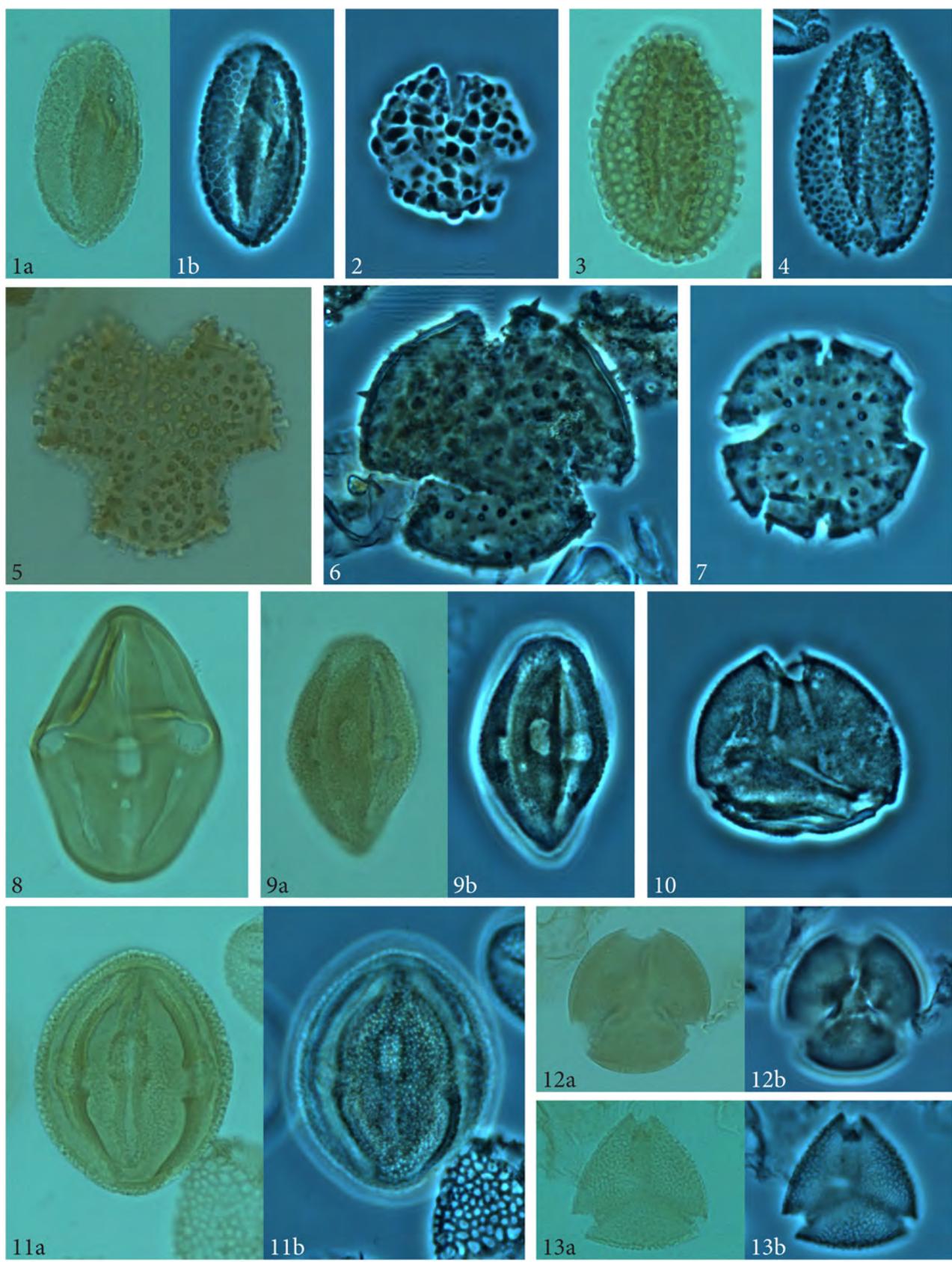


Plate 6. Tricolpate and tricolporate pollen from IODP (International Ocean Discovery Program) 364. 1. *Verrutricolpites* sp. A, 542.61 mbsf (meters below seafloor), slide 2, EFS England Finder Slide R38/1. 2. *Verrutricolpites* sp. B, 597.10 mbsf, slide 2, EFS S10/2. 3. *Clavatricolpites* aff. *C. gracilis*, 533.54 mbsf, slide 1, EFS S21/0. 4. *Clavatricolpites* aff. *C. gracilis*, 537.86 mbsf, slide 1, EFS Q26/2. 5. *Clavatricolpites* sp. A, 510.90 mbsf, slide 2, EFS O17/0. 6. *Echitricolpites* sp. A, 566.52 mbsf, slide 1, EFS N29/2. 7. *Echitricolpites* sp. A, 547.42 mbsf, slide 2, EFS M36/1. 8. *Psilatricolpites* sp. A, 555.07 mbsf, slide 1, EFS V36/1. 9. *Scabratricolporites* sp. A, 547.42 mbsf, slide 2, EFS V25/2. 10. *Scabratricolporites* sp. B, 572.75 mbsf, slide 2, EFS W29/2. 11. *Punctatricolporites* sp. A, 537.86 mbsf, slide 1, EFS S43/3. 12. *Syncolporites* sp. A, 606.61 mbsf, slide 1, EFS R23/2. 13. *Syncolporites?* sp. B, 523.92 mbsf, slide 1, EFS Q31/2. Scale bar = 10 μ m.

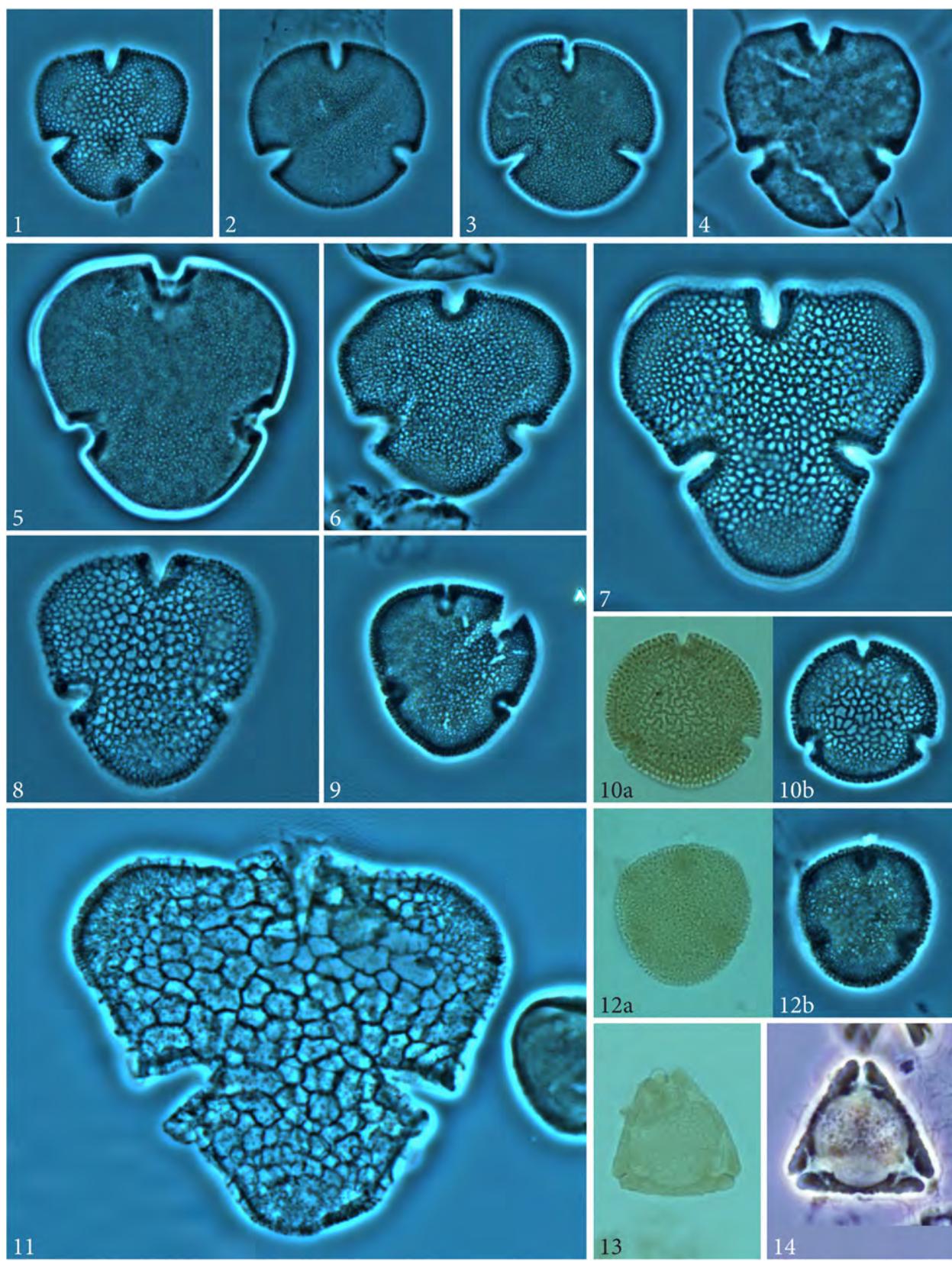


Plate 7. Tricolporate pollen from IODP (International Ocean Discovery Program) 364. 1. *Bombacacidites* sp. A, 528.69 mbsf (meters below seafloor), slide 2, EFS England Finder Slide T29/2. 2. *Bombacacidites brevis*, 537.86 mbsf, slide 1, EFS U38/0. 3. *Bombacacidites brevis*, 553.54 mbsf, slide 1, EFS Q14/1. 4. *Bombacacidites nanobrochatus*, 607.22 mbsf, slide 2, EFS F33/0. 5. *Bombacacidites nanobrochatus*, 527.08 mbsf, slide 1, EFS U14/0. 6. *Bombacacidites bombaxoides*, 512.24 mbsf, slide 2, EFS S28/2. 7. *Bombacacidites nacimientoensis*, 553.54 mbsf, slide 1, EFS Q25/2. 8. *Bombacacidites nacimientoensis*, 537.86 mbsf, slide 1, EFS T34/0. 9. *Tiliaepollenites* sp., 523.92 mbsf, slide 1, EFS S29/2. 10. *Tiliaepollenites* sp., 607.04 mbsf, slide 1, EFS S37/0. 11. *Bombacacidites* sp. B, 564.86 mbsf, slide 1, EFS F25/4. 12. *Tiliaepollenites* sp., 512.24 mbsf, slide 2, EFS N19/4. 13. *Basopollis* sp. A, 536.39 mbsf, slide 1, EFS U41/0. 14. *Basopollis* sp. A, 520.79 mbsf, slide 1, EFS P21/4. Scale bar = 10 μ m.

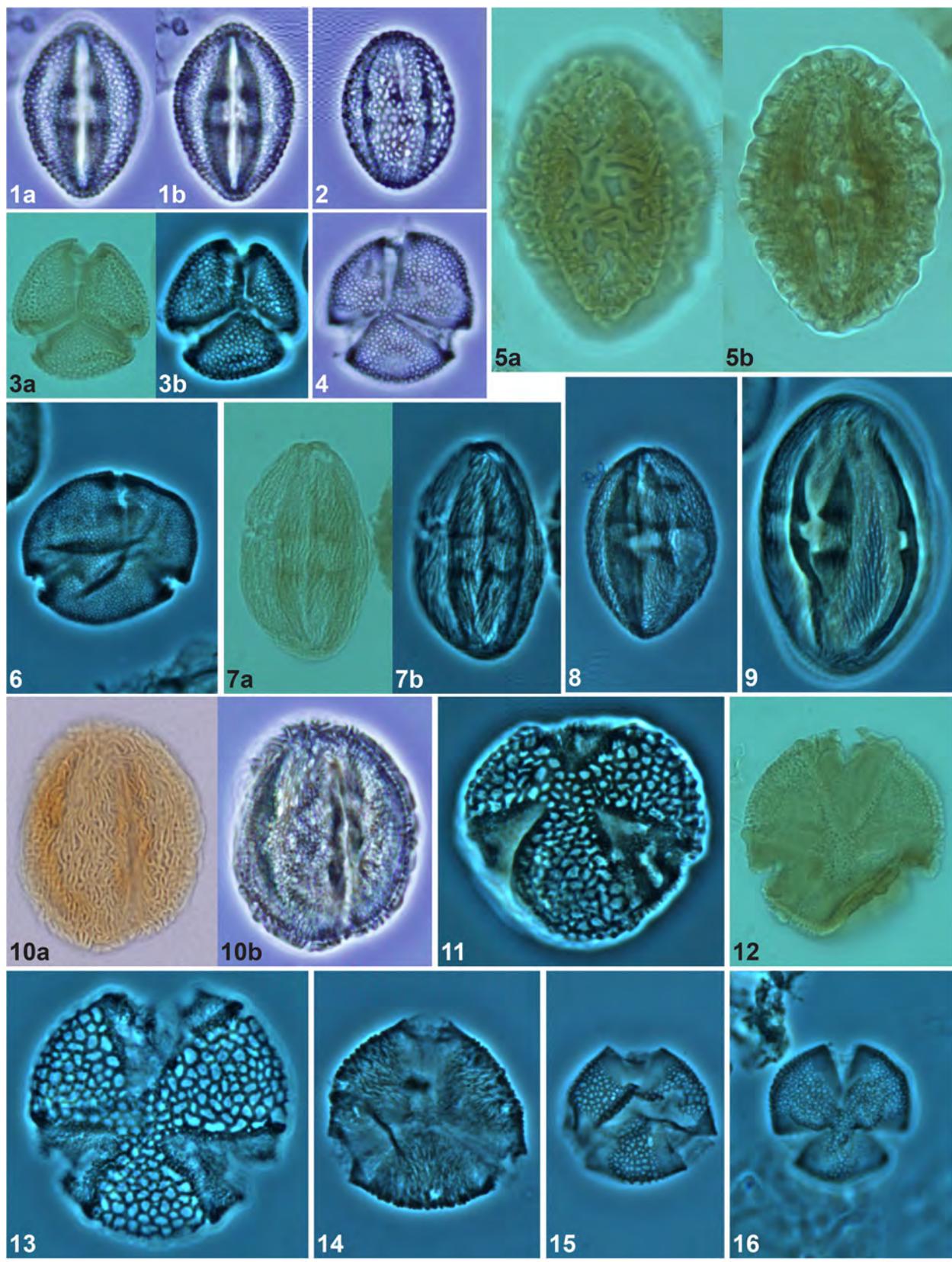


Plate 8. Tricolporate pollen from IODP (International Ocean Discovery Program) 364. 1. *Retitricolporites* sp. A, 520.79 mbsf (meters below seafloor), slide 1, EFS England Finder Slide H19/1. 2. *Retitricolporites* sp. A, 520.79 mbsf, slide 1, EFS M27/2. 3. *Retitricolporites* sp. B, 527.08 mbsf, slide 1, EFS T41/1. 4. *Retitricolporites* sp. B, 542.61 mbsf, slide 1, EFS U19/0. 5. *Retitricolporites* sp. D, 553.54 mbsf, slide 1, EFS U46/0. 6. *Retitricolporites* sp. C, 514.14 mbsf, slide 1, EFS T35/2. 7. *Striaticolporites* aff. *S. conspicuus*, 520.79 mbsf, slide 1, EFS S33/1. 8. *Rhuspollenites* sp., 607.22 mbsf, slide 2, EFS O39/1. 9. *Rhuspollenites* sp., 558.26 mbsf, slide 1, EFS R24/0. 10. *Striaticolporites* sp. A, 520.79 mbsf, slide 1, EFS J19/1. 11. *Margocolporites vanwijhei*, 520.79 mbsf, slide 1, EFS T44/0. 12. *Margocolporites* sp. A, 507.53 mbsf, slide 2, EFS S17/1. 13. *Margocolporites vanwijhei*, 523.92 mbsf, slide 1, EFS T35/1. 14. *Margocolporites* sp. C, 607.22 mbsf, slide 2, EFS G28/4. 15. *Margocolporites* sp. B, 607.22 mbsf, slide 2, EFS G28/4. 16. *Margocolporites* sp. B, 528.69 mbsf, slide 2, EFS O38/0. Scale bar = 10 μ m.

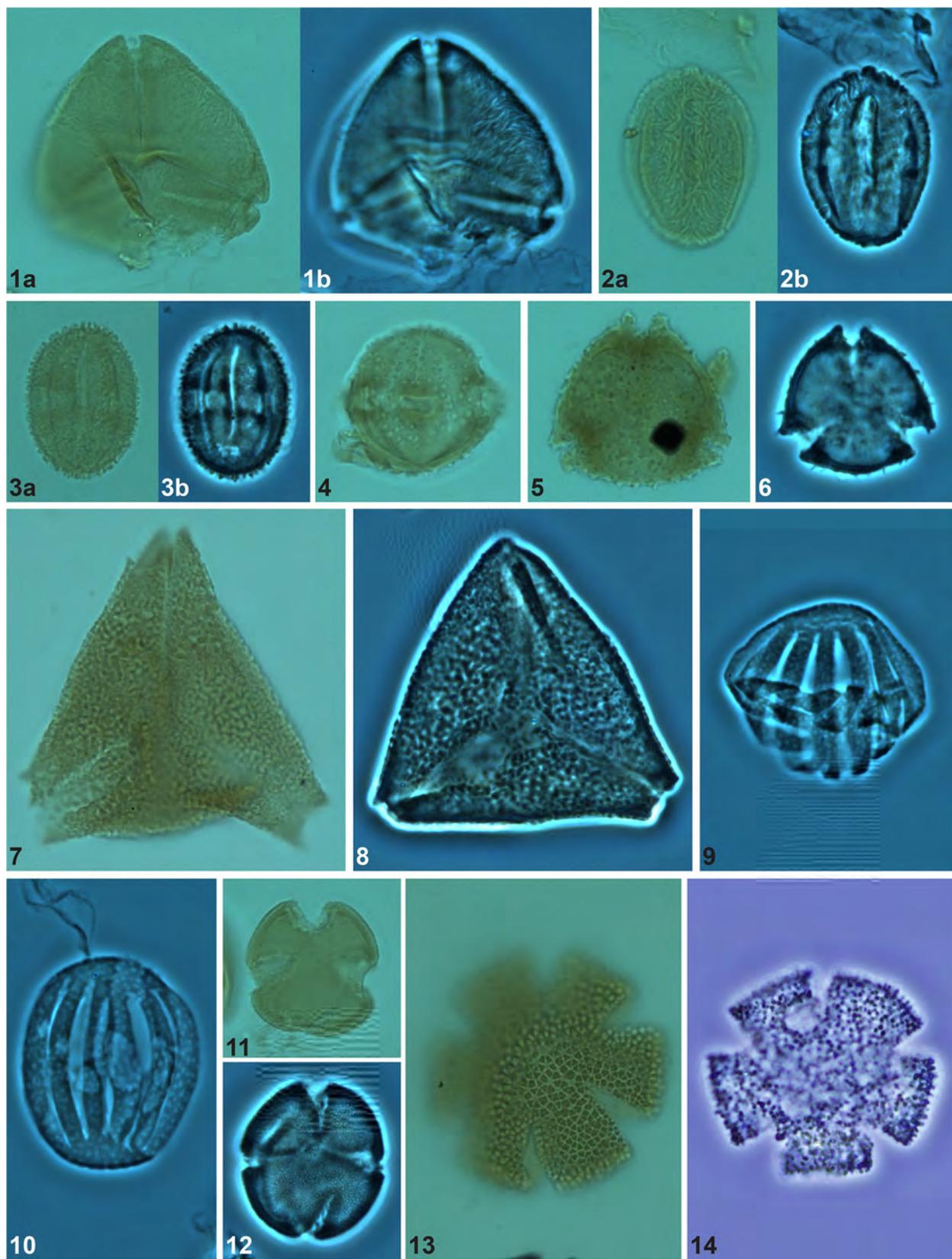


Plate 9. Tricolporate and stephanocolpate pollen from IODP (International Ocean Discovery Program) 364. 1. *Rugutricolporites* sp. A, 569.50 mbsf (meters below seafloor), slide 1, EFS England Finder Slide N27/1. 2. *Rugutricolporites* aff. *R. felix*, 512.24 mbsf, slide 2, EFS O30/1. 3. *Ilexpollenites* cf. *I. verrucatus*, 556.58 mbsf, slide 1, EFS U23/0. 4. *Echitricolporites* sp. A, 555.07 mbsf, slide 1, EFS Q17/2. 5. *Echitricolporites* sp. A, 569.50 mbsf, slide 1, EFS N34/3. 6. *Echitricolporites* sp. A, 523.92 mbsf, slide 1, EFS R24/2. 7. *Boehlensipollis* sp. A, 607.22 mbsf, slide 2, EFS T36/1. 8. *Boehlensipollis* sp. A, 607.22 mbsf, slide 2, EFS J46/1. 9. Polygalaceae? type A, 531.75 mbsf, slide 1, EFS L26/0. 10. Polygalaceae? type A, 509.17 mbsf, slide 1, EFS Q37/1. 11. *Psilastephanocolpites* sp. A, 551.98 mbsf, slide 1, EFS V24/2. 12. *Retistephanocolpites* sp. A, 606.61 mbsf, slide 2, EFS H28/2. 13. *Clavastephanocolpites* aff. *C. crotonoides*, 607.04 mbsf, slide 2, EFS K36/1. 14. *Clavastephanocolpites* aff. *C. crotonoides*, 607.22 mbsf, slide 1, EFS N24/0. Scale bar = 10 µm.

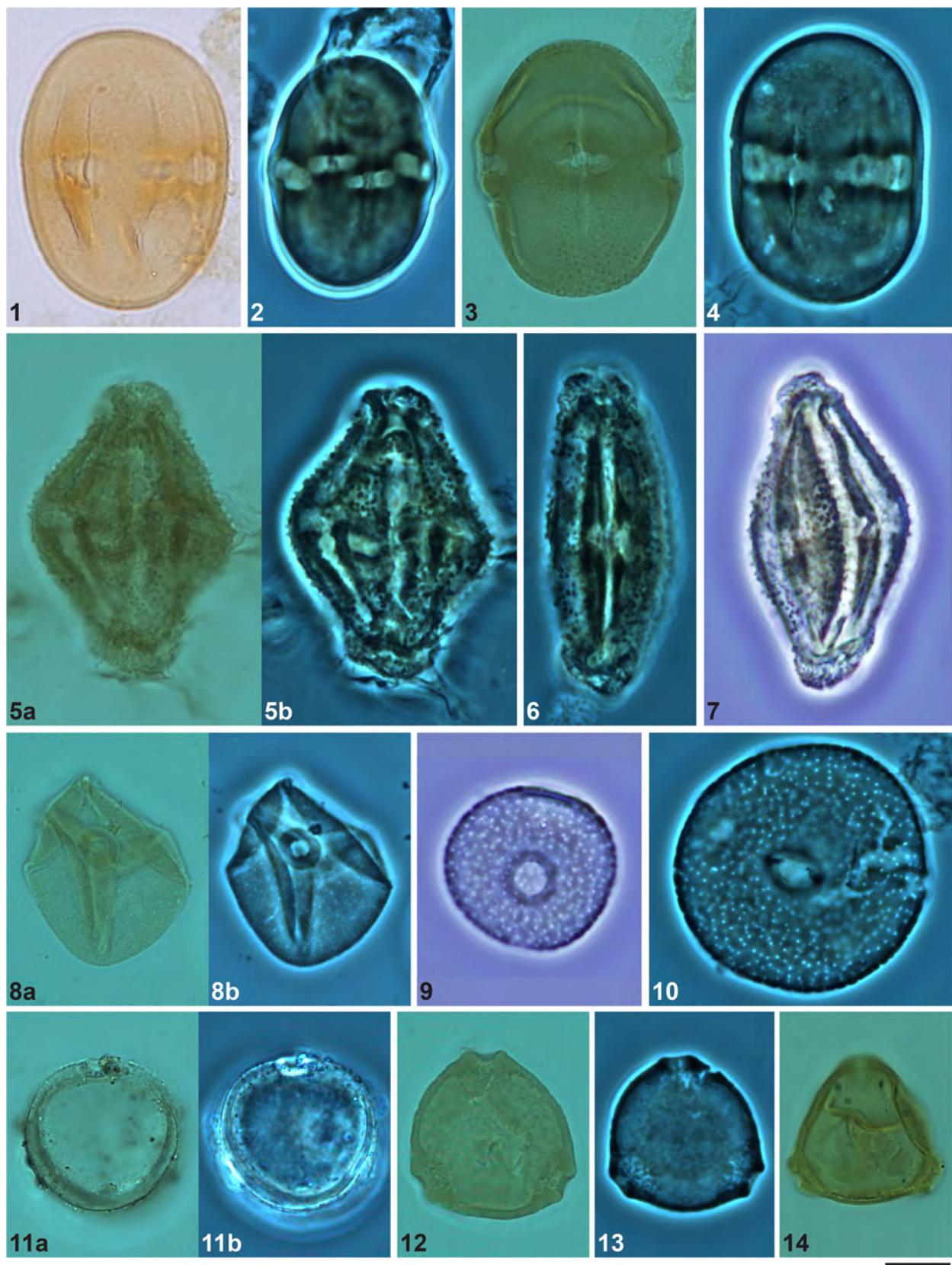


Plate 10. Stephanocolporate, monoporate, and triporate pollen from IODP (International Ocean Discovery Program) 364. 1. *Psilastephanocolporites hammenii*, sp. nov., 577.73 mbsf (meters below seafloor), slide 2, EFS England Finder Slide G19/4. 2. *Psilastephanocolporites hammenii*, sp. nov. (holotype), 597.10 mbsf, slide 1, EFS P38/1. 3. *Psilastephanocolporites hammenii*, sp. nov., 540.89 mbsf, slide 1, EFS P24/2. 4. *Psilastephanocolporites hammenii*, sp. nov., 564.86 mbsf, slide 1, EFS P36/1. 5. Stephanocolporate type A, 520.79 mbsf, slide 1, EFS X43/0. 6. Stephanocolporate type A, 505.88 mbsf, slide 1, EFS O34/1. 7. Stephanocolporate type A, 520.79 mbsf, slide 1, EFS N23/0. 8. *Monoporopollenites annulatus*, 606.61 mbsf, slide 1, EFS G28/4. 9. *Milfordia minima*, 525.48 mbsf, slide 1, EFS H33/1. 10. *Milfordia hungarica*, 569.50 mbsf, slide 1, EFS O25/2. 11. Betulaceae type A, 615.03 mbsf, slide 1, EFS R16/0. 12. Betulaceae/Myricaceae type, 533.27 mbsf, slide 1, EFS S23/0. 13. Betulaceae/Myricaceae type, 536.39 mbsf, slide 1, EFS U39/1. 14. *Trivestibulopollenites* sp. A, 607.35 mbsf, slide 1, EFS S28/2. Scale bar = 10 µm.

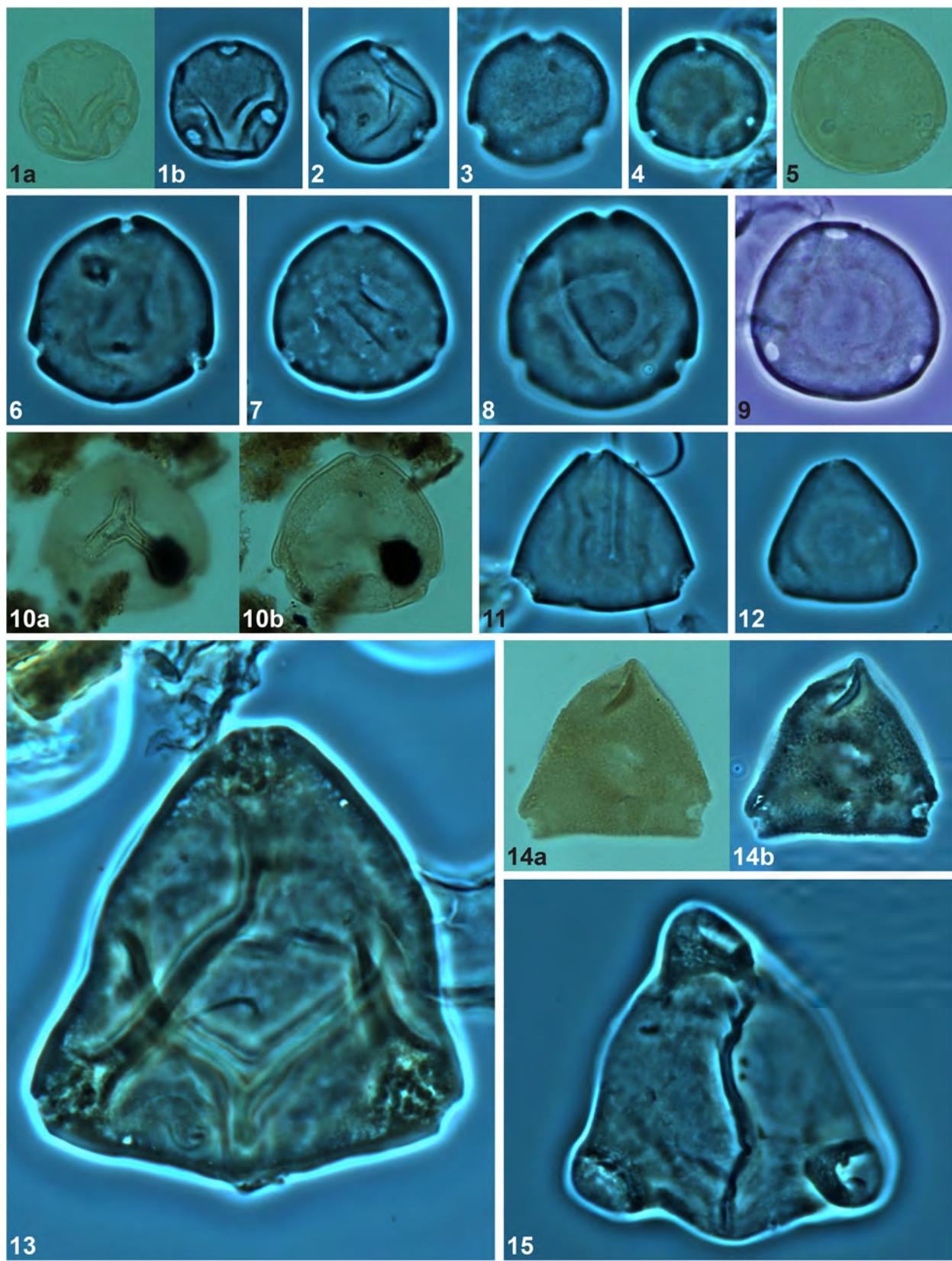


Plate 11. Triporate pollen from IODP (International Ocean Discovery Program) 364. 1. *Cricotriporites* sp. A, 507.53 mbsf (meters below seafloor), slide 2, EFS (England Finder Slide) W44/1. 2. *Cricotriporites* sp. A, 512.24 mbsf, slide 2, EFS N38/1. 3. *Scabratriporites redundans*, 514.14 mbsf, slide 1, EFS R36/1. 4. *Subtriporopollenites* cf. *S. nanus*, 527.08 mbsf, slide 1, EFS U28/2. 5. *Subtriporopollenites* cf. *S. nanus*, 536.39 mbsf, slide 1, EFS U41/0. 6. *Momipites coryloides*, 520.79 mbsf, slide 1, EFS V35/1. 7. *Momipites coryloides*, 553.54 mbsf, slide 1, EFS T33/1. 8. *Momipites amplius*, 530.24 mbsf, slide 2, EFS Q29/1. 9. *Caryapollenites veripites*, 509.17 mbsf, slide 2, EFS K23/0. 10. *Momipites triradiatus*, 566.52 mbsf, slide 2, EFS P22/2. 11. *Psilatriporites* sp. A, 527.08 mbsf, slide 1, EFS R32/4. 13. *Corsinipollenites parviangulus*, 606.61 mbsf, slide 2, EFS T17/0. 14. *Cranwellipollis?* sp. A, 607.22 mbsf, slide 2, EFS O24/2. 15. *Corsinipollenites oculusnoctis*, 561.48 mbsf, slide 1, EFS V17/1. Scale bar = 10 μ m.

particular, *Echimonocolpites chickxulubensis* is morphologically similar to pollen of the modern *Socratea hecatonandra* (Dugand) Bernal photographed by Pocknall and Jarzen (2012), who described the colpus as incomplete zonasulcate, although the echinae in *S. hecatonandra* are $\leq 1 \mu\text{m}$ in length.

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

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

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

Rugumonocolpites sp. C
Plate 2, figures 5–8

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

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

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

4.3. Tricolpate pollen

Genus *Cupuliferoidaepollenites* Potonié et al. 1950 ex Potonié 1960
Cupuliferoidaepollenites spp.
Plate 3, figure 1

Discussion. This study will follow Frederiksen (1980a) and Jardine (2011), and group all specimens of *Cupuliferoidaepollenites* into one morphotype. The type species of the genus, *Cupuliferoidaepollenites librarensis* (Thomson 1950) Potonié 1960, is smaller ($<20 \mu\text{m}$) than most specimens observed in this study. Some specimens (e.g. Plate 3, figure 1) have poles which are arguably not well rounded; this aspect of the generic circumscription has been broadly interpreted.

Occurrence. Ypresian; 535 specimens observed (3.3%). *Cupuliferoidaepollenites* is a common and widely distributed form genus in the Cenozoic, although South American

occurrences are lacking (Palynodata Inc. and White 2008). This may be due to differing taxonomic practices.

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

Paleoecology. Ramírez-Arriaga, Prámparo, et al. (2014) suggested a tropical deciduous forest paleoecology for specimens of *Cupuliferoidaepollenites* not assigned to species from the late Eocene to early Oligocene of Pueblo, Mexico. Pflug (1952) described Eocene coal beds from Germany, and interpreted pollen of *Cupuliferoidaepollenites librarensis* as indicating a lowland forest proximal to the swamp where the coal was deposited (Frederiksen 1985). The uncertainty about the botanical affinity of the IODP 364 specimens suggests caution in assigning a paleoecology.

Genus *Discoidites* Muller 1968
Discoidites sp. A
Plate 5, figures 11–13

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

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

Botanical affinity. Probably Tilioideae of the Malvaceae (see discussion of genus in *Supplementary material*).

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

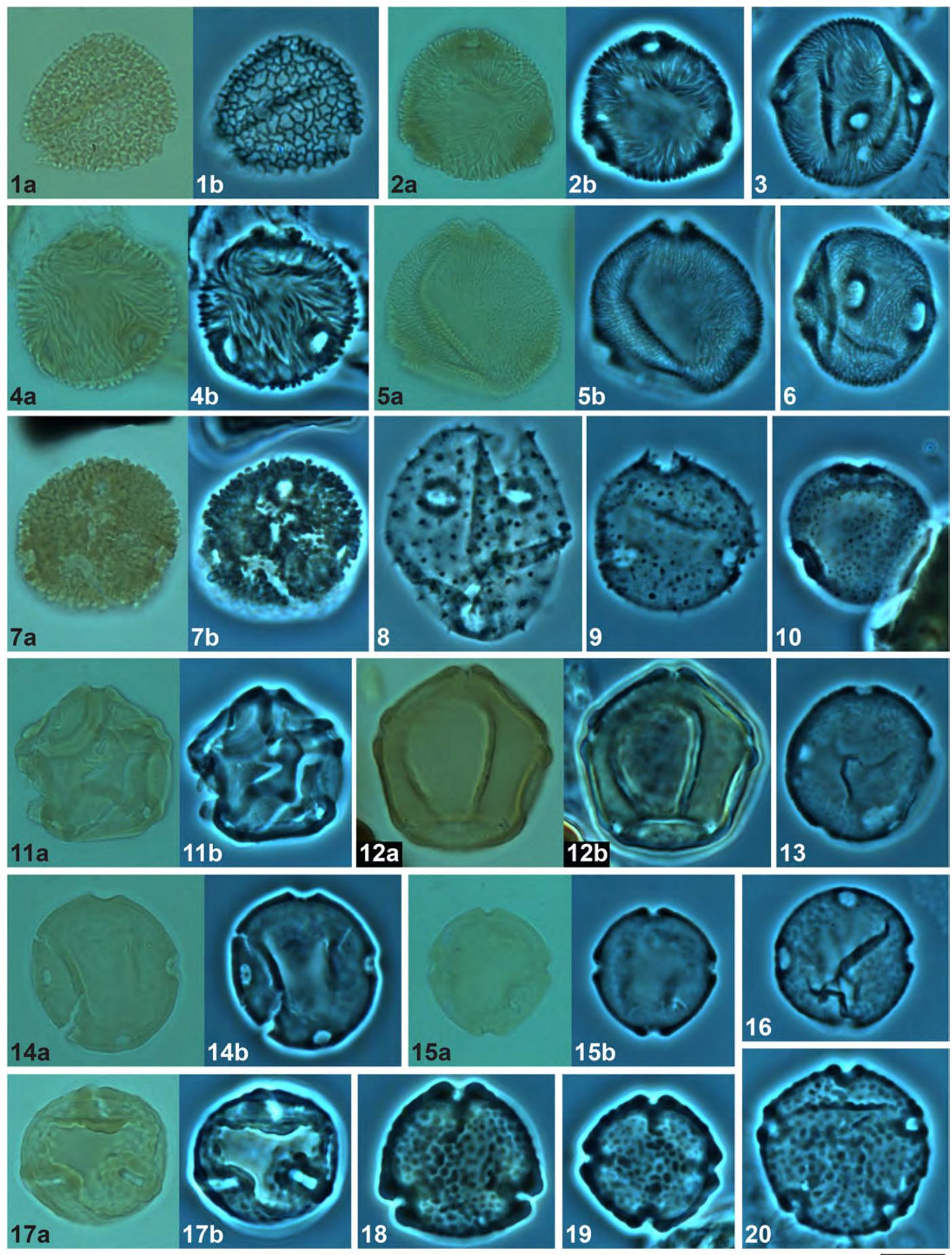
Genus *Eucommia*? Oliver
Eucommia? sp. A
Plate 3, figures 2–3; Plate 14, figure 5

Discussion. If the SEM specimen (Plate 14, figure 6) is in fact *Eucommia*? sp. A, the similarity of its fine verrucate/conate and punctate exine structure to that of *Psilatricolpites* sp. A is remarkable (Plate 14, figure 5). *Psilatricolpites* sp. A may be conspecific with *Eucommia*? sp. A, the oblate shape and equal colpi resulting from compression perpendicular to the polar axis, but these two morphologies have been identified separately due to the uncertainty of their relationship. The SEM specimen is similar to SEM specimens of *Eucommia ulmoides* in having fine conate or spinulate ornamentation, but the modern species does not have fine punctae, and verrucae may also be absent (Zavada and Dilcher 1986; Rowley et al. 1992).

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

Botanical affinity. Possibly Eucommiaceae.

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



Genus *Fraxinoipollenites* Potonié 1951 ex Potonié 1960

Fraxinoipollenites spp.

Plate 3, figures 9–11; Plate 14, figure 8

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

Occurrence. Ypresian; 2596 specimens observed (16.0%). *Fraxinoipollenites* is a common and widely distributed genus in the Cretaceous and Cenozoic (Palynodata Inc. and White 2008).

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

Genus *Psilatricolpites* Pierce 1961

Psilatricolpites sp. A

Plate 3, figures 4–5; Plate 14, figure 5

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

Occurrence. Ypresian; 1334 specimens observed (8.2%).

Botanical affinity. Eudicots, lower affinity uncertain.

Spirosyncolpites spiralis González Guzmán 1967 sensu lato

Plate 4, figures 6–7, 9; Plate 14, figure 12

Selected synonymy. *Retitricolpites amapaensis* Regali et al. 1974, pl. 16, figs 1–1c.

Discussion. The IODP 364 specimens are similar to *Spirosyncolpites spiralis* as originally described by González Guzmán (1967) and as imaged by Hoorn (1994, pl. 4, fig. 1). Jaramillo and Dilcher (2001) provide additional descriptions of this species. The ring or helical shape of the colpi as described for *S. spiralis* has not been clearly observed in these specimens, although it is often difficult to observe the colpi at all. Specimens assigned to 'Reticulataeplolis cf. intergranulata' by Graham et al. (2000, figs 35–36) are also morphologically similar to the IODP 364 specimens, although smaller and less coarsely reticulate. A single tricolporate specimen, otherwise similar to *Spirosyncolpites spiralis*, has not been assigned to a separate species. The observation of additional tricolporate specimens in future work may justify the creation of a new taxon.

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

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

Genus *Retitrescolpites* Sah 1967

Retitrescolpites sp. C

Plate 4, figures 4–5, 8; Plate 14, figure 11

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

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

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

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

Scabratricolpites sp. A

Plate 3, figures 7–8

Plate 12. Triporate and stephanoporate pollen from IODP (International Ocean Discovery Program) 364. 1. *Retitriporites* sp. A, 505.88 mbsf (meters below seafloor), slide 2, EFS England Finder Slide P36/1. 2. *Brosipollis striata*, 559.91 mbsf, slide 1, EFS V33/1. 3. *Brosipollis striata*, 547.42 mbsf, slide 2, EFS R43/0. 4. *Brosipollis* aff. *B. striata*, 553.54 mbsf, slide 1, EFS Q20/2. 5. *Brosipollis reticulatus*, sp. nov., 558.26 mbsf, slide 1, EFS R24/0. 6. *Brosipollis reticulatus*, sp. nov. (holotype), 547.42 mbsf, slide 2, EFS L25/2. 7. *Gemmatriporites* sp. A, 607.22 mbsf, slide 2, EFS F17/3. 8. *Echitriporites* sp. A, 505.88 mbsf, slide 2, EFS Q46/0. 9. *Echitriporites* sp. A, 558.26 mbsf, slide 1, EFS R26/2. 10. *Echitriporites* sp. B, 597.10 mbsf, slide 2, EFS U33/1. 11. *Alnus verus*, 522.38 mbsf, slide 2, EFS S28/4. 12. *Alnus verus*, 607.15 mbsf, slide 1, EFS N39/1. 13. *Scabrathephanopores* sp., 520.79 mbsf, slide 1, EFS U20/2. 14. *Scabrathephanopores* sp., 569.50 mbsf, slide 1, EFS L36/1. 15. *Scabrathephanopores* sp., 558.26 mbsf, slide 1, EFS S34/1. 16. *Scabrathephanopores* sp., 516.00 mbsf, slide 1, EFS T34/2. 17. *Ulmipollenites krempii*, 569.50 mbsf, slide 1, EFS L47/0. 18. *Ulmipollenites krempii*, 607.06 mbsf, slide 1, EFS J31/3. 19. *Ulmipollenites krempii*, 512.24 mbsf, slide 2, EFS S21/2. 20. *Ulmipollenites krempii*, 523.92 mbsf, slide 1, EFS R17/2. Scale bar = 10 µm.

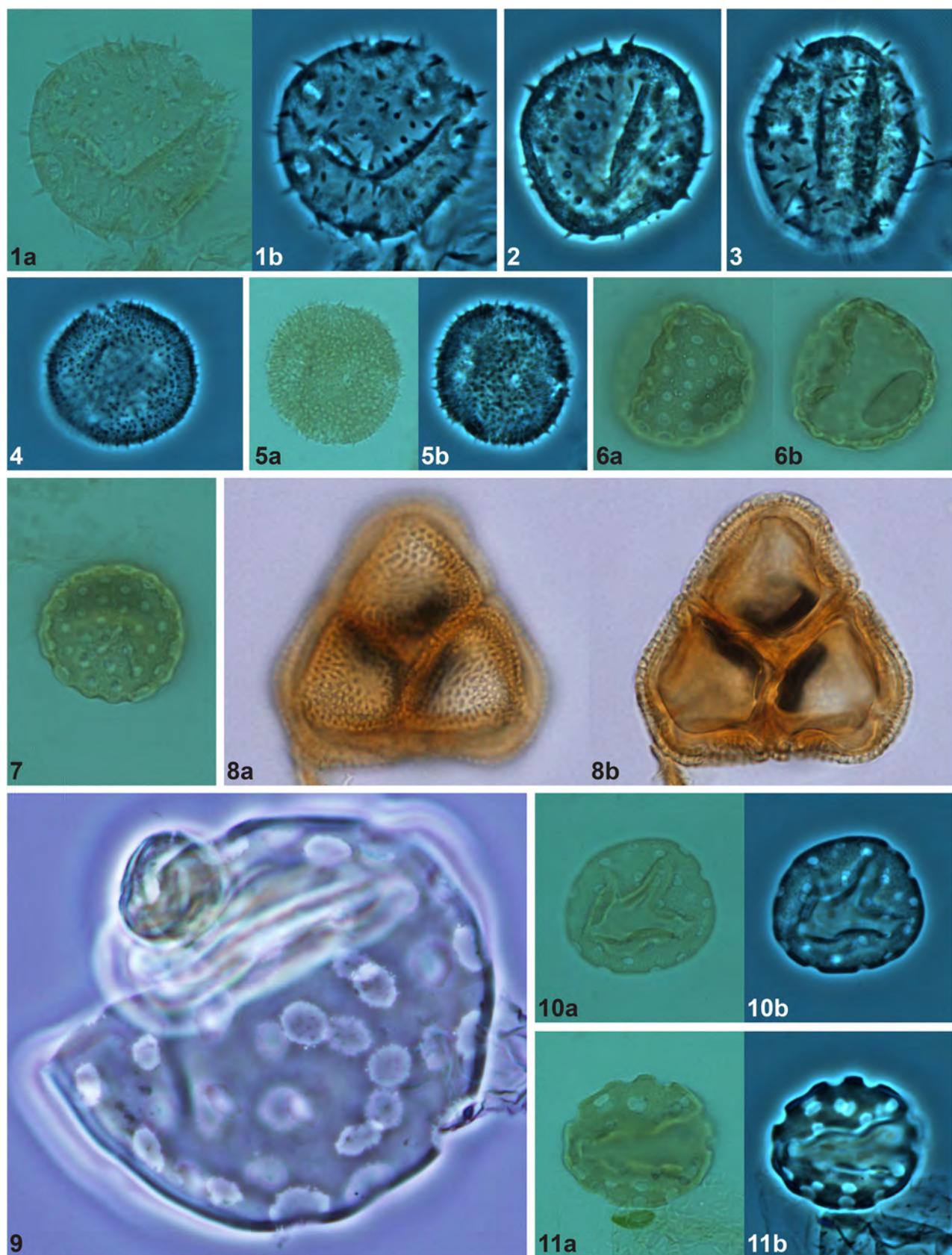


Plate 13. Stephanoporate and pantoporate pollen from IODP (International Ocean Discovery Program) 364. 1. *Malvacipollis* sp. (Euphorbiaceae type), 536.39 mbsf (meters below seafloor), slide 1, EFS England Finder Slide T42/0. 2. *Malvacipollis* sp. (Euphorbiaceae type), 520.79 mbsf, slide 1, EFS M31/0. 3. *Malvacipollis* sp. (Euphorbiaceae type), 527.08 mbsf, slide 1, EFS U24/2. 4. *Malvacipollis?* sp. A (Malvaceae type), 564.86 mbsf, slide 1, EFS N17/4. 5. *Malvacipollis?* sp. A (Malvaceae type), 556.58 mbsf, slide 1, EFS R15/2. 6. *Chenopodipollis* sp. A, 531.75 mbsf, slide 1, EFS K16/1. 7. *Chenopodipollis* sp. A, 531.75 mbsf, slide 1, EFS L29/3. 8. *Retitetradites* sp. A, 577.73 mbsf, slide 2, EFS S27/0. 9. *Psilaperiporites* sp. A, 597.10 mbsf, slide 1, EFS J34/2. 10. *Psilaperiporites suarezi*, 607.22 mbsf, slide 1, EFS T28/0. 11. *Psilaperiporites suarezi*, 579.39 mbsf, slide 1, EFS S33/1. Scale bar = 10 μ m.

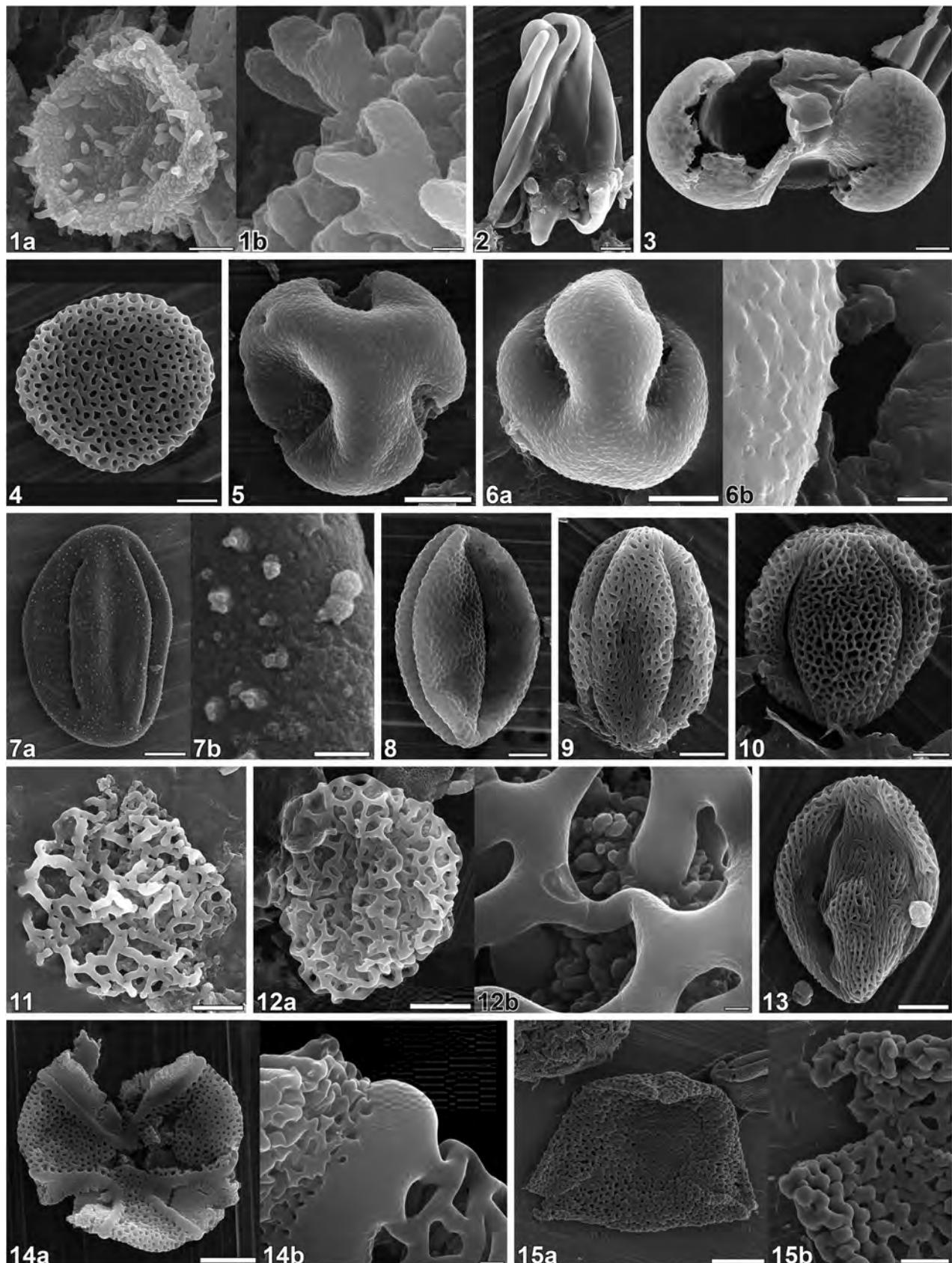


Plate 14. Scanning electron microscopy images of spores and pollen from IODP (International Ocean Discovery Program) 364. 1. *Raistrickia* sp. A, 582.78 mbsf (meters below seafloor). 2. *Gnetaceapollenites* sp. A, 577.73 mbsf. 3. Class Pinopsida, 607.18 mbsf. 4. *Retipollenites?* sp. A, 510.90 mbsf. 5. *Psilatricolpites* sp. A, 577.73 mbsf. 6. *Eucommia?* sp. A, 517.61 mbsf. 7. *Cupuliferoidea pollenites* sp., 510.90 mbsf. 8. *Fraxinoipollenites* sp., 505.88 mbsf. 9. *Retitricolpites* sp. A, 505.88 mbsf. 10. *Retitricolpites* sp. B, 505.88 mbsf. 11. *Retitrescolpites* sp. C, 517.61 mbsf. 12. *Spirosyncolpites spiralis*, 510.90 mbsf. 13. *Ailanthipites* sp. A, 542.61 mbsf. 14. *Margocolporites vanwijhei*, 510.90 mbsf. 15. *Boehlensipollis* sp. A, 510.90 mbsf. Scale bars: 1a, 2, 4, 5, 6a, 7a, 8–10, 13 = 5 μ m; 1b, 6b, 7b, 12b, 14b = 0.5 μ m; 3, 11, 12a, 14a, 15a = 10 μ m; 15b = 2 μ m.

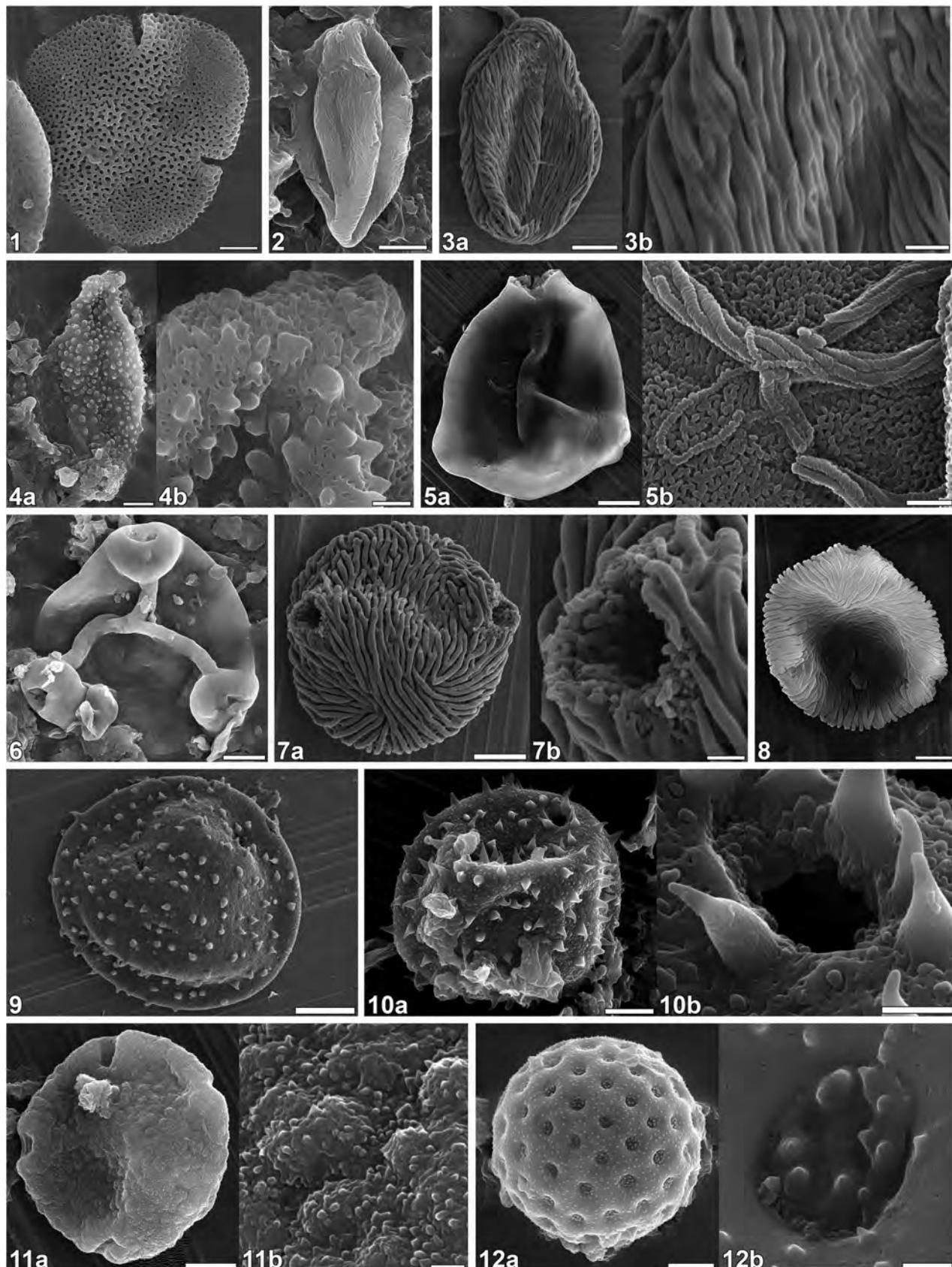


Plate 15. Scanning electron microscopy images of pollen from IODP (International Ocean Discovery Program) 364. 1. *Bombacacidites bombaxoides*, 517.61 mbsf (meters below seafloor). 2. *Rugutricolporites* aff. *R. felix*, 548.96 mbsf. 3. *Striatopolis grahamii*, sp. nov., 510.90 mbsf. 4. Stephanocolporate type A, 517.61 mbsf. 5. *Corsinipollenites parviangulus*, 510.90 mbsf. 6. *Corsinipollenites oculusnoctis*, 517.61 mbsf. 7. *Brosipollis* aff. *B. striata*, 510.90 mbsf. 8. *Brosipollis striata*, 510.90 mbsf. 9. *Malvacipollis* sp. (Euphorbiaceae type), 510.90 mbsf. 10. *Malvacipollis* sp. (Euphorbiaceae type), 577.73 mbsf. 11. *Ulmipollenites krempii*, 597.10 mbsf. 12. *Chenopodipollis* sp. A, 510.90 mbsf. Scale bars: 1, 2, 3a, 4a, 7a, 8, 9, 10a, 11a, 12a = 5 μ m; 3b, 4b, 5b, 7b, 10b = 1 μ m; 5a, 6 = 10 μ m; 11b, 12b = 0.5 μ m.

Discussion. *Scabratricolpites* sp. A resembles some species of *Quercoidites* in being tricolporate and granulate, but cannot be placed in *Quercoidites* as emended by Stanley (1965) because it lacks a geniculus and cannot be placed in *Quercoidites* as emended by Frederiksen (1980a) because it is oblate. *Psilatricolpites* sp. A is similar, but is psilate or indistinctly scabrate in LM, not granulate.

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

Botanical affinity. Eudicots, lower affinity unknown.

Genus *Striatopollis* Krutzsch 1959

Striatopollis grahamii sp. nov.

Plate 5, figures 7–9; Plate 15, figure 3

Holotype. The specimen in Plate 5, figure 8 (520.79 mbsf, slide 1, EFS S39/1).

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

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

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

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

Discussion. *Striatopollis grahamii* sp. nov. is somewhat similar to *Striatopollis catatumbus* (González Guzmán 1967) Takahashi & Jux 1989, but *S. catatumbus* is larger (49–56 μm in length) and has a thicker exine (ca. 3 μm) than *S. grahamii* sp. nov. The circumscription of *S. catatumbus* was interpreted loosely by Graham et al. (2000), who described a specimen of *S. catatumbus* 40 μm in length with a wall thickness of ca. 1 μm . *Striatopollis grahamii* sp. nov. is similar to Cenozoic Central American fossil pollen grains identified as the modern genus *Crudia* Schreb. (Fabaceae) by Graham (1988, 1989, 1991, 1999), although the specimens in this study are generally more prolate and smaller, with a thinner exine and finer, more anastomosing striae. Pollen grains with an observable pore, but otherwise similar to *Striatopollis grahamii* sp. nov., have been placed in *Striaticolporites* aff. *S. conspicuus* Muller 1968. *Striatopollis minor* (Wijmstra 1971) Jaramillo & Dilcher 2001 is distinguished from *Striatopollis grahamii* sp. nov. by its smaller size, *Striaticolpites semistriatus* González Guzmán 1967 is distinguished by having furrows that bifurcate at the poles, and *Striaticolpites saramacensis* Wijmstra 1971 has a thicker exine (2–3 μm thick) and distinct columellae.

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

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

Paleoecology. The similarity to modern *Crudia* pollen, a genus today found primarily in tropical lowlands and riverine

environments of the Amazon (Graham 1991, 2003), suggests that *Striaticolpites grahamii* sp. nov. was sourced from a tropical lowland paleoenvironment.

4.4. Tricolporate pollen

Genus *Boehlensipollis* Krutzsch 1962 emend.

Frederiksen 1983

Boehlensipollis? sp. A

Plate 9, figures 7–8; Plate 14, figure 15

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

Occurrence. Ypresian; 354 specimens observed (2.2%).

Boehlensipollis sp. A has a notably higher relative abundance in the PETM section than in the later Ypresian.

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

Genus *Bombacacidites* Couper 1960 emend. Krutzsch 1970

Bombacacidites brevis (Dueñas 1979) Muller et al. 1987

Plate 7, figures 2–3

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

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

Botanical affinity. Malvaceae, probably Bombacoideae.

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

Bombacacidites sp. A

Plate 7, figure 1

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

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

Botanical affinity. Malvaceae, probably Bombacoideae.

Paleoecology. Tropical deciduous forest.

Bombacacidites sp. B

Plate 7, figure 11

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

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

Botanical affinity. Malvaceae, probably Bombacoideae.

Paleoecology. Tropical deciduous forest.

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

Echitricolporites sp. A
Plate 9, figures 4–6

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

Occurrence. Ypresian; 54 specimens observed (0.3%). The FAD of *Echitricolporites* sp. A may be a useful regional biostratigraphic event. FAD: 572.75 mbsf; 50.5 (51.34) 53.7 Ma.

Botanical affinity. Eudicots, lower affinity unknown.

Genus *Ilexpollenites* Thiergart 1937 ex Potonié 1960

Ilexpollenites cf. *I. verrucatus* Pocknall & Mildenhall 1984
Plate 9, figure 3

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

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

Botanical affinity. Eudicots, probably Aquifoliaceae.

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

Margocolporites sp. A
Plate 8, figure 12

Discussion. The single specimen of this type is quite similar to *Margocolporites vanwijhei* Germraad et al. 1968, but the reticulum is finer, and the margocolpus is faintly scabrate.

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

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

Paleoecology. Possibly lowland tropical forest, based on the similarity to *Margocolporites vanwijhei* Germraad et al. 1968.

Margocolporites vanwijhei Germraad et al. 1968 sensu lato
Plate 8, figures 11, 13; Plate 14, figure 14

Occurrence. Ypresian; 68 specimens observed (0.4%). Germraad et al. (1968) gave the known range of *Margocolporites vanwijhei* in the Caribbean as middle Eocene to present. *Margocolporites vanwijhei* is fairly common and widely distributed in the Cenozoic (Palynodata Inc. and White 2008). These Ypresian specimens represent the earliest published occurrence of *M. vanwijhei* in Mexico, Central America, or the Caribbean (Graham 2010).

Botanical affinity. Eudicots, probably the subfamily Caesalpinoideae of the Fabaceae, possibly *Caesalpinia* L. (Germraad et al. 1968).

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

Genus *Punctatricolporites* Kedves 2000 emend.

Emended description. Punctate, tricolporate pollen.

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

Punctatricolporites sp. A
Plate 6, figure 11

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

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

Botanical affinity. Eudicots, lower affinity unknown.

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

Retitricolporites sp. A
Plate 8, figures 1–2

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

Occurrence. Ypresian; 1997 specimens observed (12.3%).

Botanical affinity. Eudicots, lower affinity unknown.

Genus *Striaticolporites* Leidelmeyer 1966

Striaticolporites aff. *S. conspicuus* Muller 1968
Plate 8, figure 7

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

Botanical affinity. Eudicots, probably Fabaceae, possibly *Crudia* (see discussion of this species in the *Supplementary material*).

Paleoecology. The similarity of these specimens to modern *Crudia* pollen, a genus today found primarily in tropical lowlands and riverine environments of the Amazon (Graham 1991, 2003), suggests that *Striaticolporites* aff. *S. conspicuus* may be indicative of tropical lowland environments. Additionally, Ramírez-Arriaga, Prámparo, et al. (2014) describe similar pollen grains of *Striaticolporites* as indicating a tropical deciduous forest paleoenvironment.

4.5. Stephanocolpate pollen

Polygalaceae? type A
Plate 9, figures 9–10

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

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

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

4.6. Stephanocolporate pollen

Genus *Psilastephanocolporites* Leidelmeyer 1966
Psilastephanocolporites hammenii sp. nov.
Plate 10, figures 1–4

Selected synonymy. *Psilastephanocolporites 'cedreloides'* Jaramillo et al. 2014, figs 262, 263

Holotype. The specimen in Plate 10, figure 2 (597.10 mbsf, slide 1, EFS P38/1).

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

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

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

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

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

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

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

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

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

Stephanocolporate type A
Plate 10, figures 5–7; Plate 15, figure 4

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

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

Botanical affinity. Eudicots, lower affinity unknown.

4.7. Monoporate pollen

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

Milfordia hungarica (Kedves 1965) Krutzsch & Vanhoorne 1970
Plate 10, figure 9

Discussion. *Milfordia minima* Krutzsch 1970 is distinguished from the otherwise similar *M. hungarica* by being less than 30 μ m in diameter (Frederiksen 1983). More detailed taxonomic discussion is given in the [Supplementary material](#).

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

Botanical affinity. Probably Restionaceae. Frederiksen (1983) considered that the botanical affinity of this genus was

possibly with the Restionaceae or *Joinvillea* (Joinvilleaceae). Akkiraz et al. (2008) considered that *Milfordia* belongs to the Restionaceae.

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

Genus *Monoporopollenites* Meyer 1956

Monoporopollenites annulatus (van der Hammen 1954)

Jaramillo & Dilcher 2001

Plate 10, figure 8

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

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

Paleoecology. Possibly arid tropical scrub (Ramírez-Arriaga, Prámparo, et al. 2014), although Macphail and Hill (2002) state that in the Paleocene–Eocene the Poaceae initially occurred in regions dominated by evergreen wet forests in paratropical conditions. If the botanical affinity is with the Restionaceae rather than the Poaceae, this would indicate an estuarine habitat.

4.8. Triporate pollen

Betulaceae/Myricaceae type sensu Jardine (2011)

Plate 10, figures 12–13

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

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

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

Genus *Brosipollis* Krutzsch 1968

Brosipollis aff. *B. striata* Frederiksen 1988

Plate 12, figure 4

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

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

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

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

Brosipollis reticulatus sp. nov.

Plate 12, figures 5–6

Holotype. Plate 12, figure 6 (547.42 mbsf, slide 2, EFS L25/2).

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

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

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

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

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

Occurrence. Ypresian; 10 specimens observed (0.1%).

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

Paleoecology. Probably lowland tropical forest.

Genus *Corsinipollenites* Nakoman 1965

Corsinipollenites oculusnoctis (Thiergart 1940) Nakoman 1965

Plate 11, figure 15

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

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

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

Corsinipollenites parviangulus Frederiksen 1983 sensu lato
Plate 11, figure 13

Discussion. The presence of viscin threads in some specimens indicates a probable affinity with the Onagraceae. A more detailed taxonomic discussion is given in the Supplementary material.

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

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

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

4.9. Stephanoporate pollen

Genus *Malvacipollis* Harris 1965 emend. Krutzsch 1966

Malvacipollis spp. (Euphorbiaceae type)
Plate 13, figures 1–3; Plate 15, figures 9–10

Discussion. There appears to be a morphological continuum in the size and distribution of the spines, as well as the exine thickness. More detailed taxonomic discussion of this taxon is given in the Supplementary material.

Occurrence. Ypresian; 1605 specimens observed (9.9%).

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

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

Malvacipollis? sp. A (Malvaceae type)
Plate 13, figures 4–5

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

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

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

Scabastephanoporites gen. nov.

Type species. *Scabastephanoporites variabilis* gen. et sp. nov.

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

Derivation of name. The form of this name follows the artificial nomenclature system of van der Hammen (1954, 1956).

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

Scabastephanoporites variabilis gen. et sp. nov.

Plate 12, figures 13–16

Holotype. The specimen in Plate 12, figure 15 (558.26 mbsf, slide 1, EFS S34/1).

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

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

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

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

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

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

Botanical affinity. Eudicots, possibly Cannabaceae or Ulmaceae. *Scabastephanoporites variabilis* gen. et sp. nov. is somewhat similar to *Ulmipollenites krempii*, and also

resembles modern pollen of *Planera aquatica* (Walt.) Gmel. (Ulmaceae), although *P. aquatica* pollen is larger (ca. 44 microns) (Kapp et al. 2000). An alternative botanical affinity for *S. variabilis* gen. et sp. nov. is suggested by the resemblance to modern *Celtis* L. pollen (Kapp et al. 2000) and the *Celtis tschudyi* (Elsik 1974) Frederiksen 1980 group (Frederiksen 1988; Jardine 2011), although the detailed pore structure described by Frederiksen (1980b) for *C. tschudyi* has not been observed in *S. variabilis* gen. et sp. nov.

Genus *Ulmipollenites* Wolff 1934 emend. Srivastava 1969

Ulmipollenites krempii (Anderson 1960) Frederiksen
1979 emend.

Plate 12, figures 17–20; Plate 15, figure 11

Selected synonymy. *Ulmoidepites krempii* Anderson 1960, pl. 6, fig. 2.

Ulmoidepites planeraeformis Anderson 1960, pl. 4, fig. 1.

Ulmoidepites tricostatus Anderson 1960, pl. 4, figs 20–21.

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

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

Discussion. A detailed taxonomic discussion is given in the Supplementary material.

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

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

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

4.10. Pantoporate pollen

Genus *Chenopodipollis* Krutzsch 1966

Chenopodipollis sp. A

Plate 13, figures 6–7; Plate 15, figure 12

Discussion. *Chenopodipollis* sp. A is quite similar to modern pollen of some species of Amaranthaceae, for example *Salicornia bigelovii* Torr. and *Amaranthus australis* (Gray) Sauer (Willard et al. 2004). The type species of the genus,

Chenopodipollis multiplex Krutzsch 1966, differs from these specimens in being infrareticulate.

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

Botanical affinity. Amaranthaceae.

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

5. Discussion and conclusions

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

Existing plant spore and pollen taxa with reasonably well-established paleogeographic ranges in the literature (see Supplementary material) suggest that the paleobotanical assemblage in the IODP 364 core has more taxa in common with North America than South America. Of these 40 Paleogene taxa, 20 occur in both North and South America, 15 occur in North America but not South America, three occur in South America but not North America, and two occur neither in North America nor in South America. *Hamulatisporis hamulatis* Krutzsch 1959 was present in Paleogene North America, but appears to have no published occurrences in Paleogene South America (Palynodata Inc. and White 2008; Graham 2010), although there is a record of *H. hamulatis* from the Cretaceous of Venezuela (Sinanoglu 1984). Pollen taxa with a botanical affinity to the Juglandaceae (*Caryapollenites* Raatz 1937 ex Potonié 1960

emend. Krutzsch 1961, *Momipites* Wodehouse 1933 emend. Nichols 1973), *Bursera* (*Brosipollis* Krutzsch 1968), and *Alnus* Ehrhart indicate a similarity to Paleocene–Eocene North American assemblages. *Bombacacidites brevis*, *Scabratriporites redundans* González Guzmán 1967, and *Spirosyncolpites spiralis* González Guzmán 1967 have published occurrences in South America but not North America. Two species, *Foveotriletes crater* Stover & Partridge 1973 and *Undulatisporites mineri* (Singh & Kumar 1972) Smith et al. 2019, have previously only been described from Australasia and India, respectively (Palynodata Inc. and White 2008; Smith et al. 2019). Some of these differences may be due to regional taxonomic practices, or convergent morphologies, but the overall resemblance of the IODP 364 assemblage to contemporaneous assemblages from North America is clear. Possibly the most unique feature of the IODP 364 angiosperm assemblage generally is the high relative abundance of *Malvacipollis* spp. with affinity to the Euphorbiaceae, approximately 9.9% of the total pollen and plant spore count (see [Supplementary material](#)). During the Paleocene and early Eocene, North and South America were widely separated, and the closest emergent landmass which could serve as a source for the pollen in the IODP 364 core was probably in either the Yucatán Peninsula or mainland Mexico (Iturralde-Vinent and MacPhee 1999).

Unfortunately, despite a large number of high-resolution samples from the basal Paleocene strata above the impact breccia, the oldest observed terrestrial palynomorphs in the IODP 364 core were two fern spores of the genus *Deltoidospora* at 615.50 mbsf (Smith et al. 2019); the age of this sample depth is constrained by foraminiferal biostratigraphy to between 65.25 and 65.72 Ma. The oldest angiosperm pollen observed in the core, a single specimen of *Betula*? sp. A and four specimens of *Chenopodipollis* sp. A occur at 615.03 mbsf; the estimated age of this sample is 65.15 Ma (see [Supplementary material](#)). Throughout the rest of the Paleocene section, pollen is either entirely absent or present in abundances too low to make any confident interpretations about the Paleocene assemblage. However, the high relative abundance of *Chenopodipollis* sp. A in the Paleocene may be evidence of a predominantly estuarine pollen source area. The near absence of palynomorphs generally in the Paleocene section stands in contrast to the calcareous microfossil record (Lowery et al. 2018; Jones et al. 2019). This indicates that the low abundance in the Paleocene section is probably the result of poor preservation of organic-walled microfossils. Gulick et al. (2019) note that based on paleogeographic reconstructions, the closest emergent land at the onset of the Paleocene (moment of impact) was 800 km westward across a relatively shallow shelf (ca. 100 m water depth). Certainly, all regional vegetation would have been annihilated by the impact event itself, and there is strong evidence that the impact caused a global mass extinction in many terrestrial plant groups (Vajda et al. 2001; Vajda and Raine 2003; McElwain and Punyasena 2007). However, due to the near absence of pollen in the Paleocene part of the section, and the lack of information about Cretaceous pollen assemblages from the Yucatán

Peninsula, it is not possible to quantitatively estimate the magnitude of the extinction event from the angiosperm pollen assemblage in the IODP 364 core.

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

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors



VANN SMITH is a PhD student in the Department of Geology and Geophysics at Louisiana State University in Baton Rouge. He completed his undergraduate degree in geology at Louisiana State University in 2011, and an MS degree in earth and environmental sciences at Tulane University in 2015. After graduating from Tulane University, he worked in the oil industry as a nannofossil biostratigrapher from 2015 to 2016. His research interests include tropical Paleogene terrestrial palynology, the K-Pg impact event, morphometrics, Cenozoic nannofossil paleontology, and quantitative biostratigraphy.



SOPHIE WARNY is an associate professor of palynology in the Department of Geology and Geophysics and a curator at the Museum of Natural Science at Louisiana State University in Baton Rouge. She has a long history with AASP as she won the AASP Student Award in 1996, served as Director-At-Large on the AASP board from 2006 to 2007, was the AASP Newsletter Editor from 2006 until 2015, and is now the AASP Chair in Palynology. She received her

PhD from the Université Catholique de Louvain, in Belgium, working with Dr. Jean-Pierre Suc on the Messinian Salinity Crisis. In 2011, she received an NSF CAREER award to conduct palynological research in Antarctica. Since being hired at LSU in 2008, she has directed 18 graduate students' theses on various Cretaceous to Cenozoic sections. Her students are now employed with the oil and gas industry (Hess, BP, Devon, Chevron, BHP Billiton Petroleum, and EOG), with the US Department of Homeland Security, with environmental companies, with IODP, or as instructors.



DAVID M. JARZEN is a research associate at the Cleveland Museum of Natural History, in paleobotany and paleoecology. He earned his BS degree in 1967 from Kent State University, and two years later received his MA degree in botany from the same institution. In 1973 he was awarded a PhD in geology from the University of Toronto. His research interests in the nature of extant and fossil plant life have provided extensive field work around the world, incorporating a global view aiming to understand the evolution of plant life during Earth's history, with an emphasis on fossil floras recorded from the Cretaceous, Paleogene and Neogene. His work has been incorporated in several radio and television productions including CBC's *Nature of Things* with David Suzuki, the PBS NOVA Series, the NHK (Japan) Series *The Miracle Planet*, the National Film Board of Canada, the Discovery Channel and other North American cable networks. David was elected as Fellow National to the Explorers Club, and in 2005 he was elected Fellow of the Ohio Academy of Science.



THOMAS DEMCHUK is an adjunct professor in the Department of Geology and Geophysics at Louisiana State University in Baton Rouge. He assists the AASP Chair in Palynology, Dr. Sophie Warny, supervising students, finding appropriate graduate projects, and teaching. Thomas is also a Business Development Manager, Geological Consultant, with RPS Energy in Houston, Texas, marketing specialist geology and biostratigraphic products to the general exploration community. He received his PhD (1992) from the University of Calgary in both palynology and organic petrography, and received his MSc (1987) from the University of Alberta in Edmonton. Thomas has over 26 years of experience in the oil industry, having spent more than 18 years with ConocoPhillips Co. and prior to that over four years with Amoco

Corporation. His current primary research interests include study of the Paleocene–Eocene boundary (PETM interval) along the US Gulf Coast, particularly the outcrops and subsurface of central and south Texas, and correlation to the deepwater Wilcox Group reservoirs. Additional research includes the organic petrography of Gulf Coast Paleocene–Eocene coals and paleoclimatic/paleogeographic reconstructions of the region. He is interested in all aspects of organic petrography and organic characterization of coals, source rocks, and unconventional resources including thermal maturity and vitrinite reflectance studies. He was the AASP-TPS Secretary-Treasurer from 1997 to 2016, and prior to that was a Director-at-Large from 1992 to 1994. He is currently the Chair and Trustee for the AASP Foundation.



VIVI VAJDA is professor in paleontology at the Swedish Museum of Natural History in Stockholm, Sweden, and she is department chair at the Department of Palaeobiology. Her research specialty is palynology, and her projects aim to determine the rate of turnover of plants across the Cretaceous–Paleogene (K-Pg) boundary, based on palynological analyses. Investigations focus on sediments from New Zealand, Colombia, and Denmark.

She also uses the palynological signal from the K-Pg boundary as a tool to interpret other mass extinction events, such as the Permian–Triassic and the Triassic–Jurassic (Australia, New Zealand, and Sweden) extinction events. Additional research includes chemical mapping of leaf fossils using vibrational microspectroscopic analyses. She is active in national and international geo-related organizations and was for several years chair of the Geological Society of Sweden and for the UNESCO sciences program IGCP. Since 2019 she has been an elected member of the Royal Swedish Academy of Sciences.



SEAN GULICK is a research professor at the Jackson School of Geosciences, University of Texas at Austin, Austin, Texas, USA. He specializes in the integration of geophysical and geological observations of impact craters, continental shelves, and tectonic plate boundaries. He received his PhD from Lehigh University in 1999. He has sailed on over 25 research expeditions including four drilling expeditions. He was the co-chief scientist of both the 2005 seismic investigation of the Chicxulub impact structure and the IODP-ICDP Expedition 364 (Drilling the K-Pg Chicxulub impact crater). His work is featured in several documentaries including PBS Nova's *Day the Dinos Died* and BBC's *The Day the Dinosaurs Died*. He currently serves as co-chair of the IODP Science Evaluation Panel and he is a Fellow of the Geological Society of America.

ORCID

Vann Smith <http://orcid.org/0000-0001-8817-2533>

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