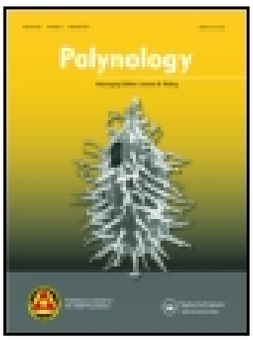

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Palaeocene–Eocene miospores from the Chicxulub impact crater, Mexico. Part 1: spores and gymnosperm pollen

Vann Smith[a,b], Sophie Warny[a,b], David M. Jarzen[c], Thomas Demchuk[a], Vivi Vajda[d] and The Expedition 364 Science Party

[a]Department of Geology and Geophysics, LSU, Baton Rouge, LA, USA; [b]Museum of Natural Science, LSU, Baton Rouge, LA, USA; [c]Cleveland Museum of Natural History, Cleveland, OH, USA; [d]Swedish Museum of Natural History, Stockholm, Sweden

ABSTRACT

In the summer of 2016, the International Ocean Discovery Program (IODP) Expedition 364 cored through the post-impact strata of the end-Cretaceous Chicxulub impact crater, Mexico. Core samples were collected from the post-impact successions for terrestrial palynological analysis, yielding a rare Danian to Ypresian high-resolution palynological assemblage. This record constitutes one of the first Palaeocene and Ypresian palynological assemblages from Central America or Mexico, representing a more coastal lowland palaeoenvironment than previous studies from mainland Mexico. Although the abundance of pollen and spores is very low in the Palaeocene carbonates, abundance increases in the more organic-rich shale layers representing the Palaeocene–Eocene Thermal Maximum (PETM) and later Ypresian. The spores and gymnosperm pollen identified from IODP 364, although rare compared to the angiosperm pollen, are a diverse mix of cosmopolitan taxa, as well as some characteristic of fossil Central American assemblages (e.g. Selaginellaceae), and others previously identified from the Paleogene northern Gulf of Mexico coastal plain. The assemblage generally indicates the presence of nearby moist to seasonally dry lowland tropical forest, with some taxa suggestive of higher elevation forests. Ephedroid pollen grains may be indicative of the presence of more arid conditions.

KEYWORDS

Mexico; miospores; Palaeocene; Eocene; Cretaceous–Paleogene boundary

1. Introduction

At the end of the Cretaceous Period, a massive asteroid collided with Earth and formed an impact crater approximately 200 km in diameter in the shallow carbonate Yucatán Platform, Mexico. This event is generally considered to be the main cause of the Cretaceous–Paleogene (K–Pg) mass extinction event (Schulte et al. 2010). Despite the catastrophic nature of the impact, the presence of trace fossils in the transitional unit between the impact breccia and the overlying Palaeocene limestone indicates that benthic life had returned to the impact crater, possibly within six years after the impact, and by 30 kyr after the impact seafloor conditions had essentially returned to normal (Lowery et al. 2018). The impact crater became a depositional basin which slowly filled in with sediment, and is no longer observable as a surface topographical feature. International Ocean Discovery Program (IODP) borehole 364 targeted the peak ring of the Chicxulub impact crater, an elevated ring inside the crater rim, with the goal of investigating the impact structure as well as the post-impact sedimentary succession (Gulick et al. 2016). Further information about the post-impact sedimentary rocks of IODP 364, including the biostratigraphical age model derived from foraminifera and calcareous nannofossils, can be found in Gulick et al. (2017). A gravity anomaly map of the Chicxulub impact crater is provided in Figure 1.

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

CONTACT Vann Smith vannpaleo@gmail.com Department of Geology and Geophysics, LSU, E-235 Howe-Russell, Baton Rouge, LA 70803, USA.

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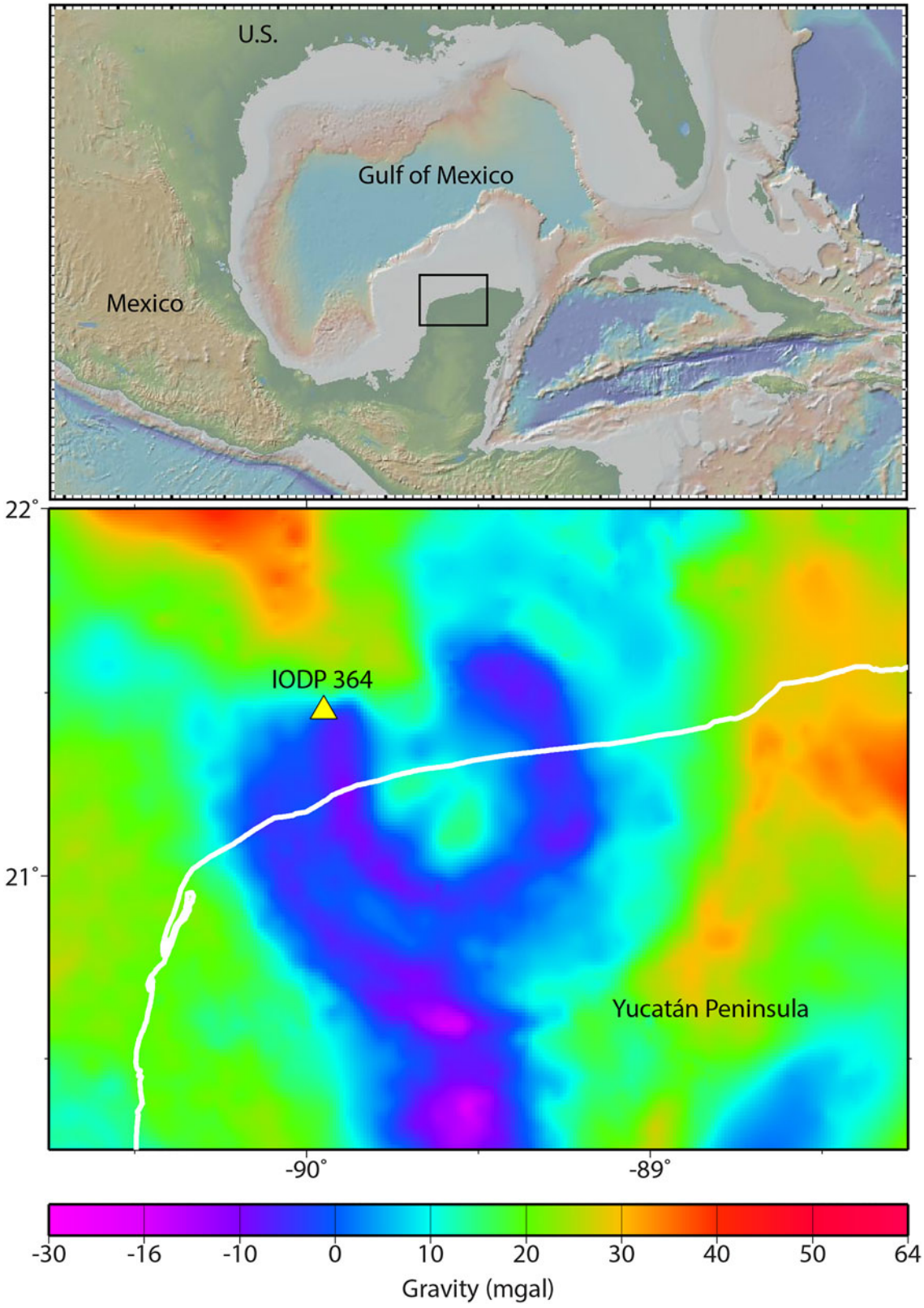

Figure 1. Location of the International Ocean Discovery Program (IODP) 364 (site MOO77A) drilling location in the Yucatán Peninsula, Mexico. The upper map shows the geographical extent of the gravity anomaly map on bottom. The position of site MOO77A is marked by a yellow triangle on the gravity anomaly map. Gravity data courtesy of G. Christeson, A. Hildebrand, and M. Pilkington.

2. Materials and methods

Approximately 15–40 g of sediment was taken at 149 sample depths from the post-impact section of the IODP 364 core and processed by Global Geolab Ltd using modifications of standard palynological techniques described by Traverse (2007). When possible, two slides were made at each depth and the residue retained for future use. Slides were scanned until 300 identifiable pollen and spore grains were counted, or until the slides at that sample depth were fully scanned. Microscopic examination

was conducted using an Olympus BX41 microscope for bright-field microscopy and phase-contrast microscopy. Pollen grains were generally photographed at 1000× magnification. Size measurements for species were made on all specimens of the species if fewer than 10 specimens were observed, and then expressed as a range. If more than 10 specimens were observed, the size ranges were based on measurements of 10 specimens and the mean size is given in parentheses.

Occurrence information is given in terms of the total number of specimens of the taxon observed in all samples; for comparison, the total number of identified angiosperm pollen, gymnosperm pollen and spores in this study is 16,247. A review of species occurrences in the literature was greatly aided by the database of Palynodata Inc. and White (2008). A list of the spore and gymnosperm pollen taxa, with their botanical affinities and interpreted palaeoecology, is given in the Supplementary materials. Quantitative counts for all spore and gymnosperm pollen taxa in the 149 samples are also given in the Supplementary materials. None of the gymnosperm pollen or spores described here have any clear biostratigraphical value for the age range covered in the IODP 364 core. Although the first observed occurrence of many species is in the Ypresian, this is probably because the Palaeocene section is nearly barren. Multiple species described in this paper have a wide geographical distribution and were present in the Mesozoic.

3. Morphology, nomenclature, and botanical affinities

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

4. Systematic palaeontology

All key palynomorphs have been photographed. The spores are illustrated in Plate 1, Plate 2, and Plate 3, and the gymnosperm pollen are illustrated in Plate 4.

4.1. Trilete spores

Genus *Ceratosporites* Cookson & Dettmann 1958

Ceratosporites sp. A
Plate 2, figures 9–10; Plate 3, figure 1

Discussion. This species is generally similar to some modern species of *Selaginella* from Panama (Roubik and Moreno 1991). Jaramillo et al. (2014, p. 194) describe an echinate trilete spore with affinity to *Selaginella* with bifurcate tips, which they informally named '*Echitriletes* "*selaginelloides*" type "'bifurcatus"'. This type differs in having a circular amb, a thicker wall, and smaller spines relative to the size of the spore. Some specimens of *Neoraistrickia* sp. A have reduced ornamentation on the proximal face and may represent gradational morphologies with *Ceratosporites* sp. A.

Occurrence. Ypresian; four specimens observed.

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

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

Genus *Cyathidites* Couper 1953

Cyathidites minor Couper 1953
Plate 1, figures 4–5

Occurrence. Ypresian; two specimens observed.

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

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

Genus *Deltoidospora* Miner 1935

Leiotriletes Naumova 1939 ex Ishchenko 1952.
Lygodiumsporites Potonié, Thomson, & Thiergart 1950 ex Potonié 1956.
Psilatriletes van der Hammen 1954 ex Potonié 1956.

Deltoidospora spp.
Plate 1, figures 1–3

Discussion. This study will follow Jardine (2011) in not identifying species of *Deltoidospora*.

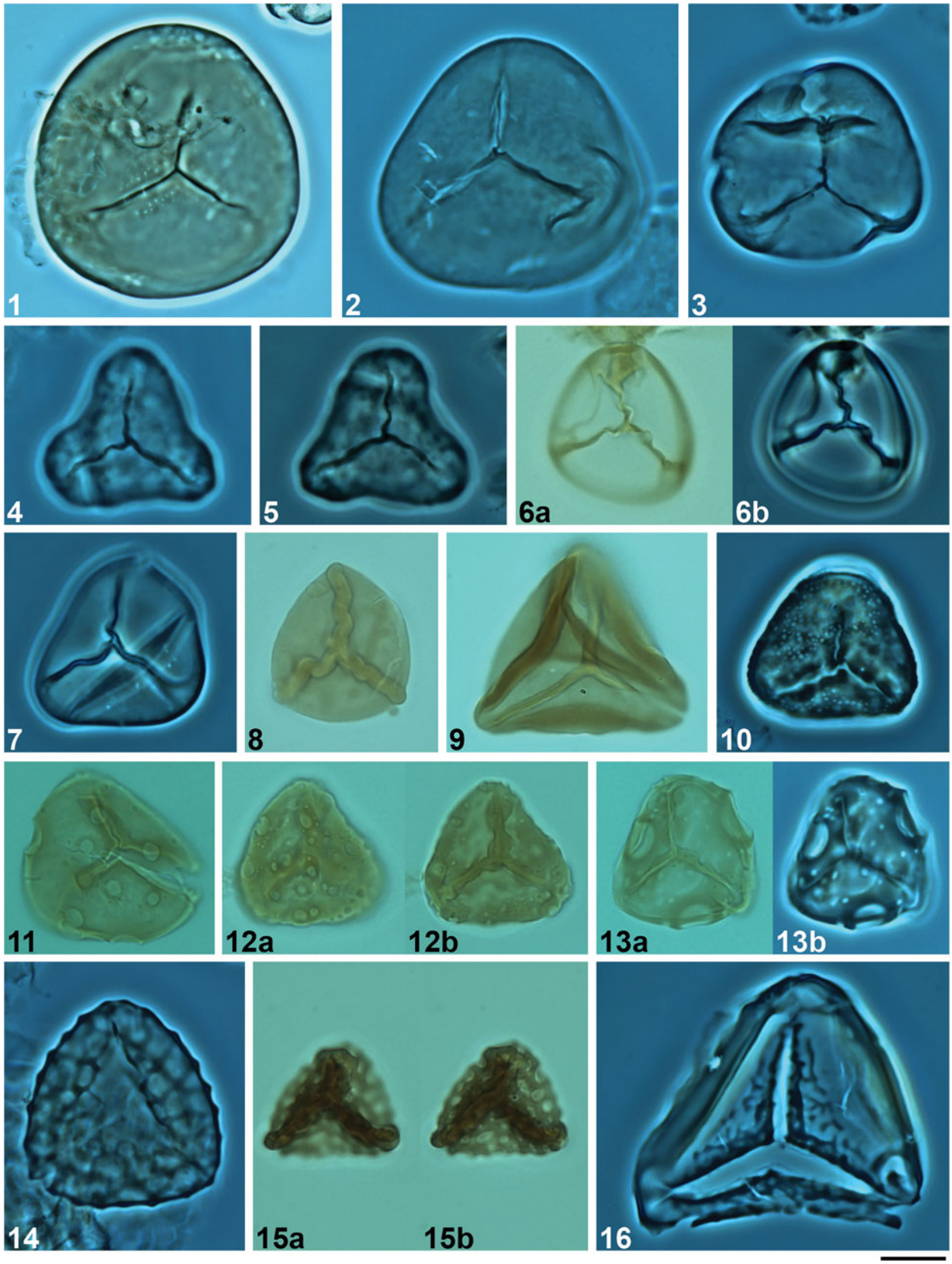

Plate 1. Trilete spores from International Ocean Discovery Program (IODP) 364. 1. *Deltoidospora* sp. 505.88 mbsf, slide 2, EFS R22/0. 2. *Deltoidospora* sp. 548.96 mbsf, slide 1, EFS P40/0. 3. *Deltoidospora* sp. 514.14 mbsf, slide 1, EFS T29/2. 4. *Cyathidites minor*. 510.90 mbsf, slide 1, EFS T29/2. 5. *Cyathidites minor*. 510.90 mbsf, slide 1, EFS P33/4. 6. *Undulatisporites mineri*. 544.11 mbsf, slide 1, EFS N26/4. 7. *Undulatisporites mineri*. 572.75 mbsf, slide 2, EFS U44/1. 8. *Undulatisporites elsikii*. 607.22 mbsf, slide 2, EFS G18/3. 9. *Gleicheniidites senonicus*. 607.22 mbsf, slide 2, EFS S38/0. 10. *Punctatriletes* sp. A. 582.78 mbsf, slide 2, EFS Q13/1. 11. *Foveotriletes crater*. 582.78 mbsf, slide 2, EFS P26/2. 12. *Foveotriletes crater*. 582.78 mbsf, slide 2, EFS V18/0. 13. *Kuylisporites waterbolkii*. 533.27 mbsf, slide 1, EFS Q30/2. 14. *Retitriletes* sp. A. 606.60 mbsf, slide 2, EFS H31/3. 15. *Retitriletes* sp. B. 607.04 mbsf, slide 2, EFS X21/2. 16. *Rugutriletes* sp. A. 563.21 mbsf, slide 1, EFS S27/2. Scale bar = 10 μm.

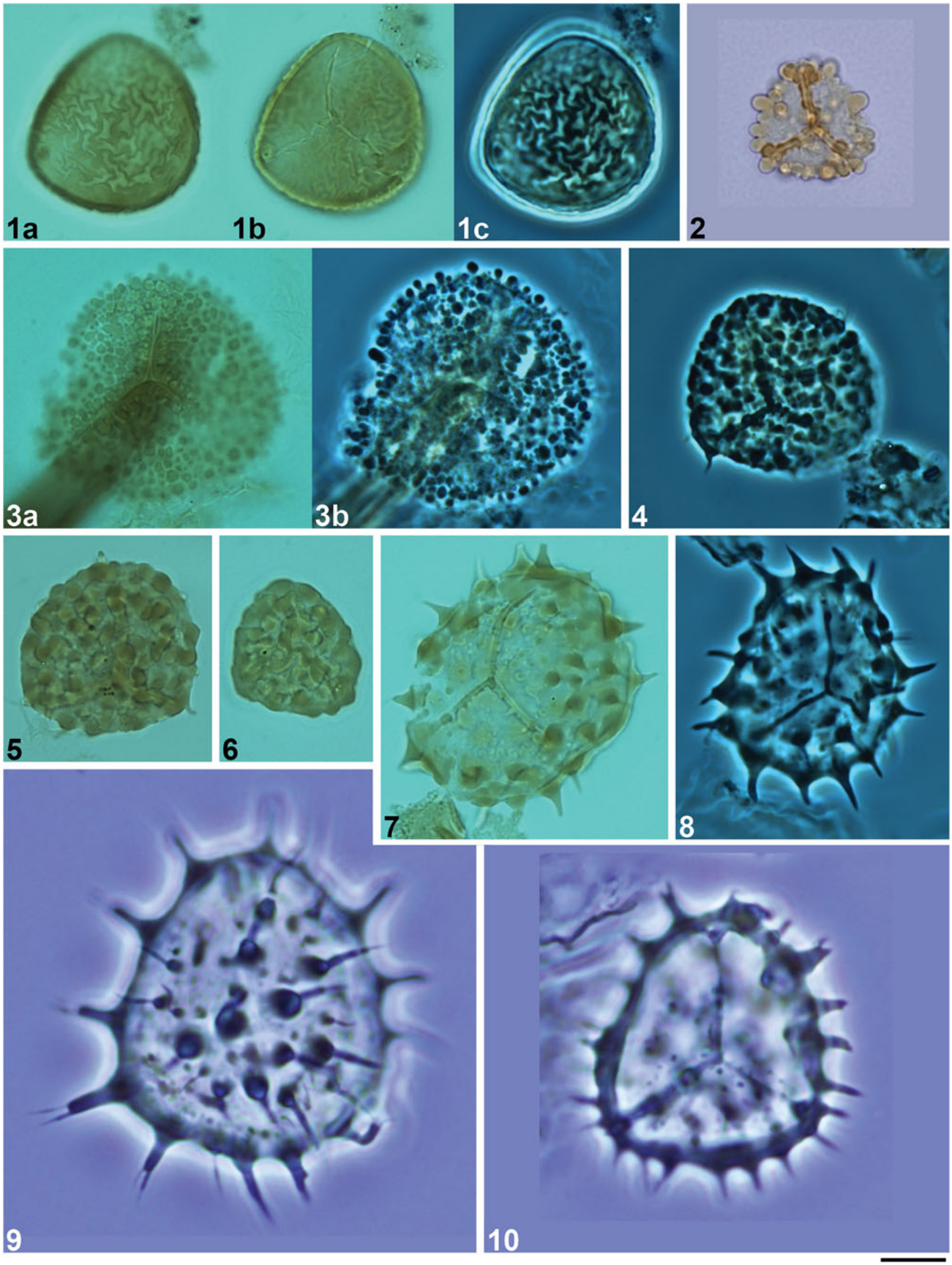

Plate 2. Trilete spores from International Ocean Discovery Program (IODP) 364. 1. *Hamulatisporis hamulatis*. 582.78 mbsf, slide 1, EFS V47/0. 2. *Gemmatriletes* sp. A. 577.73 mbsf, slide 2, EFS P31/0. 3. *Gemmatriletes* aff. *G. clavatus*. 564.86 mbsf, slide 1, EFS U19/2. 4. *Verrucosisporites* sp. A. 607.18 mbsf, slide 1, EFS 041/0. 5. *Verrucosisporites* sp. A. 607.22 mbsf, slide 2, EFS U43/0. 6. *Verrucosisporites* sp. A. 607.22 mbsf, slide 2, EFS J42/0. 7. *Echinatisporis* sp. A. 539.43 mbsf, slide 1, P23/2. 8. *Echinatisporis* sp. A. 556.58 mbsf, slide 1, EFS R37/1. 9. *Ceratosporites* sp. A. 505.88 mbsf, slide 2, EFS N43/0. 10. *Ceratosporites* sp. A. 505.88 mbsf, slide 2, EFS Q25/4. Scale bar = 10 μm.

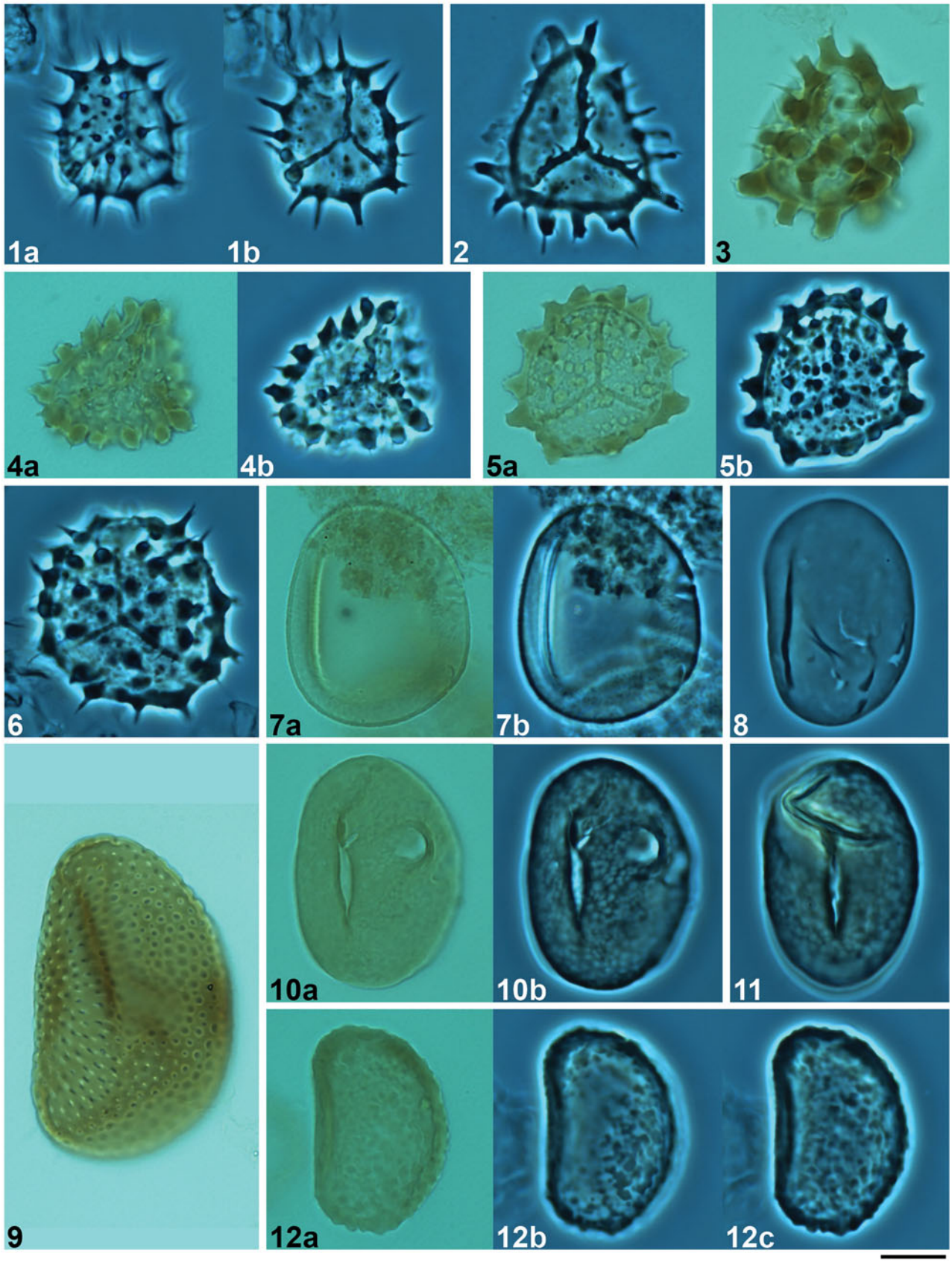

Plate 3. Trilete and monolete spores from International Ocean Discovery Program (IODP) 364. 1. *Ceratosporites* sp. A. 540.89 mbsf, slide 1, EFS T41/0. 2. *Neoraistrickia* sp. A. 516.00 mbsf, slide 1, EFS U24/0. 3. *Neoraistrickia* sp. A. 574.35 mbsf, slide 1, EFS V16/0. 4. *Neoraistrickia* sp. A. 539.43 mbsf, slides 1, EFS T33/2. 5. *Raistrickia* sp. A. 555.07 mbsf, slide 1, EFS 042/1. 6. *Raistrickia* sp. A. 576.04 mbsf, slide 1, EFS S33/1. 7. *Laevigatosporites haardtii*. 564.86 mbsf, slide 1, EFS U34/1. 8. *Laevigatosporites haardtii*. 563.29 mbsf, slide 1, EFS Q35/2. 9. *Microfoveolatosporis* cf. *M. fromensis*. 592.23 mbsf, slide 1, EFS T32/2. 10. *Reticuloidosporites pseudomurii*. 582.78 mbsf, slide 2, EFS V24/0. 11. *Reticuloidosporites pseudomurii*. 582.78 mbsf, slide 2, EFS V16/1. 12. *Polypodiisporonites* sp. A. 556.58 mbsf, slide 1, EFS Q46/0. Scale bar = 10 μm.

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

Botanical affinity. Polypodiidae, possibly *Acrostichum* (Pteridaceae) or *Antrophyum* (Pteridaceae). The botanical affinity is somewhat difficult to determine, as psilate, trilete spores are produced by a variety of ferns. The specimens illustrated here are similar to spores produced by the modern genera *Acrostichum* and *Antrophyum*; Graham (1989) noted that although *Acrostichum* spores tend to have a more scabrate exine than *Antrophyum* spores, the distinction between the two genera is difficult to make with fossil spores. It is also difficult to distinguish *Acrostichum* spores from *Lygodium* spores (Jarzen and Dilcher 2006). Ramírez-Arriaga et al. (2005) affiliated similar spores assigned to *Deltoidospora* with the Cyatheaceae. Jardine (2011) suggested a probable affinity with the Cyatheaceae, Lygodiaceae, or Schizaeaceae for thick-walled specimens of *Deltoidospora* that have not been identified to the species level. Of the psilate trilete spores described from modern Panama by Roubik and Moreno (1991), these specimens most closely resemble *Acrostichum danaifolium* Langsd. & Fisch.

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

Genus *Echinatisporis* Krutzsch 1959

Echinatisporis sp. A
Plate 2, figures 7–8

Discussion. This species is morphologically similar to *Ceratosporites* sp. A, from which it differs by having an ornamented proximal face and non-tuberculate spines. Jaramillo et al. (2014) described a similar type from the Neogene of Panama which they informally named '*Echitriletes* "*selaginelloides*" type "*muelleri*"', differing mainly in having a triangular amb.

Occurrence. Ypresian; 27 specimens observed.

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

Palaeoecology. Probably lowland tropical forest (see palaeoecology section for *Ceratosporites* sp. A).

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

Emended description. Foveolate, trilete spores. Foveolae are here defined as more or less rounded depressions more than 1 μm in diameter, generally separated from adjacent foveolae by a distance greater than their diameter (Punt et al. 2007).

Foveotriletes crater Stover & Partridge 1973
Plate 1, figures 11–12

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

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

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

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

Genus *Gemmatriletes* Pierce 1961

Gemmatriletes aff. *G. clavatus* Brenner 1968
Plate 2, figure 3

Discussion. *Gemmatriletes clavatus* is somewhat similar to this specimen, but in *G. clavatus* the clavae are not as well developed and the exine is thicker.

Occurrence. Ypresian; one specimen observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato.

Gemmatriletes sp. A
Plate 2, figure 2

Discussion. Spores somewhat similar to this species have been assigned to *Bullasporis*, for example unspeciated *Bullasporis* specimens described and illustrated by Frederiksen (1980b) and Jardine (2011), which differ from this species most obviously in having bullae which are evenly distributed over the spore surface and in having indistinct laesurae without labra.

Occurrence. Ypresian; one specimen observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato. Mildenhall et al. (2014) give the botanical affinity for the somewhat similar species *Gemmatriletes multiglobus* as Grammitidaceae. Alternatively, *Gemmatriletes* sp. A is also morphologically similar to papillate species of *Selaginella*, for example *Selaginella labordei* (Zhou et al. 2015, fig. 12 D–F), as well as spores of the modern *Actiniopteris radiata* (J. Koenig ex Sw.) Link (van Campo 1974).

Genus *Gleicheniidites* Ross 1949 emend. Skarby 1964

Gleicheniidites senonicus Ross 1949
Plate 1, figure 9

Occurrence. Danian–Ypresian; two specimens observed. *Gleicheniidites senonicus* is a very common and globally distributed form genus in the Mesozoic and Cenozoic (Palynodata Inc. and White 2008). *Gleicheniidites senonicus* has been identified from Eocene strata in Deep Sea Drilling Project (DSDP) Site 94 along the Campeche Escarpment (Barron 2015; Barron et al. 2017).

Botanical affinity. Gleicheniaceae (Jardine 2011).

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

Genus *Hamulatisporis* Krutzsch 1959 emend. Srivastava 1972

Hamulatisporis hamulatis Krutzsch 1959
Plate 2, figure 1

Occurrence. Ypresian; one specimen observed.

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

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

Genus *Kuylisporites* Potonié 1956

Kuylisporites waterbolkii Potonié 1956
Plate 1, figure 13

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

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

Palaeoecology. Probably montane forest (Trujillo and Roche 2009; Romero Valero 2014); extant *Cnemidaria* predominantly inhabits elevations between 500 and 2000 m (Mohr and Lazarus 1994).

Genus *Neoraistrickia* Potonié 1956

Neoraistrickia sp. A
Plate 3, figures 2–4

Discussion. The Chicxulub occurrences of *Neoraistrickia* sp. A and *Raistrickia* sp. A are the first Cenozoic records of these genera (Palynodata Inc. and White 2008). It is unlikely that these spores are reworked from older deposits because no other exclusively Mesozoic palynomorphs have been observed in the assemblage; also, the morphology of this species resembles some modern species of *Selaginella*. This species has similar ornamentation to *Ceratosporites* sp. A, which is distinguished by lacking ornamentation on the proximal face, and *Raistrickia* sp. A, which is distinguished by having a more circular amb. These morphologies appear to be transitional with one another to some extent, and all have probable botanical affinity with the Selaginellaceae.

Occurrence. Ypresian; six specimens observed.

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

Palaeoecology. Probably lowland tropical forest (see palaeoecology section for *Ceratosporites* sp. A).

Genus *Punctatriletes* Pierce 1961

Punctatriletes sp. A
Plate 1, figure 10

Discussion. Graham (1988) described somewhat similar punctate-foveolate spores and assigned them to *Lycopodium*; his specimens differed mainly in having a psilate proximal face.

Occurrence. Ypresian; one specimen observed.

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

Genus *Raistrickia* Schopf, Wilson & Bentall 1944

Raistrickia sp. A
Plate 3, figures 5–6

Discussion. *Raistrickia* sp. A is similar to a photograph of an undescribed spore identified as *Selaginella* from the Lower Miocene of Panama (Graham 1988), specifically in having blunt-tipped projections, although it is unclear from the photograph whether the projections are tuberculate.

Occurrence. Ypresian; six specimens observed.

Botanical affinity. Probably Selaginellaceae (Knox 1950).

Palaeoecology. Probably lowland tropical forest (see palaeoecology section for *Ceratosporites* sp. A).

Genus *Retitriletes* Pierce 1961

Retitriletes sp. A
Plate 1, figure 14

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

Occurrence. Ypresian; two specimens observed.

Botanical affinity. Probably Lycopodiaceae (see discussion).

Palaeoecology. Possibly lowland tropical forest or swamp (see palaeoecology section for *Hamulatisporis hamulatis*).

Retitriletes sp. B
Plate 1, figure 15

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

Occurrence. Ypresian; one specimen observed.

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

Genus *Rugutriletes* Pierce 1961

Rugutriletes sp. A
Plate 1, figure 16

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

Occurrence. Ypresian; one specimen observed.

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

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

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

Haradisporites Singh & Kumar 1972.

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

Undulatisporites elsikii Frederiksen 1973 sensu lato
Plate 1, figure 8

Discussion. The Chicxulub specimen has a slightly broader labrum than *U. elsikii* sensu stricto.

Occurrence. Ypresian; one specimen observed.

Botanical affinity. Probably Polypodiaceae (Frederiksen 1980b), although Galván-Escobedo et al. (2015) assigned specimens of *Undulatisporites* that had not been identified to the species level to the Ophioglossaceae.

Undulatisporites mineri (Singh & Kumar 1972) comb. nov.
Plate 1, figures 6–7

Basionym. *Haradisporites mineri* Singh & Kumar 1972, photographs of holotype specimen in Plate 1, figures 1–2.

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

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

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

Genus *Verrucosisporites* Ibrahim 1933 emend. Smith 1971
Verrucosisporites sp. A Plate 2, figures 4–6

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

Occurrence. Thanetian; 14 specimens observed.

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

4.2. Monolete spores

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

Laevigatosporites haardtii (Potonié & Venitz 1934) Thomson & Pflug 1953
Plate 3, figures 7–8

Laevigatosporites gracilis Wilson & Webster 1946.
Laevigatosporites ovatus Wilson & Webster 1946.

Occurrence. Ypresian; 11 specimens observed. *Laevigatosporites haardtii* is a common and globally distributed species in the Cenozoic (e.g. Lenoir and Hart 1988; Vajda and Raine 2003, Palynodata Inc. and White 2008; Smith et al. 2018), with some Mesozoic occurrences (e.g. Palynodata Inc. and White 2008; Garzon et al. 2012; Akyuz et al. 2016). Its nondescript morphology is similar to that of

modern Gleicheniaceae and Polypodiaceae spores from Panama (Roubik and Moreno 1991).

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

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

Genus *Microfoveolatosporis* Krutzsch 1959

Microfoveolatosporis cf. *M. fromensis* (Cookson 1957) Harris 1965
Plate 3, figure 9

Discussion. This specimen differs from the type species, *Microfoveolatosporis pseudodentatus* Krutzsch 1959, in lacking a two-layered wall structure. This specimen is quite similar to a specimen of *Microfoveolatosporis fromensis* photographed by Scholtz (1985), who stated that *M. fromensis* is indistinguishable from spores of the modern *Actinostachys pennula* (Sw.) Hook. (Schizaeaceae).

Occurrence. Ypresian; one specimen observed.

Botanical affinity. Schizaeaeceae (see discussion).

Genus *Polypodiisporonites* Potonié 1931

Polypodiisporonites sp. A
Plate 3, figure 12

Discussion. The type species, *Polypodiisporonites favus* Potonié 1931, differs in possessing a negative reticulum. *Polypodiisporonites alienus* (Potonié 1931) Frederiksen 1980 and *Polypodiisporonites afavus* (Krutzsch 1959) Frederiksen 1980 are larger (> 40 μm long). *Polypodiisporites usmensis* (van der Hammen 1956) Khan & Martin 1972 has higher verrucae (approx. 1 μm) than this specimen. *Polypodiisporites minimus* (Couper 1960) Khan & Martin 1971 emend. Pocknall & Mildenhall 1984 is similar in size to *Polypodiisporonites* sp. A, but again the verrucae are higher (approx. 1 μm).

Occurrence. Ypresian; one specimen observed.

Botanical affinity. Probably Polypodiaceae; Jardine (2011) gave the probable botanical affinity as Polypodiaceae for a visually similar specimen of *Polypodiosporonites* that had not been described or assigned to a species. Verrucate monolete spores are found in modern Polypodiaceae and Schizaeaceae from Panama (Roubik and Moreno 1991).

Palaeoecology. Possibly lowland tropical forest or swamp; Wakefield and Monteil (2002) give a suggested palaeoecology of tropical fern swamp for the similar species *P. afavus* from the Cretaceous–Tertiary of Pakistan.

Genus *Reticuloidosporites* Pflug in Thomson & Pflug 1953

Reticuloidosporites pseudomurii Elsik 1968
Plate 3, figures 10–11

Discussion. Elsik (1968) described the surface sculpture in *Reticuloidosporites pseudomurii* as foveolate, but Frederiksen (1980a) considered that the species was reticulate on the basis that the lumina are much wider than the muri. Leffingwell (1970) and Pocknall and Nichols (1996) have described this species as being verrucate and rugulate as well as foveolate; the specimens observed in this study are foveolate but not clearly verrucate or rugulate.

Occurrence. Ypresian; four specimens observed.

Botanical affinity. Bryophyta/Pteridophyta sensu lato.

4.3. Gymnosperm pollen

Genus *Cycadopites* Wodehouse 1933 ex Wilson & Webster 1946

Cycadopites follicularis Wilson & Webster 1946
Plate 4, figure 9

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

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

Botanical affinity. Cycadaceae (Wodehouse 1933).

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

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

Ephedripites (*Distachyapites*) *eocenipites* (Wodehouse 1933) Krutzsch 1961 sensu lato
Plate 4, figure 1

Discussion. This species is distinguished from other ephedroid pollen grains in the assemblage by having fused plicae with branched pseudosulci. A broad species concept for *Ephedripites eocenipites* is used here, which includes specimens smaller than the original size range given by Wodehouse (1933) of 57–74 μm in length.

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

Botanical affinity. Ephedraceae, probably *Ephedra*.

Palaeoecology. Dry and warm tropical scrub. Modern *Ephedra* is a xerophytic plant, but the palynological record indicates a greater ecological range for this group in the geological past. Frederiksen (1985) provides an extensive discussion on the palaeoecology of fossil pollen referable to the Ephedraceae. A great variety of *Ephedripites* were recovered

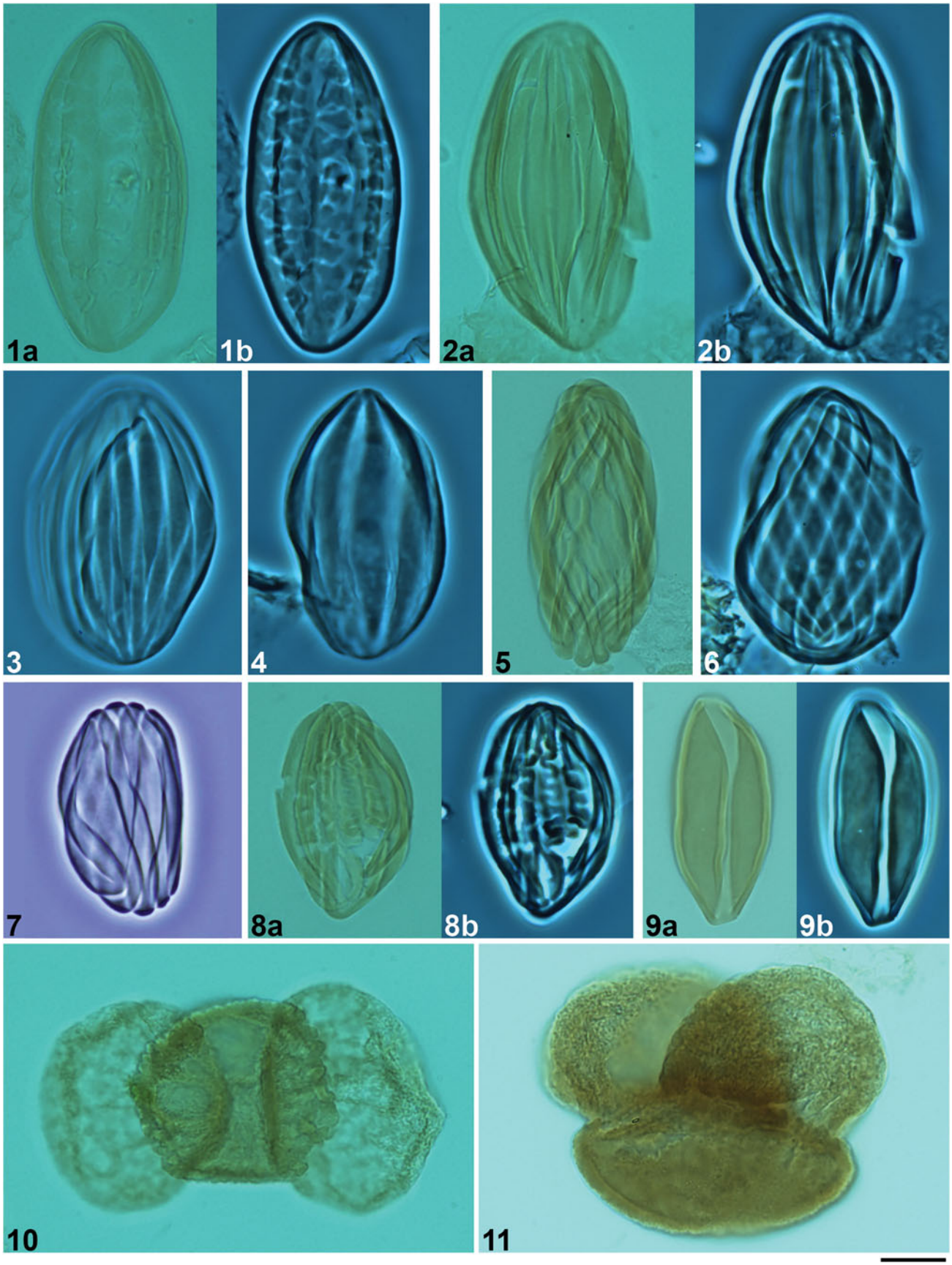

Plate 4. Gymnosperm pollen from International Ocean Discovery Program (IODP) 364. 1. *Ephedripites eocenipites*. 545.67 mbsf, slide 1, EFS V33/1. 2. *Ephedripites* (*Ephedripites*) sp. 533.27 mbsf, slide 1, EFS W44/0. 3. *Ephedripites* (*Ephedripites*) sp. 555.07 mbsf, slide 1, EFS Q46/0. 4. *Ephedripites* (*Ephedripites*) sp. 509.17 mbsf, slide 1, EFS P32/1. 5. *Gnetaceaepollenites* sp. A. 569.50 mbsf, slide 1, EFS Q39/1. 6. *Gnetaceaepollenites* sp. A. 519.31 mbsf, slide 2, EFS S29/2. 7. *Gnetaceaepollenites* sp. A. 525.48 mbsf, slide 1, EFS L36/0. 8. *Gnetaceaepollenites* sp. B. 547.42 mbsf, slide 2, EFS Q14/1. 9. *Cycadopites follicularis*. 563.29 mbsf, slide 1, EFS R24/2. 10. Class Pinopsida. 569.50 mbsf, slide 1, EFS R36/1. 11. Class Pinopsida. 592.23 mbsf, slide 2, EFS J41/1. Scale bar = 10 μm.

from a Turonian section from Tanzania, during an interval of time that was clearly warm and relatively dry, as indicated notably by the rarity of humidity-dependent bryophytes and pteridophytes (Warny et al. 2018). Akkiraz et al. (2008) considered that Eocene *Ephedra* and *Ephedripites* were indicative of back-mangrove estuarine environments; this study will follow Ramírez-Arriaga et al. (2014) and Warny et al. (2018) in considering that *Ephedripites* spp. indicates dry and warm scrub.

Ephedripites (*Ephedripites*) spp.
Plate 4, figures 2–4

Discussion. The taxonomy of *Ephedripites* subgenus *Ephedripites* is complex; many species have overlapping definitions, and arguably the group is oversplit. This subgenus was not assigned to species due to its taxonomic complexity and the lack of any clear biostratigraphical or palaeoecological rationale for splitting the subgenus.
Occurrence. Ypresian; 29 specimens observed. *Ephedripites* subgenus *Ephedripites* is common and globally distributed in the Mesozoic and Cenozoic (Palynodata Inc. and White 2008).
Botanical affinity. Ephedraceae, probably *Ephedra*.
Palaeoecology. Likely indicative of dry and warm climate. See the palaeoecology section for *Ephedripites eocenipites*.

Genus *Gnetaceaepollenites* Thiergart 1938 emend. Jansonius 1962

Gnetaceaepollenites sp. A
Plate 4, figures 5–8

Discussion. This species is synonymous with grains identified as '*Ephedripites* subgenus *Spiralipites* spp.' by Jardine (2011, p. 226), although this study follows Han et al. (2016) in assigning these grains to the genus *Gnetaceaepollenites*. Many of these specimens are probably also conspecific with *Ephedra voluta* Stanley 1965, which has been regularly identified from the Paleogene of the Gulf Coastal Plain (Palynodata Inc. and White 2008). *Gnetaceaepollenites* sp. B is distinguished by having plicae with a sinusoidal pattern.
Occurrence. Ypresian; 90 specimens observed.
Botanical affinity. Ephedraceae, possibly *Ephedra* (Jardine 2011).
Palaeoecology. Probably an arid tropical scrub environment. See the palaeoecology section for *Ephedripites eocenipites*.

Gnetaceaepollenites sp. B
Plate 4, figure 8

Discussion. This species is similar to *Ephedripites* (*Distachyapites*) *zigzagus* Sun & He 1980, and a grain identified as '*Ephedra* sp. 1' by Frederiksen et al. (1983), in possessing plicae which undulate in a sinusoidal pattern. This specimen differs from those two species most notably in having plicae which are not fused at the tips of the grain. A new species has not been erected because only one specimen was observed.
Occurrence. Ypresian; one specimen observed.
Botanical affinity. Ephedraceae.
Palaeoecology. Probably arid tropical scrub. See the palaeoecology section for *Ephedripites eocenipites*.

Class Pinopsida
Plate 4, figures 10–11

Discussion. The general morphology of most of these specimens is similar to that of modern *Pinus* pollen, particularly in the grain size and the shape of the sacci. This study will follow Pocknall and Nichols (1996), Nichols (2002), and Jardine (2011) in not assigning species names to bisaccate pollen grains referable to the Class Pinopsida.
Occurrence. Danian–Ypresian; 37 specimens observed.
Botanical affinity. Pinopsida, probably Pinaceae, possibly *Pinus*.
Palaeoecology. Probably montane forest. More specifically, upland evergreen forest (*Pinus* forest), according to Ramírez-Arriaga et al. (2014); however, Frederiksen (1985) cautioned that some modern species of *Pinus* live in lowland swamps, and may have lived in similar environments in the Paleogene.

5. Conclusions

Palynological analysis of Danian–Ypresian post-impact rocks from the IODP 364 core yielded a diverse assemblage of 23 plant spore taxa and six gymnosperm pollen taxa. The spore and gymnosperm pollen assemblage exhibits a low relative abundance in comparison to the angiosperm pollen assemblage, representing only about 2% of the total pollen and spore counts. The low relative abundance of spores is suggestive of generally arid or seasonally dry environmental conditions, similar to modern conditions in the northern Yucatán Peninsula, Mexico. None of the gymnosperm pollen or spores had any clear biostratigraphical value in the core interval. Most species were not observed in the Palaeocene section of the core due to low abundance, with the exception of *Gleicheniidites senonicus* and bisaccate Pinopsida pollen, which were both observed in the Danian. Palaeoecologies suggested by the spore and gymnosperm pollen assemblage include lowland tropical forest, estuarine or mangrove environment, warm and dry tropical scrub, and montane forest.

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

In the IODP 364 core, the oldest sample with observed terrestrial palynomorphs, specifically two specimens of *Deltoidospora*, is at 615.50 mbsf. Foraminiferal biostratigraphy constrains the age of this sample depth to between 65.25

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

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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 palaeontology, 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 (LSU) 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 palaeobotany and palaeoecology. 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 motivated 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 Paleogene, Neogene and Cretaceous. His work has been incorporated into several radio and television productions, including CBC's *The Nature of Things* with David Suzuki, the PBS *NOVA* Series, the NHK (Japan) Series *The Miracle Planet*, and others by the National Film Board of Canada, the Discovery Channel and other North American cable networks. He 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, with supervising students, finding appropriate graduate projects, and teaching. He is also a business development manager and a geological consultant with RPS Energy in Houston, Texas, marketing specialist geological and biostratigraphical products to the general exploration community. He received his PhD (1992) from the University of Calgary in both palynology and organic petrography, and earlier received his MSc (1987) from the University of Alberta in Edmonton. He has over 26 years of experience in the oil industry, having spent more than 18 years with ConocoPhillips Co., and prior to that over 4 years with Amoco Corp. His current primary research interests include study of the Palaeocene–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 Palaeocene–Eocene coals and palaeoclimatic/palaeogeographical reconstructions of the region. He is interested in all aspects of organic petrography and organic characterisation 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 a professor in palaeontology at the Swedish Museum of Natural History in Stockholm, Sweden, and department chair of the Department of Palaeobiology. Her research speciality 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 organisations and was for several years chair of the Geological Society of Sweden and the UNESCO sciences programme IGCP. In 2019 she became an elected member of the Royal Swedish Academy of Sciences.

ORCID

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

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