CHAPTER 8

PALYNOLOGICAL RECORD OF THE LAST 20 MILLION YEARS IN PANAMA

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ABSTRACT

The Isthmus of Panama illustrates how the vegetation of a newly created landscape in a tropical setting evolves over time. It also allows us to investigate biological invasions, because the landscape was first connected to temperate North America, and later connected to tropical South America. Using a large number of outcrops newly exposed during the recent expansion of the Panama Canal, we were able to complement the extensive palynological research that Alan Graham conducted in Panama over the past 25 years. We analyzed the palynological record of the interval 19.5–1.2 Ma, represented by 282 samples containing 27,910 grains (pollen/spores) with 496 morphotypes. Further, a revision of the plant macrofossil literature of Panama and analysis of the carbon isotope content of 14 samples were carried out. Our results indicate that since the Early Miocene, Panamanian forests have been dominated by Gondwana-Amazonian taxa, suggesting that plants were able to cross the Central American Seaway much earlier than mammals. The landscape was dominated by tropical rainforest and lower montane to montane forest, contrary to the dry and open habitats that some previous studies have proposed. Plant diversity seems to have increased over the past 10 My, but it is unclear if this increase is due to a taphonomic bias. Further studies are needed to understand the relationships of the Early Miocene Panamanian mammals derived from North American temperate forest lineages as they faced new habitats in Panama dominated by South American–derived tropical rainforest.

Key words: biogeography, GABI, Neogene, paleobotany, palynology.

A century ago, during the initial excavations for the Panama Canal, the Smithsonian Institution conducted intensive natural history and geological investigations, resulting in some of the first major collections that documented the high biodiversity of the American Neotropics (e.g., Vaughan, 1919). Almost a century later, starting in 2007, after a public referendum, the government of Panama decided to widen the Panama Canal. The $5 billion project is scheduled for

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completion in 2014. The Smithsonian Tropical Research Institute and the University of Florida have taken advantage of this extraordinary opportunity to collect fossils and geological information to better understand the uplift of the Isthmus of Panama, which had far-reaching biological, climatic, and tectonic implications. The recently exposed rocks have allowed us to compile large amounts of new geological and paleontological data that otherwise would have been impossible to collect, given that most of the Panamanian landscape is covered by tropical rainforest. Many highly fossiliferous sedimentary strata were exposed, giving us a glimpse of the evolution of the landscape, the formation of the isthmus, and the ecosystem, flora, and biota of Panama during the past 20 million years.

The Panamanian fossil vertebrate collections provide a good record of Miocene North American mammal immigrants, including horses, beardogs, camels, rhinocerids, peccaries, and rodents (Whitmore & Stewart, 1965; Slaughter, 1981; MacFadden & Higgins, 2004; MacFadden, 2006a, 2006b, 2009, 2010; MacFadden et al., 2012; Rincon et al., 2012, 2013); South American immigrants include turtles, snakes, and crocodiles (Cadena et al., 2012; Head et al., 2012; Hastings et al., 2013). The geological history of the Isthmus of Panama can be divided broadly into four segments (Coates et al., 1992, 2003, 2004; Coates & Obando, 1996; Farris et al., 2011; Montes et al., 2012a, 2012b; Sepulchre et al., 2014): (1) a pre-22 Ma interval during which most of Panama was underwater, except some Late Eocene and Oligocene volcanic islands; (2) an initial collision with South America around 22–21 Ma with an associated broad-scale land exhumation and a narrowing of the Central American Seaway (CAS) to ca. 200 km (CAS is defined here as the oceanic seaway along the tectonic boundary of the South American plate and the Panamanian microplate); (3) a final and major exhumation at 12–10 Ma, when most of the Panamanian landscape was exhumed above sea level and the CAS was fully closed, ending deep and intermediate water exchange between the Caribbean and Pacific; (4) an intermittent exchange between 10 and 3.5 Ma of shallow waters between the Pacific and the Caribbean (Coates et al., 1992; Coates & Obando, 1996; Haug & Tiedemann, 1998) along places other than the CAS. At 4.2–3.5 Ma a full closure of the isthmus occurred (Coates et al., 1992; Haug et al. 2001, 2004). The complete isthmus formation facilitated exchange of faunas and floras of South America with those of Central and North America, in a process that has been named GABI (the Great American Biotic Interchange; Stehli & Webb, 1985; Coates & Obando, 1996). Modern Neotropical biodiversity and biogeographic distributions are deeply affected by this interchange.

Our study presents an overall view of the vegetation evolution of the isthmus for the past 20 My, using both palynological and macrofossil data. We attempt to answer four questions, namely: (1) what are the vegetation types that have dominated the Isthmus of Panama over the past 20 Ma?, (2) are there any lines of evidence for widespread savannas or dry forests?, (3) what is the biogeographic origin of the floras found in Panama?, and (4) how has plant diversity changed? In particular, we hypothesized that the earlier floras would have been dominated by North American (Laurasian) families, due to the relatively late physical connection with South America brought on by full closure of the isthmus at ca. 3.5 Ma.

This investigation was based on the analysis of 282 palynological samples together with the extensive palynological research of Dr. Alan Graham on Panamanian sedimentary formations (Graham, 1977, 1988a, 1988b, 1989, 1991a, 1991b, 1991c, 1992, 1995, 1999, 2010, 2011). Our palynological work focused on the Cucaracha, Culebra, Gatun, and Chagres formations that outcrop along the canal in central Panama, together with samples from western Panama (Bocas del Toro) and eastern Panama (Darien). Macrobotanical information is derived from newly discovered fossil assemblages (leaves, fruits, and wood) from the Cucaracha and Gatun formations, together with a review of previous published work.

GRAHAM CONTRIBUTIONS

Graham has been a pioneer in the study of the floristic evolution of Central America and the Caribbean, publishing extensively across many regions and time periods. See Graham (2010, 2011) for an excellent synthesis of his impressive research over the past 40 years. In a series of papers, he described the palynofloras of central Panama, including La Boca, Culebra, Cucaracha, and Gatun formations. His study of La Boca Formation (Graham, 1989), was not included here because the precise stratigraphic position of this site in relation to our stratigraphic work could not be determined, and it could correspond to the Lower Culebra or Cascadas formations. The original site, which is in an area with high structural complexities, no longer exists, since it was depleted before our study in the Panama Canal started.

From the La Boca Formation (Graham, 1989), Graham found 54 morphotypes, including 39 where natural affinities could be assessed. The sediments were mostly marine, and some samples were dominated by mangrove elements (*Rhizophora* L.) and some dinoflagellates. The flora reflects low-lying volcanic islands fringed by mangroves, with freshwater and palm swamp, marshes, and tropical wet/moist and premontane forest. There is no evidence of dry habitats, including savannas or high elevations (> 1500 m). The flora is similar to extant coastal Panamanian floras. Climate was humid-tropical, similar to that of modern southern Central America.

Study of the Culebra Formation (upper Culebra) (Graham 1987, 1988b), where 41 palynomorphs were identified, indicated an estuarine sequence. Ferns constitute 25% of the flora, palms 4%, and lowland vegetation 71%. Tropical moist forest, represented by 30 genera, dominated the assemblages of premontane wet forest (25 genera), tropical wet forest (22 genera), and some forms of premontane moist forest (12 genera). Communities of higher elevations and dry to arid habitats (including savannas) are poorly represented to absent. Climate was similar to modern Panama, with 2.7–3.2 m rainfall annually, and tropical temperatures. All 41 taxa identified are still represented in the modern flora of Panama.

The study of the Cucaracha Formation (Graham, 1988a) identified 19 palynomorphs accumulated in an estuarine sequence. Paleocommunities included fern/palm marshes, mangroves, tropical wet/moist forests, and premontane forests. There is no evidence for high-altitude (> 1500 m) vegetation or dry vegetation (savanna). The affinity of the palynoflora showed connection to North American and Central American floras, and paleoclimatic conditions were interpreted as similar to modern Panama (tropical temperatures and high levels of rainfall). Graham (1988a) proposed that the volcanic activity might have produced disruptions in the vegetation, with resulting short-term open communities (savannas) that are suggested by the presence of browsers and grazers in the mammalian faunas of the Cucaracha Formation.

Graham (1991a, 1991b, 1991c) dated the Gatun Formation as Middle Miocene, but more recent work has indicated a Late Miocene age (Hendy, 2013). Graham identified 110 palynomorphs from several habitats, including shallow marine communities, mangroves, freshwater swamps/marshes, tropical wet/moist forests, premontane rainforests/moist forests, lower montane moist forests, and tropical dry forest. There was an increase in diversity compared to earlier floras, an increase of grasses (but only up to 7.5%), more developed dry forest, better representation of lower montane forest, and possibly, the first indication of differentiation between a wetter Atlantic side and a drier Pacific side in Panama.

VEGETATION TYPES IN THE ISTHMUS OF PANAMA

Today there are several types of forests in Panama, reflecting a variety of environmental differences—mainly differences in the mean annual precipitation (MAP) and the amount of precipitation during the dry season. Forests include lowland wet forest (> 300 mm of rain during the dry season), seasonal lowland moist forest (100–300 mm during the dry season), and lowland dry forest (≤ 1600 mm MAP and ≤ 100 mm during the dry season) (Pyke et al., 2001; Condit et al., 2004). The Caribbean side is also much wetter than the Pacific side. Additional forest types include swamp forest, seasonally flooded riparian forest, mangrove forest, and montane and premontane forests. An extensive review of each of those forest types has been provided by Graham in a number of seminal works in the past few years (Graham, 1991c, 2010). We have used his vegetation classification approach to assess the types of forest found in the fossil record (Table 1).

METHODS

SAMPLES

A total of 282 palynological samples were analyzed. Samples came from three sources: (1) Fifty-five samples were from a measured and described stratigraphic section of the full span of Culebra and Cucaracha formations from the new excavations of the Panama Canal (Emperador section for the Lower Culebra, and Hodges Hill section for the Upper Culebra and Cucaracha) (Figs. 1, 2, Table 2). (2) Two hundred samples previously collected by the Panama Paleontology Project (PPP) (Collins & Coates, 1999) were processed for palynological analyses. These were collected from central Panama (from Gatun and Chagres formations), eastern Panama (Darien region), and western Panama (Bocas del Toro) (Figs. 1, 2, Table 2). (3) Palynological information previously published by Graham (1987, 1988a, 1988b, 1991a, 1991b, 1991c) was added to our stratigraphic framework (Montes et al., 2012b; Hendy, 2013), including 11 samples from the Culebra Formation, seven samples from the Cucaracha Formation, and nine samples from the Gatun Formation (Figs. 1, 2, Table 2). The stratigraphic position as well as the label of each sample is given in the Supplementary Appendix (<http://dx.doi.org/10.5479/data.stri.jaramillo-2014>). Palynological samples were prepared by digesting 30 g of sediment in HCl and HF, then oxidizing if necessary (Traverse, 2007), and all slides were added to the Alan Graham Palynological Collection, the extensive pollen collection donated by Alan Graham to the Smithsonian Institution a few years ago.

AGE

The age for the Culebra and Cucaracha has been estimated as 19.5–18.5 Ma using uranium-lead (U-Pb) geochronology and magnetostratigraphy (MacFadden et al., 2012; Montes et al., 2012a, 2012b): 19.5–19 Ma for Culebra Formation and 19–18.5 Ma for Cucaracha Formation. For the age of individual samples within these formations, a linear and constant accumulation rate was assumed, since there are no major lithological changes within each formation (Supplementary Appendix). Age for each PPP sample has been determined using planktonic foraminifera and calcareous nannoplankton (Collins & Coates, 1999). Ages of 12 to ca. 8.5 Ma (Middle to Late Miocene) for the Gatun Formation and 6.5–5.5 Ma (Late Miocene) for the Chagres Formation have been determined using foraminifera, nannoplankton, and molluskan biostratigraphy (Collins & Coates, 1999; Hendy, 2013). See Figures 1, 2, Table 2, and Supplementary Appendix.

ECOLOGICAL PREFERENCES AND BIOGEOGRAPHIC ORIGINS

Ecological preferences for fossil taxa follow mainly Graham (1991c), with additional input (Germeraad et al., 1968; Croat, 1978; Henderson et al., 1995; Correa & Valdespino, 1998; March-

TABLE 1. Ecological preferences for fossil taxa, based primarily on Graham (1991c), with additional input from Germeraad et al. (1968), Croat (1978), Henderson et al. (1995), Correa and Valdespino (1998), Marchant et al. (2001), Correa et al. (2004), Carrasquilla (2006), and Henderson (2011).

Taxa	TRFO	PMF	MF	TDFO	SV	FW	MG	MR
Acacia Mill.	1		1	1				
Acalypha diversifolia Jacq.	1	1	1					
Aegiphila Jacq.	1	1						
Alchornea Sw.	1	1						
Alfaroa Standl.			1					
Alfaroa/Oreomunnea Standl./Oerst.	1	1	1					
Allophylus L.	1	1		1				
Alnus Mill.			1					
Alsophila R. Br.	1	1	1					
Amanoa Aubl.	1	1						
Bernoullia Oliv.	1	1						
Bombacopsis Pittier	1			1				
Borreria G. Mey.	1		1	1				
Bucida L.	1							
Bucida L.						1		
Bursera Jacq. ex L.	1	1		1				
Cabomba Aubl.						1		
Caesalpinia L.				1				
Casearia Jacq.				1				
Catopsis Griseb.	1							
Cayaponia Silva Manso	1		1					
Cedrela P. Browne	1	1		1				
Ceiba Mill.	1	1		1				
Ceratopteris Brongn.						1		
cf. *Aguiaria* Ducke	1							
cf. *Cionosicys* Griseb.	1	1						
cf. *Glycydendron* Ducke	1							
cf. *Jatropha* L.				1				
cf. *Stillingia* Garden ex L.	1	1						
cf. *Jatropha* L.	1							
Chelonanthus (Griseb.) Gilg	1	1						
Chomelia Jacq.	1							
Chrysophyllum L.	1			1				
Cnemidaria C. Presl	1	1	1					
Combretum Loefl.				2				
Combretum Loefl./*Terminalia* L.	1	1						
Cordia L.	1	1						
Cosmibuena Ruiz & Pav.	1	1						
Crudia Schreb.	1	1						
Cryosophila Blume	1	1						
Ctenitis (C. Chr.) C. Chr.	1	1	1					
Cupania L.	1	1						

TABLE 1. (*continued*)

Taxa	TRFO	PMF	MF	TDFO	SV	FW	MG	MR
Cyathea Kaulf.	I	I	I					
Cymbopetalum Benth.	I	I						
Danaea Sm.	I	I						
Desmoncus-type Mart.	I							
Dinoflagellates								I
Dioclea reflexa Hook. f.	I							
Dioscorea L./*Rajania* L.	I							
Doliocarpus Rol.	I	I		I				
Erythrina L.	I	I						
Eugenia L.				I				
Eugenia L./*Myrcia* DC.	I	I						
Euterpe Mart.	I							
Faramea Aubl.	I	I						
Foram lining								I
Genipa americana L.	I	I		I				
Glycydendron Ducke	I							
Gomphrena L.	I	I						
Grammitis Sw.			I					
Guarea F. Allam. ex L.	I							
Hampea Schltdl.		I						
Hampea Schltdl./*Hibiscus* L.	I							
Hauya DC.		I						
Hedyosmum Sw.	I	I	I					
Hemitelia R. Br./*Cnemidaria* C. Presl	I							
Hibiscus L.							I	
Humiria Aubl.	I							
Ilex L.		I	I					
Iriartea deltoidea Ruiz & Pav.	I							
Jamesonia Hook. & Grev.			I					
Jatropha L.	I			I				
Ludwigia L.	I			I				
Lycopodium L.	I	I	I					
Lygodium Sw.	I							
Lygodium microphyllum (Cav.) R. Br.						I		
Machaerium Pers.	I							
Manicaria-type Gaertn.	I							
Matayba Aubl.	I			I				
Mauritia L. f.	I							
Mauritia flexuosa L. f.	I							
Miconia Ruiz & Pav.		I						
Monolete fern spore types 1-2 (Blechnaceae)						I		
Mortoniodendron Standl. & Steyerm.	I							
Mutisieae type Cass.				I				

(*continued*)

TABLE 1. (*continued*)

Taxa	TRFO	PMF	MF	TDFO	SV	FW	MG	MR
Myrcia DC.	1							
Oenocarpus Mart.	1	1						
Ophioglossum L.	1	1	1					
Oryctanthus (Griseb.) Eichler	1	1		1				
Pachira aquatica Aubl.	1							
Palmae type 1						1		
Paullinia L.	1	1						
Pelliciera Planch. & Triana							1	
Petrea L.	1	1						
Phytelephas Ruiz & Pav.	1							
Poaceae				1	1			
Podocarpus L'Hér. ex Pers.			1					
Polypodiaceae/Pteridaceae						1		
Posoqueria Aubl.	1	1		1				
Pouteria Aubl.	1							
Protium Burm. f.	1	1						
Pseudobombax Dugand	1	1		1				
Psidium L.	1							
Pteris L.	1	1	1					
Quercus L.	1	1	1					
Rhizophora L.							1	
Rourea Aubl.	1	1		1				
Sabicea Aubl.	1	1						
Sapium Jacq.	1	1						
Sapium caudatum Pittier	1	1						
Scheelea zonensis L. H. Bailey	1	1	1					
Selaginella P. Beauv.	1	1	1					
Serjania Mill.		1		1				
Serjania cf. Mill.	1							
Spondias L.	1	1		1				
Stenochlaena palustris (Burm. f.) Bedd.						1		
Stillingia Garden ex L.	1							
Symphonia globulifera L. f.	1	1						
Symplocos Jacq.	1	1						
Tetrorchidium macrophyllum Müll. Arg.	1							
Trichilia P. Browne	1							
Utricularia L.						1		
Vernonia Schreb.	1	1	1					
Vochysia Aubl.	1							

Abbreviations: TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest; SV = savanna; FW = freshwater marsh community; MG = mangrove swamps; MR = shallow water marine community.

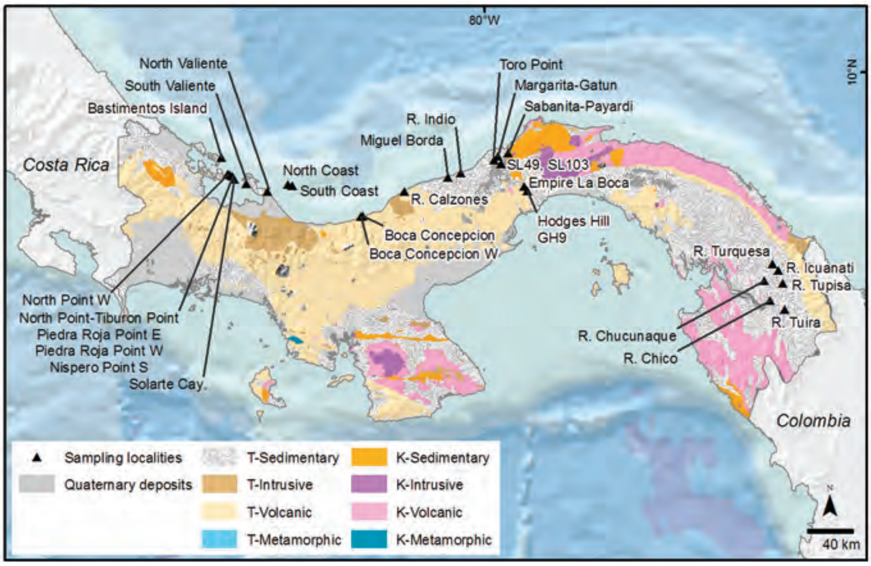

FIGURE 1. Sampling localities displayed on Panama's regional geology. "North Coast" and "South Coast" localities are on Escudo de Veraguas Island. Geology is from the National Environmental Authority (ANAM). Elevation data are from the Shuttle Radar Topography Mission (U.S.G.S., 2004) and bathymetry is from the ETOPO1 dataset (Amante & Eakins, 2009).

ant et al., 2001; Correa et al., 2004; Carrasquilla, 2006; Henderson, 2011) (Table 1).

For biogeographic origins, we followed the approach of Gentry (1982). Plant families were given a biogeographic origin provided by Gentry, including Gondwana-Amazonian families, Gondwana-northern Andean, Gondwana-southern Andean, Laurasian, or unassigned (Table 3). Modern vegetational abundance data and species composition were derived from the 50-ha plot of Barro Colorado Island in Panama (Condit et al., 2004) (Appendix 1). The data from this plot include approximately 240,000 stems of 303 species of trees and shrubs more than 1 cm in diameter at breast height, representing ca. 96% of the biomass in the plot (Chave et al., 2003, 2005). Pollen traps in the soil within the plot also have shown than pollen spectra produce a representative sample of the vegetation within the plot (Bush & Rivera, 1998; Haselhorst et al., 2013), consequently making the pollen record a good proxy to understand the forest.

STABLE CARBON ISOTOPES

We used stable carbon isotopes to identify C3 versus C4 photosynthetic pathways, as a means to identify the presence of C4 savannas (rich in C4 grasses) versus trees (C3). Sediment samples were freeze-dried and crushed with a mortar and pestle. Total carbon and total nitrogen were measured using a Carlo Erba (Milan, Italy) NA1500 CNS elemental analyzer with a zero blank autosampler. Carbonate carbon was determined by coulometric titration using an automated acidification prep device coupled with a UIC CO2 coulometer. Percentage of organic carbon was calculated by subtraction of carbonate carbon from total carbon. Samples for isotopic analyses were treated with 2 N HCl to remove carbonate and then washed with distilled water to remove chloride. Approximately 50 mg of carbonate-free bulk sediment was loaded into tin sample capsules and placed in a 50-position automated sample zero blank carousel on the elemental analyzer. Combustion gases were carried in a helium stream through

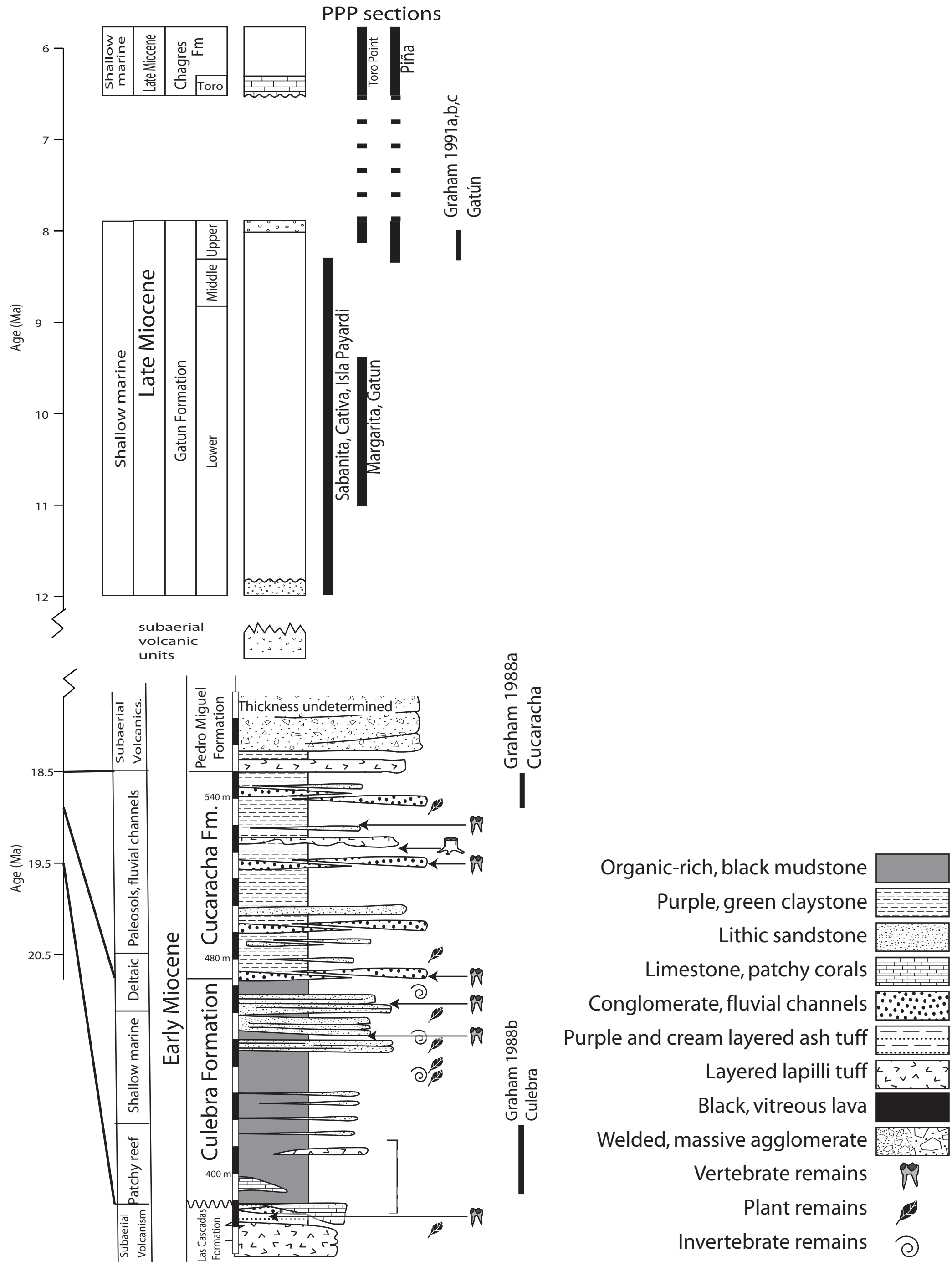

FIGURE 2. Stratigraphic profile of the main formations and sections studied in central Panama. Stratigraphy and age of Cucaracha and Culebra formations after Montes et al. (2012b) and MacFadden et al. (2012); Gatun Formation after Hendy (2013). PPP = Panama Paleontology Project.

TABLE 2. Geographical location of the studied samples.

Region	Section name	Formation name	Latitude	Longitude	Source
Central Panama	Empire section La Boca	Culebra	9.0827	–79.6789	this study
Central Panama	Hodges Hill section	Culebra/Cucaracha	9.05	–79.6534	this study
Central Panama	01-Sabanita to Payardi	Gatun	9.351083333	–79.808	PPP samples
Central Panama	02-Margarita to Gatun	Gatun	9.32575	–79.89133333	PPP samples
Central Panama	03-Toro point	Gatun	9.296083333	–79.92466667	PPP samples
Central Panama	05- Rio Indio	Chagres	9.192138889	–80.19133333	PPP samples
Central Panama	06-Miguel de la Borda	Gatun	9.154833333	–80.29133333	PPP samples
Central Panama	07-Boca de Concepcion	Gatun	8.847583333	–80.97466667	PPP samples
Central Panama	08-Boca de Concepcion West	Gatun	8.841416667	–80.99133333	PPP samples
Central Panama	09 -Calzones River	Gatun	9.045083333	–80.64133333	PPP samples
Western Panama	10-North Coast	Escudo Veraguas	9.101444444	–81.57466667	PPP samples
Western Panama	11-South Coast	Escudo Veraguas	9.089944444	–81.54133333	PPP samples
Western Panama	12-North Valiente	Shark Hole Point	9.042777778	–81.74133333	PPP samples
Western Panama	15-South Valiente	Shark Hole Point	9.106666667	–81.908	PPP samples
Western Panama	16-North Point West	Cayo Agua	9.18	–82.058	PPP samples
Western Panama	17-Piedra Roja Point West	Cayo Agua	9.141083333	–82.008	PPP samples
Western Panama	18-Piedra Roja Point East	Cayo Agua	9.143138889	–82.008	PPP samples
Western Panama	19- North Point-Tiburon Point	Cayo Agua	9.174888889	–82.04133333	PPP samples
Western Panama	20-Nispero Point South	Cayo Agua	9.167527778	–82.02466667	PPP samples
Western Panama	22-Bastimentos Island	unnamed	9.317777778	–82.108	PPP samples
Western Panama	23-Bastimentos Island	unnamed	9.317277778	–82.108	PPP samples
Western Panama	24- Solarte Cay	unnamed	9.142194444	–82.008	PPP samples
Eastern Panama	Rio Chico	Tuira?	8.17075	–77.708	PPP samples
Eastern Panama	Rio Chucunaque	Chucunaque	8.331138889	–77.758	PPP samples
Eastern Panama	Rio Icuanati	Lara	8.410416667	–77.64133333	PPP samples
Eastern Panama	Rio Tuira	Tuira	8.097	–77.59133333	PPP samples
Eastern Panama	Rio Tupisa	Tuira	8.308611111	–77.608	PPP samples
Eastern Panama	Rio Turquesa	Tuira	8.465722222	–77.69133333	PPP samples
Central Panama	Core SL103	Gatun	9.266666667	–79.86666667	Graham, 1991c
Central Panama	Core SL49	Gatun	9.266666667	–79.86666667	Graham, 1991c
Central Panama	GH9	Culebra	9.05	–79.6534	Graham, 1988a
Central Panama	Roadside K2	Cucaracha	9.05	–79.6	Graham, 1988b

Abbreviation: PPP = Panama Paleontology Project.

a Conflo II interface to a Finnigan-MAT 252 isotope ratio mass spectrometer (PRISM). All carbon isotopic results are expressed in standard delta notation relative to Vienna Pee Dee Belemnite (VPDB).

PALYNOLOGICAL NOMENCLATURE

Morphological characteristics of the palynomorphs were compared with illustrations and descriptions from literature and summarized in Jaramillo and Rueda (2013). Major nomenclatural usages follow those in Jaramillo and Dilcher (2001). Informal species are those between quotation marks. In the taxonomic section (Appendix 2), 414 morphotypes are briefly described and/or illustrated. The taxa encountered and their counts are listed in the Supplementary Appendix,

TABLE 3. Biogeographic affinities after Gentry (1982) for the families present in either the Barro Colorado Island 50-ha plot or the fossil record presented in this report.

Biogeographic Province	Family
Dry area Gondwanan group	Erythroxylaceae
Gondwana-Amazonian	Anacardiaceae, Annonaceae, Apocynaceae, Arecaceae, Bombacoideae, Burseraceae, Byttneroideae, Caesalpinioideae, Chrysobalanaceae, Combretaceae, Connaraceae, Dilleniaceae, Ebenaceae, Elaeocarpaceae, Euphorbiaceae, Fabaceae, Faboideae, Grewioideae, Humiriaceae, Lacistemataceae, Lauraceae, Lecythidaceae, Malpighiaceae, Meliaceae, Mimosoideae, Moraceae, Myristicaceae, Ochnaceae, Olacaceae, Phyllanthaceae, Polygalaceae, Rhizophoraceae, Sapindaceae, Sapotaceae, Simaroubaceae, Sterculiaceae, Tetrameristaceae, Tiliaceae, Violaceae, Vochysiaceae
Gondwana-northern Andean	Acanthaceae, Araceae, Araliaceae, Asteraceae, Bromeliaceae, Clusiaceae, Ericaceae, Loranthaceae, Monimiaceae, Nyctaginaceae, Piperaceae, Rubiaceae, Urticaceae
Gondwana-southern Andean	Bignoniaceae, Myrtaceae, Onagraceae, Podocarpaceae, Solanaceae
Laurasian	Achariaceae, Aquifoliaceae, Betulaceae, Boraginaceae, Celastraceae, Chloranthaceae, Fagaceae, Gentianaceae, Juglandaceae, Labiatae, Lythraceae, Melastomataceae, Rhamnaceae, Salicaceae, Staphyleaceae, Symplocaceae, Ulmaceae
Unassigned	Amaranthaceae, Cabombaceae, Cucurbitaceae, Cyperaceae, Dioscoreaceae, Dryopteridaceae, Lamiaceae, Lentibulariaceae, Malvaceae, Malvoideae, Nymphaeaceae, Picramniaceae, Poaceae, Polygonaceae, Rutaceae, Verbenaceae

as well as in Table 4, where possible natural affinities are provided. We employ a nomenclature using fossil names for each taxon, even when the natural affinities are known. This approach differs from that used by Graham in all his publications where the fossils were referred to extant families and genera when possible. We feel that using a fossil taxon naming approach would be more useful when comparing to fossil floras elsewhere in the tropics, where fossil morphotaxa have mostly been used. Also, using natural affinities as the name of a fossil taxon can bring nomenclatural problems in the future, because the affinity of a given fossil species can change when further research is done, specially using SEM and TEM. It would be more practical to have a fossil morphotaxon name with an informally suggested natural affinity; that is, a hypothesis of relationship can change over time, but the morphotaxon name will not.

DIVERSITY ANALYSES

A number of techniques were used to analyze the patterns of pollen and spore diversity and floral composition. Diversity is used here to denote the number of species (Rosenzweig, 1995). Diversity within a sample was estimated using rarefaction, an interpolation technique that estimates how many species may have been found if the sample had been smaller (Raup, 1975). The rarefaction was calculated with the fungal spores excluded because they can represent a large proportion of the palynological sum and thus can mask possible vegetation patterns; this exclusion from the diversity analyses was also appropriate, because little taxonomic work has been undertaken on Neotropical Neogene fungi.

Species accumulation curves (Gilinsky, 1991), using the collector method, were used to calculate how diversity increases as more samples are analyzed. The collector method adds sites in the order they happen to be in the data (Oksanen et al., 2010). It was used to compare the three time intervals that we analyzed (see below), because each interval represents a different time span, and comparison of them would have biased the diversity toward the interval with the longest duration (i.e., the longest duration interval would have a greater probability to accumulate more species).

TABLE 4. List of all species used in the analysis with their possible natural affinities. The Graham taxon name corresponds to the names used by Graham in his publications. Informal species are those within quotation marks.

Taxon	Category	Graham taxon name	Family	Genus
Acanthaceae aff. "hygrophilensis"	angiosperm		Acanthaceae	*Hygrophila*
Alnipollenites verus (Potonie, 1931) ex Potonie, 1934	angiosperm		Betulaceae	*Alnus*
Anacardiaceae "morenensis"	angiosperm		Anacardiaceae	*Spondias*
Anacardiaceae "sanchenzis"	angiosperm		Anacardiaceae	
Annonaceae (*Cymbopetalum*) Benth.	angiosperm	*Cymbopetalum*	Annonaceae	*Cymbopetalum*
Araceae type	angiosperm		Araceae	
Arecipites "perfectus"	angiosperm		Arecaceae	
Arecipites regio (Van der Hammen and Garcia, 1966) Jaramillo and Dilcher, 2001	angiosperm		Arecaceae	
Baculipollenites "inciertus"	angiosperm			
Bignoniaceae type	angiosperm		Bignoniaceae	
Bombacaceae (cf. *Aguiaria*) Ducke	angiosperm	cf. *Aguiaria*	Bombacoideae	*Aguiaria*
Bombacacidites "bombacopsiformis"	angiosperm		Bombacoideae	*Bombacopsis*
Bombacacidites "colpiechinatus"	angiosperm			
Bombacacidites "problematicus"	angiosperm			
Bombacacidites "pseudobombiformis"	angiosperm	*Pseudobombax*	Bombacoideae	*Pseudobombax*
Bombacacidites araracuarensis Hoorn, 1994	angiosperm	*Ceiba*	Bombacoideae	*Ceiba*
Bombacacidites baculatus Muller et al., 1987	angiosperm		Bombacoideae	*Pachira aquatica*
Bombacacidites brevis (Dueñas, 1980) Muller et al., 1987	angiosperm	Unknown Type 10	Bombacoideae	
Bombacacidites nacimientoensis (Anderson, 1960) Elsik, 1968	angiosperm	*Bernoullia*	Bombacoideae	*Bernoullia*
Brevitricolpites "panamensis"	angiosperm			
Brevitricolpites "triangulatus"	angiosperm	Unknown Type 9		
Brevitricolporites "scabratus"	angiosperm		Fabaceae	
Brevitricolpites sp. Gonzalez, 1967	angiosperm	Unknown Type 8		
Bromeliacidites sp. 1	angiosperm		Bromeliaceae	
Bromeliacidites sp. 2	angiosperm		Bromeliaceae	*Catopsis*
Burseraceae "protiumensis"	angiosperm		Burseraceae	*Protium*
Cabombaceae (*Cabomba*) Aubl.	angiosperm	*Cabomba*	Cabombaceae	*Cabomba*
Chelonanthus type (Griseb.) Gilg	angiosperm		Gentianaceae	*Chelonanthus*
Cichoreacidites longispinosus (Lorente, 1986) Silva-Caminha et al., 2010	angiosperm		Asteraceae	
Clavainaperturites clavatus Van der Hammen and Wymstra, 1964	angiosperm			
Clavainaperturites microclavatus Hoorn, 1994b	angiosperm		Chloranthaceae	*Hedyosmum*
Clavaperiporites "crotonoides"	angiosperm			
Clavapollenites "circularis"	angiosperm		Euphorbiaceae	
Clavapollenites "triangulatus"	angiosperm			
Clavatricolpites "infinitus"	angiosperm			
Clavatricolpites "tectatum"	angiosperm	*Tetrorchidium*	Euphorbiaceae	*Tetrorchidium*
Clavatricolpites sp. Van Hoeken Klinkenberg, 1964	angiosperm			
Colombipollis "guerrillensis"	angiosperm			

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Combretaceae (cf. *Bucida*) L.	angiosperm	cf. *Bucida*	Combretaceae	*Bucida*
Compositae (*Mutisieae* type) Cass.	angiosperm	Mutisieae type	Asteraceae	*Mutisieae*
Corsinipollenites psilatus Jaramillo and Dilcher, 2001	angiosperm		Onagraceae	*Ludwigia*
Crassiectoapertites columbianus Dueñas, 1980; emend. Lorente, 1986	angiosperm		Fabaceae	*Dioclea reflexa*
Cricotriporites "chagrensis"	angiosperm			
Cricotriporites "minimus"	angiosperm			
Cricotriporites aff. *macroporus* Jaramillo and Dilcher, 2001	angiosperm			
Crototricolpites "euphorbiensis"	angiosperm		Euphorbiaceae	
Crototricolpites "pseudodaemoni"	angiosperm			
Cucurbitaceae (cf. *Cionosicys*) Griseb.	angiosperm	cf. *Cionosicys*	Cucurbitaceae	*Cionosicys*
Cucurbitaceae type	angiosperm		Cucurbitaceae	*Cayaponia*
Cyperaceae	angiosperm		Cyperaceae	
Dioscorea L./*Rajania* L.	angiosperm	*Dioscorea/Rajania*	Dioscoreaceae	*Dioscorea-Rajania*
Echimonocolpites "dariensis"	angiosperm		Arecaceae	
Echimonocolpites "mauritiformis"	angiosperm		Arecaceae	
Echimonocolpites "mosquitensis"	angiosperm		Arecaceae	
Echimonocolpites "panamensis"	angiosperm		Arecaceae	*Mauritia*
Echiperiporites "aquaticus"	angiosperm			
Echiperiporites "ipomoensis"	angiosperm			
Echiperiporites "pantagruelicus"	angiosperm			
Echiperiporites akanthos Van der Hammen and Wymstra, 1964	angiosperm			
Echiperiporites estelae Germeraad et al., 1968	angiosperm	*Hampea/Hibiscus*	Malvoideae	*Hampea-Hibiscus*
Echiperiporites sp. Van der Hammen and Wymstra, 1964	angiosperm	Unknown Type 1		
Echistephanoporites "saggitarianus"	angiosperm			
Echitricolporites "chiquitinus"	angiosperm		Asteraceae	
Echitricolporites "devriesi"	angiosperm			
Echitricolporites "microspinosus"	angiosperm		Boraginaceae	*Cordia*
Echitricolporites "vesiculoides"	angiosperm	Compositae	Asteraceae	
Echitricolporites mcneillyi Germeraad et al., 1968	angiosperm		Asteraceae	*Ambrosia*
Echitricolporites sp. (Van der Hammen) Germeraad, Hopping & Muller 1968	angiosperm			
Echitricolporites spinosus Van der Hammen, 1956	angiosperm		Asteraceae	
Echitricolporites spinosus var. microspinosus	angiosperm		Asteraceae	
Echitriporites "abutiloensis"	angiosperm		Malvoideae	*Abutilon*
Echitriporites "megaexinatus"	angiosperm			
Echitriporites aff. "eocenicus"	angiosperm			
Ericaceae Type 1	angiosperm	Ericaceae Type 1	Ericaceae	
Ericaceae Type 2	angiosperm	Ericaceae Type 2	Ericaceae	
Ericipites "baculatus"	angiosperm		Ericaceae	
Ericipites "psilatus"	angiosperm	Ericaceae Type 2	Ericaceae	

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Erythrina L.	angiosperm	*Erythrina*	Fabaceae	*Erythrina*
Euphorbiaceae (cf. *Glycydendron*) Ducke	angiosperm	cf. *Glycydendrum*	Euphorbiaceae	*Glycydendron*
Euphorbiaceae (cf. *Jatropha*) L.	angiosperm	cf. *Jatropha*	Euphorbiaceae	*Jatropha*
Euphorbiaceae (cf. *Stillingia*) Garden ex L.	angiosperm	cf. *Stillingia*	Euphorbiaceae	*Stillingia*
Fagaceae (*Quercus*) L.	angiosperm	*Quercus*	Fagaceae	*Quercus*
Fenestrites "silanensis"	angiosperm		Asteraceae	
Fenestrites spinosus Van der Hammen, 1956	angiosperm		Asteraceae	*Vernonia*
Foveomonocolpites "panamensis"	angiosperm	*Desmoncus*-type	Arecaceae	*Desmoncus*
Foveostephanocolpites CU488	angiosperm	Unknown Type 4		
Foveotricolporites "brevicolpatus"	angiosperm			
Foveotricolporites "cingulatum"	angiosperm		Euphorbiaceae	*Sapium caudatum*
Foveotricolporites "colonensis"	angiosperm	*Doliocarpus*	Dilleniaceae	*Doliocarpus*
Foveotricolporites "longaporatus"	angiosperm			
Foveotriporites "bocencis"	angiosperm	Unknown Type 11 and 12		
Foveotriporites "ochromensis"	angiosperm			
Foveotriporites "protohammenii"	angiosperm	*Sabicea*	Rubiaceae	*Sabicea*
Gemmatricolporites sp. Leidelmeyer, 1966	angiosperm	Unknown Type 6		
Gemmatriporites "matisialis"	angiosperm			
Gomphrena sp. L.	angiosperm		Amaranthaceae	*Gomphrena*
Grimsdalea "aparecida"	angiosperm		Arecaceae	
Hauya DC.	angiosperm	*Hauya*	Onagraceae	*Hauya*
Heterocolpites "combretoides"	angiosperm		Combretaceae	*Combretum*
Heterocolpites "irregularis"	angiosperm		Melastomataceae	
Heterocolpites "melastomicus"	angiosperm		Melastomataceae	
Heterocolpites "minutus"	angiosperm		Melastomataceae	
Heterocolpites incomptus Hoorn, 1993	angiosperm		Melastomataceae	*Miconia*
Heterocolpites rotundus Hoorn, 1993	angiosperm	*Combretum/ Terminalia*	Combretaceae	*Combretum-Terminalia*
Heterocolpites sp. Van der Hammen, 1956	angiosperm			
Horniella "longicolpatus"	angiosperm			
Ilexpollenites "chiquitus"	angiosperm			
Ilexpollenites "clavavariatus"	angiosperm	*Ilex*	Aquifoliaceae	*Ilex*
Ilexpollenites "larguitus"	angiosperm		Aquifoliaceae	*Ilex*
Ilexpollenites "redonditus"	angiosperm			
Inaperturopollenites "crotonoides"	angiosperm			
Inaperturopollenites "grandiosus"	angiosperm			
Inaperturopollenites "reticulatus"	angiosperm	*Chomelia* type	Rubiaceae	*Chomelia*
Ladakhipollenites simplex (Gonzalez, 1967) Jaramillo and Dilcher, 2001	angiosperm			
Lanagiopollis crassa (Van der Hammen and Wymstra, 1964) Frederiksen, 1988	angiosperm		Tetrameristaceae	*Pelliciera rhizophorae*

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Leguminosae	angiosperm	Leguminosae	Fabaceae	
Lentibulariaceae	angiosperm	Lentibulariaceae	Lentibulariaceae	
Lingulodinium machaerophorum (Deflandre and Cookson 1955) Wall, 1967	angiosperm			
Longapertites "foveolatus"	angiosperm	*Cryosophila* type	Arecaceae	*Cryosophila*
Loranthaceae "atriensis"	angiosperm			
Loranthaceae "marginalis"	angiosperm		Loranthaceae	
Loranthaceae "oryctanthusis"	angiosperm		Loranthaceae	*Oryctanthus*
Loranthaceae Type 1	angiosperm	Loranthaceae Type 1	Loranthaceae	
Loranthaceae Type 2	angiosperm	Loranthaceae Type 2	Loranthaceae	
Magnastriatites grandiosus (Kedves and Sole de Porta, 1963) Dueñas, 1980	angiosperm	*Ceratopteris*	Pteridaceae	*Ceratopteris*
Malpighiaceae "bunchoensis"	angiosperm		Malpighiaceae	
Malpighiaceae Type 2	angiosperm	Malpighiaceae Type 2	Malpighiaceae	
Margocolporites "hematoxyformis"	angiosperm		Caesalpinioideae	*Caesalpinia*
Margocolporites "simpliporatus"	angiosperm			
Margocolporites vanwijhei Germeraad et al., 1968	angiosperm		Fabaceae	
Mauritiidites franciscoi var. *franciscoi* (Van der Hammen, 1956) Van Hoeken Klinkenberg, 1964	angiosperm		Arecaceae	*Mauritia flexuosa*
Mauritiidites franciscoi var. *minutus* Van der Hammen and Garcia, 1966	angiosperm		Arecaceae	
Melastomataceae	angiosperm	Melastomataceae	Melastomataceae	
Momipites "panamensis"	angiosperm	*Alfaroa*/*Engelhardia*	Juglandaceae	*Alfaroa-Engelhardia*
Momipites africanus Van Hoeken Klinkenberg, 1966	angiosperm		Betulaceae	*Corylus*
Monocolpopollenites "canalensis"	angiosperm	*Synechanthus*-type	Arecaceae	*Synechanthus*
Monoporopollenites "minutus"	angiosperm		Poaceae	
Monoporopollenites annulatus (Van der Hammen, 1954) Jaramillo and Dilcher, 2001	angiosperm	Gramineae	Poaceae	
Multimarginites vanderhammenii Germeraad et al., 1968	angiosperm		Acanthaceae	*Sanchezia klugii*
Myrtaceae type	angiosperm		Myrtaceae	*Psidium*
Nymphaeaceae	angiosperm	Nymphaeaceae	Nymphaeaceae	
Ochnaceae type	angiosperm		Ochnaceae	
Onagraceae	angiosperm	Onagraceae	Onagraceae	
Pachydermites diederixi Germeraad et al., 1968	angiosperm		Clusiaceae	*Symphonia globulifera*
Palmae Type 1	angiosperm	Palmae Type 1	Arecaceae	
Palmapollenites "iriartoides"	angiosperm		Arecaceae	*Iriartea deltoidea*
Palmapollenites "microperforatus"	angiosperm	Palmae Type 2	Arecaceae	*Oenocarpus*
Palmapollenites "phytelephensis"	angiosperm		Arecaceae	*Phytelephas*
Palmapollenites "scheeleaensis"	angiosperm		Arecaceae	*Scheelea zonensis*

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Papilionoideae	angiosperm	Papilionoideae	Faboideae	
Parsonsidites "multiporatus"	angiosperm			
Perisyncolporites "gemmatus"	angiosperm			
Perisyncolporites pokornyi Germeraad et al., 1968	angiosperm	Malpighiaceae	Malpighiaceae	
Poloretitricolpites "centenarius"	angiosperm	*Pouteria*	Sapotaceae	*Pouteria*
Polyadopollenites "minutus"	angiosperm		Mimosoideae	*Acacia*
Polyadopollenites mariae Dueñas, 1980	angiosperm	*Acacia*	Mimosoideae	*Acacia*
Pouteria "mamey"	angiosperm			
Proteacidites triangulatus Lorente, 1986	angiosperm	*Allophylus*	Sapindaceae	*Allophylus*
Proxapertites "scabra?"	angiosperm		Araceae	
Proxapertites psilatus Sarmiento, 1992	angiosperm		Araceae	
Psilabrevitricolpites aff. *flexibilis* van Hoeken-Klinkenberg, 1966	angiosperm		Humiriaceae	
Psilabrevitricolporites "magnoporatus"	angiosperm			
Psilabrevitricolporites "vestibulatus"	angiosperm			
Psilabrevitricolpites aff. *rotundus* Van Hoeken-Klinkenberg, 1966	angiosperm		Apocynaceae	
Psilabrevitricolporites devriesi (Lorente, 1986) Silva-Caminha et al., 2010	angiosperm		Humiriaceae	*Humiria*
Psilabrevitricolporites triangularis (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm		Sapindaceae	
Psiladiporites "faramensis"	angiosperm			
Psiladiporites "infragranulatus"	angiosperm			
Psiladiporites "annulatus"	angiosperm			
Psiladiporites sp. Varma & Rawat, 1963	angiosperm			
Psilamonocolpites "longiformis"	angiosperm			
Psilamonocolpites amazonicus Hoorn, 1993	angiosperm		Arecaceae	*Euterpe*
Psilamonocolpites medius (Van der Hammen, 1956) Van der Hammen and Garcia, 1966	angiosperm		Arecaceae	
Psilamonocolpites rinconii Duenas, 1986	angiosperm		Arecaceae	*Oenocarpus*
Psilaperiporites "juglands"	angiosperm			
Psilaperiporites minimus Regali et al., 1974	angiosperm	Chenopodiaceae/ Amaranthaceae	Amaranthaceae	
Psilastephanocolpites "janduforius"	angiosperm	Unknown Type 5		
Psilastephanocolporites "acalyphoides"	angiosperm		Euphorbiaceae	*Acalypha diversifolia*
Psilastephanocolporites "cedreloides"	angiosperm	*Cedrela*	Meliaceae	*Cedrela*
Psilastephanocolporites fissilis Leidelmeyer, 1966	angiosperm		Polygalaceae	
Psilastephanoporites "crassiannulatus"	angiosperm			
Psilastephanoporites "magnus"	angiosperm		Apocynaceae	
Psilastephanoporites "microcaribiensis"	angiosperm			
Psilastephanoporites "pareado"	angiosperm			
Psilastephanoporites "punctatus"	angiosperm			
Psilastephanoporites herngreenii Hoorn, 1993	angiosperm		Apocynaceae	

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Psilasyncolpites "recticolpatus"	angiosperm			
Psilasyncolporites "reticolpatus"	angiosperm			
Psilatricolpites CU490	angiosperm	Unknown Type 2		
Psilatricolpites sp. (Van der Hammen) Pierce, 1961	angiosperm			
Psilatricolporites "colpiconstrictus"	angiosperm			
Psilatricolporites "communis"	angiosperm			
Psilatricolporites "crassiexinatus"	angiosperm			
Psilatricolporites "faboides"	angiosperm			
Psilatricolporites "hornii"	angiosperm		Apocynaceae	
Psilatricolporites "poriperfectus"	angiosperm			
Psilatricolporites "rotund"	angiosperm			
Psilatricolporites "sphericus"	angiosperm			
Psilatricolporites "vest"	angiosperm			
Psilatricolporites "vestibulatus"	angiosperm			
Psilatricolporites costatus Dueñas, 1980	angiosperm	*Casearia*	Salicaceae	*Casearia*
Psilatricolporites sp. Van der Hammen ex. Pierce, 1961	angiosperm			
Psilatriporites "anilloides"	angiosperm			
Psilatriporites "lobatus"	angiosperm			
Psilatriporites "moraceoides"	angiosperm			
Psilatriporites "ulmoides"	angiosperm		Ulmaceae	
Psilatriporites "vestibulatum"	angiosperm			
Ranunculacidites operculatus (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm	*Alchornea*	Euphorbiaceae	*Alchornea*
Retibrevitricolporites "vestibulatum"	angiosperm			
Retidiporites "cordiaeformis"	angiosperm			
Retidiporites "vestibulatum"	angiosperm			
Retimonocolpites "colpimarginatus"	angiosperm			
Retimonocolpites "heteroretifossulatus"	angiosperm	*Manicaria*-type	Arecaceae	*Manicaria*
Retimonocolpites "palmatus"	angiosperm		Arecaceae	*Cryosophila*
Retipericolporites sp.	angiosperm			
Retipollenites "minutus"	angiosperm		Araceae	
Retistephanocolpites "brevicolpatus"	angiosperm		Rubiaceae	*Borreria*
Retistephanocolpites "hexalabiatus"	angiosperm			
Retistephanocolpites "octolabiatus"	angiosperm		Labiatae	
Retistephanocolporites "bombacoides"	angiosperm			
Retistephanocolporites "borrerioides"	angiosperm		Rubiaceae	*Borreria*
Retistephanocolporites "crassimuratus"	angiosperm			
Retistephanoporites aff. *crassiannulatus* Lorente, 1986	angiosperm		Malvaceae	
Retitrescolpites "amanoensis"	angiosperm		Phyllanthaceae	*Amanoa*
Retitrescolpites "amplibrochatus"	angiosperm			
Retitrescolpites "deformis"	angiosperm			
Retitrescolpites "homogeneus"	angiosperm			
Retitrescolpites "usualis"	angiosperm			

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Retitrescolpites? irregularis (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm		Phyllanthaceae	*Amanoa*
Retitricolpites "generalis"	angiosperm			
Retitricolpites "pseudosimplex"	angiosperm			
Retitricolpites "spiraloides"	angiosperm	Unknown Type 14		
Retitricolpites simplex Gonzalez, 1967	angiosperm	*Sapium*	Euphorbiaceae	*Sapium*
Retitricolpites sp. (Van der Hammen) Pierce, 1961	angiosperm			
Retitricolporites "amplibrochatus"	angiosperm			
Retitricolporites "colpimarginatus"	angiosperm			
Retitricolporites "communis"	angiosperm	*Rourea*	Connaraceae	*Rourea*
Retitricolporites "crassiannulatus"	angiosperm		Rubiaceae	*Genipa americana*
Retitricolporites "hlongorate"	angiosperm			
Retitricolporites "minibrochatus"	angiosperm			
Retitricolporites "papilioniformis"	angiosperm		Faboideae	*Machaerium*
Retitricolporites "pluricolumellatus"	angiosperm	Unknown Type 7		
Retitricolporites "poricostatus"	angiosperm			
Retitricolporites "pseudoperculatus"	angiosperm			
Retitricolporites "simplibaculatus"	angiosperm			
Retitricolporites "spheroidalis"	angiosperm			
Retitricolporites "triangularis"	angiosperm			
Retitricolporites "zonoaperturatus"	angiosperm			
Retitricolporites "zonocolpatus"	angiosperm			
Retitricolporites CU456	angiosperm	*Cupania*	Sapindaceae	*Cupania*
Retitricolporites CU456-2	angiosperm	*Guazuma*	Byttneroideae	*Guazuma*
Retitricolporites CU57	angiosperm	Unknown Type 1		
Retitricolporites sp. Van der Hammen & Wymstra, 1964	angiosperm			
Retitriporites "erythrinoides"	angiosperm			
Retitriporites "heterobrochatus"	angiosperm			
Retitriporites "vestibulatum"	angiosperm		Rubiaceae	
Retitriporites aff. *poricostatus* Jaramillo and Dilcher, 2001	angiosperm			
Rhoipites "colpizonatus"	angiosperm			
Rhoipites "poricostatus"	angiosperm			
Rhoipites aff. *Cienagensis* (Dueñas, 1980) Barreda, 1997	angiosperm			
Rhoipites guianensis (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm		Malvaceae	
Rousea "cristatus"	angiosperm			
Rubiaceae (*Cosmibuena*) Ruiz & Pav.	angiosperm	*Cosmibuena*	Rubiaceae	*Cosmibuena*
Rubiaceae (*Faramea*) Aubl.	angiosperm	*Faramea*	Rubiaceae	*Faramea*
Rubiaceae (*Posoqueria*) Aubl.	angiosperm	*Posoqueria*	Rubiaceae	*Posoqueria*
Rubiaceae (Type 1)	angiosperm	Rubiaceae Type 1	Rubiaceae	
Rubiaceae (Type 2)	angiosperm	Rubiaceae Type 2	Rubiaceae	
Rubiopollis "muellerii"	angiosperm			

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Rutaceae (*Casimiroa*) La Llave & Lex.	angiosperm	*Casimiroa*	Rutaceae	*Casimiroa*
Sapindaceae (*Paullinia*) L.	angiosperm	*Paullinia*	Sapindaceae	*Paullinia*
Sapindaceae (*Serjania*) Mill.	angiosperm	*Serjania*	Sapindaceae	*Serjania*
Sapotaceae (cf. *Bumelia*) Sw.	angiosperm	cf. *Bumelia*	Sapotaceae	*Bumelia*
Scabraperiporites "nothofaguiformis"	angiosperm			
Scabrastephanoporites "apocynaceous"	angiosperm			
Siltaria "comunis"	angiosperm			
Siltaria dilcheri Silva-Caminha et al., 2010	angiosperm			
Stephanocolporites "lalongatus"	angiosperm			
Stephanoporites "scabratus"	angiosperm			
Striatopollis catatumbus (Gonzalez, 1967) Takahashi and Jux, 1989	angiosperm	*Crudia*	Caesalpinioideae	*Crudia*
Striatricolporites "burseriformis"	angiosperm	*Bursera*	Burseraceae	*Bursera simarouba*
Striatricolporites digitatus Jaramillo and Dilcher, 2001	angiosperm			
Striatricolporites melenae Dueñas, 1980	angiosperm		Anacardiaceae	
Striatricolporites tenuissimus Dueñas, 1980	angiosperm		Caesalpinioideae	*Crudia*
Symplocaceae (*Symplocos*) Jacq.	angiosperm	*Symplocos*	Symplocaceae	*Symplocos*
Syncolporites "paraisus"	angiosperm	*Matayba*	Sapindaceae	*Matayba*
Syncolporites "silvais"	angiosperm			
Syncolporites poricostatus van Hoeken Klinkenberg, 1966	angiosperm	*Eugenia/Myrcia*	Myrtaceae	*Eugenia-Myrcia*
Tetracolpites "rectangularis"	angiosperm			
Tetracolporites "guareaensis"	angiosperm	*Guarea*	Meliaceae	*Guarea*
Tetracolporites "meliaciformis"	angiosperm			
Tetracolporites "trichiliensis"	angiosperm		Meliaceae	*Trichilia*
Tetracolporites "vestibulatum"	angiosperm			
Tetracolporopollenites aff. *spongiosus* Jaramillo and Dilcher, 2001	angiosperm			
Tetracolporopollenites maculosus (Regali et al., 1974) Jaramillo and Dilcher, 2001	angiosperm		Sapotaceae	*Chrysophyllum*
Tetracolporopollenites transversalis (Dueñas, 1980) Jaramillo and Dilcher 2001	angiosperm		Sapotaceae	
Tiliaceae (*Mortoniodendron*) Standl. & Steyerm.	angiosperm	*Mortoniodendron*	Grewioideae	*Mortoniodendron*
Tricolpites "minutibacularis"	angiosperm			
Tricolpites "punctatus"	angiosperm	Unknown Type 3		
Tricolporites "annulatus"	angiosperm			
Tricolporites "caveatus"	angiosperm			
Tricolporites "colpidigitatus"	angiosperm			
Tricolporites "ericipitiformis"	angiosperm			
Tricolporites "megaporatus"	angiosperm			
Unknown 1	angiosperm	Unknown 1		
Unknown 2	angiosperm	Unknown 2		
Unknown 3	angiosperm	Unknown 3		
Unknown 4	angiosperm	Unknown 4		

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Unknown 5	angiosperm	Unknown 5		
Unknown 6	angiosperm	Unknown 6		
Unknown 7	angiosperm	Unknown 7		
Unknown 8	angiosperm	Unknown 8		
Unknown 9	angiosperm	Unknown 9		
Unknown 10	angiosperm	Unknown 10		
Unknown 11	angiosperm	Unknown 11		
Unknown 12	angiosperm	Unknown 12		
Unknown 13	angiosperm	Unknown 13		
Unknown 14	angiosperm	Unknown 14		
Unknown 15	angiosperm	Unknown 15		
Unknown 16	angiosperm	Unknown 16		
Unknown 17	angiosperm	Unknown 17		
Unknown 18	angiosperm	Unknown 18		
Unknown 19	angiosperm	Unknown 19		
Unknown 20	angiosperm	Unknown 20		
Unknown 21	angiosperm	Unknown 21		
Unknown 22	angiosperm	Unknown 22		
Unknown 23	angiosperm	Unknown 23		
Unknown 24	angiosperm	Unknown 24		
Unknown 25	angiosperm	Unknown 25		
Unknown 26	angiosperm	Unknown 26		
Unknown 27	angiosperm	Unknown 27		
Utricularia L.	angiosperm	*Utricularia*	Lentibulariaceae	*Utricularia*
Venezuelites "centroamericanus"	angiosperm			
Verbenaceae (*Aegiphila*) Jacq.	angiosperm	*Aegiphila*	Lamiaceae	Aegiphila
Verbenaceae (*Petrea*) L.	angiosperm	*Petrea*	Verbenaceae	Petrea
Verrutricolporites "desmodiensis"	angiosperm			
Verrutricolporites "faboides"	angiosperm			
Verrutricolporites "poricircularis"	angiosperm			
Verrutricolporites sp. Van der Hammen & Wymstra, 1964	angiosperm			
Vochysia type Aubl.	angiosperm		Vochysiaceae	Vochysia
Zonocostites "elongatus"	angiosperm			
Zonocostites ramonae Germeraad et al., 1968	angiosperm	*Rhizophora*	Rhizophoraceae	*Rhizophora*
Podocarpidites "globosus"	gymno-sperm	*Podocarpus*	Podocarpaceae	*Podocarpus*
Dinoflagellate	marine			
Foram lining	marine			
Anthocerotaceae	spore		Anthocerotaceae	
Apiculatasporites obscurus Jaramillo and Dilcher, 2001	spore	*Selaginella*	Selaginellaceae	*Selaginella*
Baculatisporites "circularis"	spore			
Baculatisporites "triangularis"	spore			
Camarozonoporites "crassus"	spore			

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Chomotriletes minor (Kedves, 1961) Pocock, 1970	spore			
Cicatricosisporites "bocatorensis"	spore			
Cingulatisporites "distafossulatus"	spore			
Cingulatisporites "gemmatus"	spore			
Cingulatisporites "pteriformis"	spore			
Cingulatisporites "rugulatus"	spore			
Cingulatisporites "verrutiformis"	spore			
Cingulatisporites psilatus Groot and Penny	spore			
Concavissimisporites "kyrtomatus"	spore			
Concavissimisporites fossulatus Duenas, 1980	spore			
Crassoretitriletes vanraadshooveni Germeraad et al., 1968	spore		Schizaeaceae	*Lygodium microphyllum*
Cyatheaceae (*Alsophila*) R. Br.	spore	*Alsophila*	Cyatheaceae	*Alsophila*
Cyatheaceae (*Cnemidaria*) C. Presl	spore	*Cnemidaria*	Cyatheaceae	*Cnemidaria*
Cyatheaceae (Type 1)	spore	Type 1	Cyatheaceae	
Cyatheaceae (Type 2)	spore	Type 2	Cyatheaceae	
Cyatheacidites annulatus Cookson, 1967	spore			
Cyathidites "typicus"	spore	*Cyathea*	Cyatheaceae	*Cyathea*
Leiotriletes adriennis (Potonie & Gelletich 1933) Krutzsch, 1959	spore			
Distaverrusporites "usmensis"	spore			
Dryopteridaceae (*Ctenitis*) (C. Chr.) C. Chr.	spore	*Ctenitis*	Dryopteridaceae	*Ctenitis*
Dryopteridaceae Type 1	spore	Dryopteridaceae Type 1	Dryopteridaceae	
Dryopteridaceae Type 2	spore	Dryopteridaceae Type 2	Dryopteridaceae	
Dryopteridaceae Type 3	spore	Dryopteridaceae Type 3	Dryopteridaceae	
Echinosporis sp. Krutzsch, 1967	spore			
Echinatisporis muelleri (Regali et al., 1974) Silva-Caminha et al., 2010	spore			
Echinomonoletes "amplimarginatus"	spore			
Echinomonoletes "bifurcatus"	spore			
Echinomonoletes "hirsutus"	spore			
Echinomonoletes "megaechinatus"	spore			
Echinomonoletes "sphericus"	spore			
Echitriletes "dasilviensis"	spore			
Echitriletes "densispinosus"	spore			
Echitriletes "minispinosus"	spore			
Echitriletes "minutuechinulatus"	spore			
Echitriletes "selaginelloides" type "bacularis"	spore		Selaginellaceae	
Echitriletes "selaginelloides" type "bifurcatus"	spore		Selaginellaceae	
Echitriletes "selaginelloides" type "echiplanatus"	spore		Selaginellaceae	
Echitriletes "selaginelloides" type "muelleri"	spore		Selaginellaceae	

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Echitriletes "selaginelloides" type "regularis"	spore		Selaginellaceae	
Echitriletes sp. Potonie, 1956	spore	*Selaginella*	Selaginellaceae	*Selaginella*
Fossutriletes "communis"	spore			
Fossutriletes "guapissimus"	spore			
Foveotriletes "arrugatus"	spore			
Foveotriletes "laterodepressus"	spore			
Foveotriletes "proximopsilatus"	spore	*Lycopodium*	Lycopodiaceae	*Lycopodium*
Foveotriletes "pseudoornatus"	spore			
Foveotriletes aff. *ornatus* Regali et al., 1974	spore			
Foveotriletes ornatus Regali et al., 1974	spore	Trilete fern spores Type 1 and 2		
Grammitisporites "verruminutus"	spore	*Grammitis*	Polypodiaceae	*Grammitis*
Kuylisporites "irregularis"	spore			
Kuylisporites "miniorodate"	spore			
Kuylisporites "multiorodate"	spore			
Kuylisporites waterbolki Potonié, 1956	spore		Cyatheaceae	*Hemitelia-Cnemidaria*
Laevigatosporites "magnus"	spore			
Laevigatosporites catanejensis Mullet et al., 1987	spore			
Laevigatosporites tibuensis (Van der Hammen, 1956a) Jaramillo and Dilcher, 2001	spore	Monolete fern spores Type 1 and 2		
Lycopodiaceae	spore	*Lycopodium* type 1	Lycopodiaceae	*Lycopodium*
Lycopodiaceae	spore	*Lycopodium* type 2	Lycopodiaceae	*Lycopodium*
Lycopodiaceae	spore	*Lycopodium* type 3	Lycopodiaceae	*Lycopodium*
Lycopodiaceae	spore	*Lycopodium* type 4	Lycopodiaceae	*Lycopodium*
Lycopodiumsporites "clavaelongatus"	spore		Lycopodiaceae	
Lycopodiumsporites "clavatus"	spore		Lycopodiaceae	
Lycopodiumsporites "morenoi"	spore		Lycopodiaceae	
Lycopodiumsporites "spinosus"	spore		Lycopodiaceae	
Lycopodiumsporites sp. Thiergart ex Delcourt & Sprumont, 1955	spore		Lycopodiaceae	
Matonisporites mulleri Playford, 1982	spore			
Monolete fern spore Type 1	spore	Monolete fern spore Type 1		
Monolete fern spore Type 2	spore	Monolete fern spore Type 2		
Monolete fern spore Type 3	spore	Monolete fern spore Type 3		
Monolete fern spore Type 4	spore	Monolete fern spore Type 4		
Monolete fern spore Type 5	spore	Monolete fern spore Type 5		
Nijssenosporites "pteridoides"	spore			
Nijssenosporites fossulatus Lorente, 1986	spore	*Pityrogramma*	Adianthaceae	*Pityrogramma*

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Ophioglossaceae (*Ophioglossum*) L.	spore	*Ophioglossum*	Ophioglossaceae	*Ophioglossum*
Perinomonoletes "aciculiformis"	spore			
Perinomonoletes "microechinulatus"	spore			
Perinomonoletes "minispinosus"	spore			
Perinomonoletes "minutus"	spore			
Perinomonoletes "pseudoreticulatus"	spore			
Perinomonoletes "reticuloacicularis"	spore			
Perinomonoletes sp. Krutzsch, 1967	spore			
Planisporites sp. 2 Jaramillo and Dilcher, 2001	spore			
Polypodiaceoisporites pseudopsilatus Lorente, 1986	spore			
Polypodiaceoisporites "circularis"	spore			
Polypodiaceoisporites "reticulatus"	spore			
Polypodiaceoisporites fossulatus Jaramillo and Dilcher, 2001	spore			
Polypodiaceoisporites pseudopsilatus Lorente, 1986	spore		Pteridaceae	*Pteris*
Polypodiaceoisporites? fossulatus Jaramillo and Dilcher, 2001	spore	*Pteris*	Pteridaceae	*Pteris*
Polypodiisporites "microverrucate"	spore			
Polypodiisporites "planus"	spore			
Polypodiisporites "reniformis"	spore			
Polypodiisporites scabraproximatus Silva-Caminha et al., 2010	spore			
Polypodiisporites "verruplanatus"	spore			
Polypodiisporites aff. *echinatus* Jaramillo and Dilcher, 2001	spore			
Polypodiisporites aff. sp. 2 J & D Jaramillo and Dilcher, 2001	spore			
Polypodiisporites aff. *specious* Sah, 1967	spore	Monolete fern spore Type 3		
Polypodiisporites scabraproximatus Silva-Caminha et al., 2010	spore	Monolete fern spores Type 2		
Polypodiisporites usmensis (Van der Hammen, 1956a) Khan and Martin, 1972	spore		Blechnaceae	*Stenochlaena palustris*
Polypodiisporites? planus Silva-Caminha et al., 2010	spore			
Psilatriletes "brevilaesuratus"	spore	*Antrophyum*	Pteridaceae	*Antrophyum*
Psilatriletes "camerata"	spore			
Psilatriletes "crassitriangulatus"	spore			
Psilatriletes "enormis"	spore	*Lygodium*	Lygodiaceae	*Lygodium*
Psilatriletes "minor"	spore			
Psilatriletes < 25 μm	spore			
Psilatriletes > 50 μm	spore			
Psilatriletes 25–50 μm	spore	*Cyathea*	Cyatheaceae	*Cyathea*
Psilatriletes lobatus Hoorn, 1994	spore			
Psilatriletes peruanus Hoorn, 1994	spore		Pteridaceae	*Jamesonia*
Pteridaceae (Type 1)	spore	Pteridaceae Type 1	Pteridaceae	

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Pteridaceae (Type 2)	spore	Pteridaceae Type 2	Pteridaceae	
Pteridaceae (Type 3)	spore	Pteridaceae Type 3	Pteridaceae	
Pteridaceae (Type 4)	spore	Pteridaceae Type 4	Pteridaceae	
Pteridaceae (Type 5)	spore	Pteridaceae Type 5	Pteridaceae	
Retitriletes "perforatus"	spore			
Retitriletes sommeri Regali et al., 1974	spore	Trilete fern spores Type 3	Lycopodiaecae	
Rugulatisporites "irregularis"	spore			
Rugulatisporites "minutus"	spore			
Scabramonoletes "elongatus"	spore			
Scabratriletes "complicatus"	spore			
Schizaea "mosquitensis"	spore			
Selaginellasporites "cingulatus"	spore		Selaginellaceae	
Selaginellasporites "crestatus"	spore		Selaginellaceae	
Selaginellasporites "psilatus"	spore		Selaginellaceae	
Selaginellasporites "variechinatus"	spore		Selaginellaceae	
Striatomonoletes "inciertus"	spore			
Striatriletes "saccolomicites"	spore			
Trilete fern spore Type 1	spore	Trilete fern spore Type 1		
Trilete fern spore Type 2	spore	Trilete fern spore Type 2		
Undulatisporites "undulapolus"	spore			
Verrucatotriletes etayoi Duenas, 1980	spore			
Verrucatotriletes sp. van Hoeken-Klinkenberg, 1964	spore			
Verrutriletes "bullatus"	spore			
Verrutriletes "densiverrucatus"	spore			
Verrutriletes "magnoviruelensis"	spore			
Verrutriletes "perforatus"	spore			
Verrutriletes "uniformis"	spore			
Verrutriletes "variverrucatus"	spore			
Verrutriletes sp. Pierce, 1961	spore	Trilete fern spores Type 4		
Baculatriletes "palmiformis"	spore			
Echimonoletes "panamensis"	spore	*Danaea*	Marattiaceae	*Danaea*

Samples were divided into three groups (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma) because, as mentioned previously, they represent three major periods in the geological evolution of the isthmus history. All comparisons are the result of two-sided *t*-tests to evaluate the equality of means in two unpaired samples. Probability (P) is reported for each test, along with degrees of freedom (df) calculated using the Welch modification to account for different variances in the groups being compared. All analyses were done using R Project for Statistical Computing (R Development Core Team, 2012) and the package "vegan" (Oksanen et al., 2010). All R codes used here are presented in Appendix 3. Samples with less than 80 grains (excluding fungi) were excluded from most of the analyses.

RESULTS

OVERALL PATTERN

A total of 27,910 grains (pollen/spores), yielding 496 morphotypes in 282 samples, were registered (Tables 4, 5, Supplementary Appendix, Appendix 2). Angiosperm abundance per sample did not change substantially across the 19.5–3.5 Ma interval (40% in the 19.5–10 Ma interval, 36% in the 10–3.5 Ma interval, $P = 0.2$, $df = 109$), and slightly decreased in the last 3.5 Ma (26%), although the difference is not significant ($P = 0.07$, $df = 17$) (Fig. 3). Ferns represent 59% of the abundance per sample in the 19.5–10 Ma interval, and 62% in the 10–3.5 Ma interval ($P = 0.3$, $df = 108$), increasing slightly in the last 3.5 Ma (73%, $P = 0.07$, $df = 17$), although the difference is not significant (Fig. 3).

Biogeographic affinities. The biogeographic affinity of each individual extant tree and shrub in the Barro Colorado Island (BCI) 50-ha vegetation plot is dominated by Gondwana-Amazonian families: 68% of individuals are Gondwana-Amazonian, 20.5% are Gondwana-northern Andean, 3.2% are Gondwana-southern Andean, and only 6.1% are Laurasian (2.2% are unassigned to families) (Fig. 4, Appendix 1). We analyzed the biogeographic affinities of the entire fossil dataset (496 taxa) but only in samples with counts larger than 80 grains ($N = 124$). The mean of Gondwana-Amazonian individuals in a sample is 27% (SD = 16.9); Gondwana-northern Andean, 1% (SD = 1.7); Gondwana-southern Andean, 0.5% (SD = 1.3); and Laurasian-centered, 1.8% (SD = 0.2) (Fig. 4, Table 5). There was still a large proportion of individuals excluded from this calculation (69%, SD = 16.6), because either the family does not have a distinct biogeographic origin (23 taxa) or the family that the individual belongs to is still unknown (315 taxa). Does this proportion change when time slots are analyzed independently? Gondwana-Amazonian taxa are significantly more abundant prior to 3.5 Ma (> 3.5 Ma: 28%; < 3.5 Ma: 17%; $P = 0.03$, $df = 12$). Conversely, Laurasian taxa (> 3.5 Ma: 1.7%; < 3.5 Ma: 2.5%) and northern Andean taxa (> 3.5 Ma: 1%; < 3.5 Ma: 1.7%) are slightly less abundant prior to 3.5 Ma, although these differences are not significant ($P = 0.2$, $df = 12$ and $P = 0.1$, $df = 16$, respectively) (Fig. 4). Amazonian taxa are slightly more abundant prior to 10 Ma, compared to the 10–3.5 Ma interval, although the difference is not significant (19.5–10 Ma: 31.8%; 10–3.5 Ma: 24.6%; $P = 0.02$, $df = 108$), while Laurasian taxa are significantly more abundant in the 10–3.5 Ma interval compared to older strata (10–3.5 Ma: 2.8%; 19.5–10 Ma: 0.8%; $P = 0.001$, $df = 92$); the same pattern is depicted by northern Andean taxa (10–3.5 Ma: 1.9%; 19.5–10 Ma: 0.3%; $P = 0.001$, $df = 63$) (Fig. 4).

Extant species on BCI are dominated by South American families: 66.4% of species are Gondwana-Amazonian, 13.1% are Gondwana-northern Andean, and 4.8%, Gondwana-southern Andean, while only 10.9% are Laurasian (4.4% are unassigned families) (Fig. 5, Appendix 1). The biogeographic affinity of each fossil taxon is very similar to the pattern described for extant plants: the Gondwana-Amazonian mean is 26.7% (SD

TABLE 5. Summary table. The following values correspond to pollen/spore grains and species counted in each sample, and abundances (given as percentages) of species grouped by both biogeographic and ecological categories. Samples with counts of < 80 grains are included here but were not considered for the biogeographic and ecological analyses.

Area	Formation	Sample age (Ma)	N^I	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Bocas del Toro	Swan Cay	1.285	34	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	1.810	81	30	29.8	0.14	0.02	0.04	0.06	0.74	0.20	0.20	0.15	0.05	0.00	0.00	0.05	0.01	0.72
Bocas del Toro	Nancy Point	1.820	57	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	2.000	123	17	15.15	0.12	0.02	0.00	0.02	0.84	0.04	0.02	0.02	0.00	0.00	0.00	0.08	0.00	0.88
Bocas del Toro	Escudo Veraguas	2.051	111	31	24.8	0.44	0.04	0.00	0.04	0.49	0.26	0.23	0.17	0.04	0.00	0.00	0.29	0.01	0.43
Bocas del Toro	Escudo Veraguas	2.052	78	31	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	2.053	76	27	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	2.054	158	36	24.56	0.32	0.01	0.01	0.01	0.64	0.29	0.27	0.20	0.08	0.01	0.00	0.19	0.00	0.49
Bocas del Toro	Escudo Veraguas	2.055	326	47	26.85	0.23	0.02	0.02	0.05	0.68	0.19	0.16	0.12	0.04	0.01	0.00	0.12	0.00	0.67
Bocas del Toro	unnamed	2.300	45	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	2.400	298	31	17.79	0.05	0.01	0.01	0.05	0.88	0.18	0.16	0.14	0.00	0.01	0.00	0.03	0.01	0.77
Bocas del Toro	unnamed	2.500	21	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	2.651	297	46	26.44	0.06	0.02	0.01	0.04	0.86	0.24	0.23	0.23	0.01	0.01	0.00	0.04	0.00	0.68
Bocas del Toro	unnamed	2.652	141	20	15.92	0.08	0.01	0.00	0.01	0.91	0.04	0.02	0.02	0.00	0.00	0.00	0.06	0.00	0.90
Bocas del Toro	unnamed	2.653	105	12	10.75	0.02	0.00	0.00	0.00	0.98	0.03	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.96
Bocas del Toro	Escudo de Veraguas	2.751	22	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.752	105	18	15.63	0.36	0.01	0.00	0.01	0.62	0.06	0.04	0.01	0.01	0.00	0.00	0.33	0.00	0.61
Bocas del Toro	Escudo de Veraguas	2.753	14	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.754	297	40	19.41	0.04	0.01	0.00	0.00	0.95	0.18	0.15	0.15	0.00	0.00	0.00	0.01	0.00	0.79
Bocas del Toro	Escudo de Veraguas	2.755	31	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.756	39	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.757	13	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.758	26	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	3.450	72	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	3.451	38	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

(continued)

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N^{I}	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Bocas del Toro	Escudo de Veraguas	3.551	52	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.551	38	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.551	79	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	3.551	68	29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	3.551	61	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	70	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	32	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	37	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	65	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	308	38	21.82	0.16	0.02	0.01	0.00	0.81	0.17	0.14	0.13	0.00	0.00	0.00	0.12	0.00	0.71
Bocas del Toro	Escudo de Veraguas	3.552	52	24	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	3.552	67	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.552	31	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.552	77	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	94	28	25.95	0.23	0.05	0.00	0.02	0.69	0.16	0.12	0.10	0.00	0.00	0.00	0.18	0.00	0.65
Bocas del Toro	Cayo Agua	3.553	71	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	70	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	9	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	111	27	24.29	0.23	0.07	0.01	0.07	0.61	0.29	0.27	0.16	0.05	0.00	0.00	0.09	0.00	0.59
Bocas del Toro	Cayo Agua	3.553	264	48	23.37	0.41	0.03	0.01	0.01	0.54	0.22	0.21	0.19	0.01	0.00	0.02	0.19	0.00	0.56
Bocas del Toro	Cayo Agua	3.553	101	25	21.74	0.06	0.01	0.00	0.06	0.87	0.16	0.11	0.14	0.01	0.00	0.01	0.02	0.00	0.75
Bocas del Toro	Cayo Agua	3.553	32	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	42	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	46	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	3.554	109	30	24.69	0.16	0.05	0.00	0.06	0.74	0.38	0.37	0.32	0.06	0.01	0.00	0.06	0.00	0.53
Bocas del Toro	unnamed	3.554	5	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Bocas del Toro	unnamed	3.554	279	35	21.08	0.08	0.00	0.00	0.03	0.89	0.23	0.19	0.16	0.00	0.01	0.00	0.00	0.00	0.75
Bocas del Toro	unnamed	3.554	171	37	26.22	0.07	0.03	0.01	0.02	0.87	0.19	0.14	0.13	0.02	0.01	0.00	0.02	0.00	0.77
Bocas del Toro	Shark Hole Point	4.000	206	40	25.4	0.20	0.01	0.00	0.01	0.78	0.22	0.19	0.14	0.04	0.01	0.00	0.08	0.00	0.69
Bocas del Toro	Cayo Agua	4.250	196	34	22.45	0.35	0.03	0.00	0.01	0.61	0.18	0.17	0.11	0.05	0.01	0.00	0.25	0.00	0.56
Bocas del Toro	Cayo Agua	4.250	41	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.250	6	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.250	11	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	7	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	23	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	21	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	45	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	35	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	35	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	70	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	22	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	36	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.251	17	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.252	67	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.252	92	28	26.59	0.18	0.05	0.00	0.10	0.66	0.21	0.21	0.21	0.02	0.00	0.02	0.07	0.00	0.63
Bocas del Toro	Cayo Agua	4.252	140	32	25.59	0.21	0.02	0.02	0.06	0.69	0.24	0.22	0.20	0.03	0.01	0.00	0.16	0.00	0.57
Bocas del Toro	Cayo Agua	4.252	85	23	22.29	0.44	0.08	0.02	0.02	0.44	0.20	0.20	0.19	0.02	0.00	0.00	0.35	0.01	0.40
Bocas del Toro	Cayo Agua	4.252	76	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.252	37	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.252	149	15	11.05	0.03	0.00	0.01	0.00	0.97	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.98
Bocas del Toro	Cayo Agua	4.252	26	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.252	323	63	30.52	0.21	0.02	0.01	0.05	0.70	0.31	0.28	0.23	0.02	0.00	0.00	0.11	0.00	0.56
Bocas del Toro	Cayo Agua	4.252	7	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	21	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	174	29	20.48	0.04	0.03	0.01	0.01	0.91	0.19	0.17	0.17	0.00	0.00	0.02	0.02	0.00	0.76
Bocas del Toro	Cayo Agua	4.253	88	20	19.14	0.11	0.01	0.00	0.00	0.88	0.14	0.11	0.09	0.00	0.00	0.00	0.07	0.00	0.80
Bocas del Toro	Cayo Agua	4.253	148	21	15.7	0.06	0.03	0.00	0.01	0.91	0.30	0.27	0.26	0.01	0.00	0.01	0.04	0.00	0.63
Bocas del Toro	Cayo Agua	4.253	95	24	22.23	0.05	0.00	0.01	0.05	0.88	0.16	0.18	0.20	0.00	0.00	0.00	0.04	0.01	0.73

(*continued*)

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N^{I}	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Bocas del Toro	Cayo Agua	4.253	48	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	15	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	49	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	57	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	34	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	4.254	33	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	4.400	25	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	4.610	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	4.620	164	36	27.52	0.15	0.01	0.00	0.02	0.82	0.13	0.14	0.13	0.01	0.00	0.01	0.05	0.00	0.76
Bocas del Toro	Shark Hole Point	4.630	99	26	23.8	0.07	0.01	0.00	0.03	0.89	0.15	0.15	0.15	0.01	0.00	0.00	0.01	0.00	0.81
Bocas del Toro	Nancy Point	5.650	132	25	19.57	0.32	0.02	0.01	0.00	0.66	0.20	0.19	0.14	0.05	0.01	0.00	0.23	0.00	0.55
Panama Central	Gatun	6.000	114	25	21.51	0.43	0.10	0.01	0.04	0.43	0.25	0.22	0.16	0.04	0.00	0.00	0.22	0.01	0.50
Panama Central	Chagres	6.010	156	29	21.14	0.13	0.01	0.00	0.02	0.83	0.36	0.31	0.26	0.05	0.01	0.00	0.03	0.00	0.60
Panama Central	Chagres	6.020	106	22	20.04	0.06	0.01	0.01	0.00	0.92	0.12	0.08	0.08	0.00	0.00	0.00	0.01	0.00	0.86
Bocas del Toro	Nancy Point	6.051	10	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.052	22	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.300	16	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.400	54	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	6.400	36	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	6.410	40	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Pucro	6.950	22	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Pucro	6.950	18	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.950	9	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Chucunaque	6.950	16	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	5	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	32	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	82	22	21.73	0.23	0.00	0.00	0.01	0.76	0.02	0.02	0.02	0.00	0.00	0.00	0.15	0.00	0.83

Darien	Tuira	6.951	16	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	47	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	44	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	269	31	19.16	0.30	0.02	0.01	0.06	0.62	0.19	0.18	0.16	0.01	0.00	0.00	0.24	0.00	0.56
Darien	Tuira	6.951	23	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	46	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	12	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.952	7	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.952	13	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.952	219	27	17.67	0.25	0.01	0.00	0.00	0.73	0.22	0.21	0.17	0.03	0.00	0.01	0.18	0.00	0.57
Darien	Tuira	6.952	28	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.952	226	24	15.5	0.59	0.00	0.02	0.03	0.36	0.10	0.10	0.11	0.00	0.00	0.00	0.54	0.00	0.33
Darien	Tuira	6.952	70	18															
Darien	Chucunaque	6.952	225	29	19.79	0.29	0.02	0.01	0.03	0.66	0.14	0.13	0.12	0.01	0.01	0.00	0.13	0.00	0.70
Darien	Lara	6.952	112	19	16.13	0.66	0.01	0.01	0.00	0.32	0.04	0.04	0.02	0.01	0.00	0.00	0.60	0.01	0.35
Darien	Tuira	6.952	24	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.952	24	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.953	51	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.953	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.953	35	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.953	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Pucro	6.953	53	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Pucro	6.953	82	26	25.61	0.16	0.00	0.00	0.00	0.84	0.06	0.06	0.01	0.04	0.00	0.00	0.04	0.01	0.89
Darien	Pucro	6.953	57	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.953	30	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.953	10	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.953	12	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.954	34	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	6.954	20	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Chucunaque	7.050	105	25	21.29	0.55	0.01	0.01	0.01	0.42	0.16	0.11	0.10	0.05	0.00	0.01	0.40	0.00	0.40
Bocas del Toro	Nancy Point	7.150	15	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.300	165	24	19.33	0.21	0.00	0.01	0.03	0.75	0.18	0.15	0.05	0.00	0.01	0.00	0.02	0.00	0.79

(continued)

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N^{I}	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Panama Central	Gatun	8.400	163	25	21.35	0.30	0.03	0.09	0.03	0.55	0.32	0.32	0.10	0.00	0.09	0.08	0.04	0.00	0.43
Panama Central	Gatun	8.407	182	25	17.32	0.46	0.02	0.07	0.02	0.43	0.29	0.29	0.03	0.00	0.07	0.22	0.03	0.00	0.36
Panama Central	Gatun	8.412	240	88	42.74	0.24	0.05	0.08	0.04	0.59	0.26	0.26	0.10	0.03	0.04	0.08	0.04	0.00	0.55
Panama Central	Gatun	8.418	199	15	9.881	0.90	0.00	0.01	0.01	0.08	0.07	0.05	0.02	0.02	0.00	0.04	0.82	0.00	0.06
Panama Central	Gatun	8.472	176	23	19.86	0.30	0.00	0.03	0.04	0.63	0.20	0.23	0.16	0.00	0.00	0.19	0.11	0.09	0.37
Panama Central	Gatun	8.473	179	21	16.34	0.35	0.01	0.00	0.00	0.64	0.14	0.10	0.09	0.01	0.01	0.30	0.11	0.08	0.36
Panama Central	Gatun	8.474	182	16	15.07	0.37	0.02	0.00	0.05	0.55	0.16	0.15	0.14	0.00	0.00	0.31	0.10	0.08	0.30
Panama Central	Gatun	8.563	184	18	15.18	0.33	0.02	0.00	0.03	0.63	0.08	0.11	0.08	0.00	0.00	0.25	0.09	0.00	0.55
Panama Central	Gatun	8.596	179	14	12.45	0.16	0.02	0.02	0.04	0.77	0.11	0.16	0.14	0.01	0.00	0.20	0.08	0.00	0.56
Panama Central	Gatun	8.610	10	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.620	13	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.630	23	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.640	8	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.650	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.660	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.670	49	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.726	265	21	14.36	0.19	0.00	0.00	0.01	0.80	0.23	0.23	0.17	0.01	0.00	0.00	0.08	0.00	0.67
Panama Central	Gatun	8.753	156	25	19.16	0.14	0.00	0.00	0.01	0.85	0.17	0.15	0.08	0.00	0.00	0.01	0.01	0.00	0.81
Panama Central	Gatun	8.754	287	35	21.85	0.25	0.00	0.03	0.03	0.68	0.09	0.06	0.01	0.00	0.00	0.00	0.09	0.00	0.81
Panama Central	Gatun	8.754	69	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.770	363	58	25.52	0.27	0.01	0.01	0.01	0.69	0.31	0.26	0.16	0.02	0.01	0.00	0.02	0.00	0.65
Panama Central	Gatun	8.773	746	66	21.39	0.34	0.00	0.00	0.04	0.61	0.23	0.22	0.07	0.01	0.00	0.00	0.08	0.00	0.67
Panama Central	Gatun	9.398	41	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.401	11	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.402	24	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.412	219	22	14.28	0.32	0.00	0.00	0.00	0.67	0.09	0.07	0.06	0.00	0.00	0.00	0.24	0.00	0.67
Panama Central	Gatun	9.424	58	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Panama Central	Gatun	9.432	83	24	23.56	0.05	0.04	0.00	0.10	0.82	0.24	0.25	0.23	0.02	0.00	0.01	0.00	0.00	0.71
Panama Central	Gatun	9.464	63	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.500	34	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.519	37	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.552	50	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.589	137	29	21.78	0.09	0.00	0.00	0.05	0.86	0.07	0.09	0.06	0.03	0.00	0.01	0.02	0.00	0.86
Panama Central	Gatun	9.737	171	36	26.73	0.25	0.01	0.01	0.04	0.70	0.44	0.32	0.29	0.05	0.00	0.00	0.04	0.00	0.48
Panama Central	Gatun	9.932	207	37	22.78	0.15	0.03	0.01	0.02	0.79	0.17	0.14	0.10	0.02	0.00	0.00	0.02	0.00	0.79
Panama Central	Gatun	9.932	17	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.932	129	26	21.23	0.15	0.00	0.00	0.05	0.80	0.23	0.22	0.20	0.02	0.00	0.00	0.05	0.00	0.69
Panama Central	Gatun	10.143	323	43	21.97	0.25	0.02	0.01	0.05	0.67	0.29	0.27	0.22	0.03	0.00	0.01	0.14	0.00	0.55
Darien	Tuira	10.151	50	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.152	44	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.153	49	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.154	30	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.155	47	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.156	23	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.157	19	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	10.874	91	19	18.09	0.04	0.01	0.00	0.09	0.86	0.46	0.47	0.48	0.02	0.00	0.00	0.00	0.00	0.49
Panama Central	Gatun	10.877	299	29	18.93	0.24	0.00	0.00	0.01	0.75	0.10	0.09	0.03	0.00	0.00	0.00	0.03	0.00	0.86
Panama Central	Gatun	10.878	129	26	20.73	0.05	0.00	0.00	0.02	0.93	0.16	0.13	0.11	0.00	0.00	0.00	0.00	0.00	0.84
Panama Central	Gatun	10.881	268	32	19.4	0.08	0.01	0.00	0.01	0.90	0.07	0.05	0.03	0.00	0.00	0.00	0.00	0.00	0.93
Panama Central	Gatun	10.883	51	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	11.553	185	43	29.46	0.22	0.04	0.00	0.02	0.72	0.29	0.26	0.20	0.05	0.02	0.02	0.06	0.01	0.60
Panama Central	Gatun	11.674	139	29	22.79	0.08	0.01	0.00	0.06	0.85	0.20	0.18	0.17	0.03	0.00	0.00	0.00	0.00	0.78
Darien	Tuira	12.601	12	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	12.602	13	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	12.603	15	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	12.604	7	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	18.834	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	18.915	86	8	8	0.65	0.00	0.00	0.00	0.35	0.13	0.09	0.03	0.35	0.00	0.00	0.07	0.00	0.45
Panama Central	Cucaracha	18.925	6	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

(*continued*)

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N^{I}	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Panama Central	Culebra	18.928	82	11	10.95	0.43	0.00	0.00	0.00	0.57	0.20	0.16	0.06	0.04	0.01	0.00	0.10	0.00	0.66
Panama Central	Culebra	18.931	86	14	13.65	0.53	0.00	0.00	0.01	0.45	0.38	0.38	0.27	0.13	0.00	0.00	0.10	0.00	0.37
Panama Central	Culebra	18.935	94	13	12.66	0.43	0.00	0.00	0.00	0.57	0.37	0.35	0.21	0.13	0.00	0.00	0.05	0.00	0.45
Panama Central	Culebra	18.948	182	38	28.08	0.35	0.01	0.00	0.03	0.62	0.35	0.35	0.15	0.04	0.01	0.02	0.03	0.00	0.58
Panama Central	Culebra	18.953	182	19	13.79	0.41	0.00	0.00	0.01	0.59	0.37	0.32	0.18	0.02	0.00	0.00	0.02	0.00	0.61
Panama Central	Culebra	18.954	181	32	26.04	0.33	0.00	0.02	0.04	0.61	0.40	0.37	0.20	0.06	0.00	0.00	0.06	0.00	0.48
Panama Central	Culebra	18.961	185	25	19.62	0.36	0.01	0.01	0.01	0.63	0.32	0.24	0.18	0.05	0.00	0.02	0.09	0.00	0.53
Panama Central	Culebra	18.962	162	17	15.04	0.27	0.00	0.00	0.00	0.73	0.41	0.33	0.23	0.04	0.01	0.00	0.04	0.00	0.51
Panama Central	Culebra	18.962	187	12	10.64	0.29	0.00	0.00	0.00	0.71	0.25	0.21	0.16	0.11	0.00	0.00	0.04	0.00	0.59
Panama Central	Culebra	18.962	180	13	11.77	0.27	0.00	0.00	0.00	0.73	0.49	0.40	0.31	0.07	0.00	0.00	0.12	0.00	0.33
Panama Central	Cucaracha	18.974	323	9	5.957	0.76	0.00	0.00	0.00	0.24	0.03	0.03	0.01	0.00	0.00	0.21	0.00	0.00	0.76
Panama Central	Cucaracha	18.974	223	15	10.53	0.48	0.00	0.00	0.00	0.52	0.04	0.04	0.02	0.00	0.00	0.07	0.01	0.00	0.89
Panama Central	Cucaracha	18.981	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.061	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.086	299	16	10.89	0.54	0.00	0.00	0.00	0.46	0.14	0.14	0.10	0.00	0.00	0.10	0.00	0.00	0.77
Panama Central	Cucaracha	19.100	10	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.143	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.173	298	22	13.91	0.35	0.00	0.00	0.00	0.65	0.16	0.16	0.14	0.00	0.01	0.03	0.00	0.00	0.81
Panama Central	Cucaracha	19.175	167	18	13.46	0.44	0.00	0.00	0.00	0.56	0.21	0.21	0.20	0.00	0.01	0.07	0.00	0.00	0.78
Panama Central	Cucaracha	19.196	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.201	179	26	17.63	0.22	0.00	0.00	0.00	0.78	0.25	0.23	0.21	0.00	0.00	0.08	0.02	0.00	0.66
Panama Central	Cucaracha	19.203	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.210	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.215	117	21	18.01	0.30	0.00	0.00	0.01	0.69	0.27	0.26	0.23	0.01	0.00	0.02	0.00	0.00	0.70
Panama Central	Cucaracha	19.230	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.241	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.241	172	19	15.12	0.19	0.01	0.00	0.01	0.80	0.32	0.29	0.27	0.01	0.00	0.05	0.00	0.00	0.63

Panama Central	Cucaracha	19.251	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.254	108	20	17.92	0.27	0.00	0.00	0.00	0.73	0.28	0.24	0.23	0.01	0.00	0.01	0.00	0.00	0.72
Panama Central	Cucaracha	19.262	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.264	326	10	8.192	0.30	0.00	0.00	0.00	0.70	0.15	0.15	0.02	0.00	0.00	0.04	0.00	0.00	0.80
Panama Central	Culebra	19.268	101	23	20.33	0.22	0.00	0.00	0.00	0.78	0.26	0.13	0.12	0.02	0.01	0.04	0.00	0.00	0.69
Panama Central	Cucaracha	19.269	321	8	5.935	0.31	0.00	0.00	0.00	0.69	0.13	0.13	0.00	0.00	0.00	0.14	0.00	0.00	0.74
Panama Central	Cucaracha	19.278	132	20	16.84	0.09	0.00	0.00	0.00	0.91	0.21	0.19	0.20	0.01	0.01	0.05	0.00	0.00	0.73
Panama Central	Culebra	19.281	54	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.290	140	17	13.38	0.11	0.01	0.00	0.00	0.89	0.34	0.34	0.34	0.00	0.01	0.19	0.01	0.00	0.54
Panama Central	Culebra	19.294	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.308	171	16	12.39	0.37	0.00	0.00	0.01	0.61	0.29	0.30	0.30	0.01	0.00	0.22	0.11	0.00	0.58
Panama Central	Cucaracha	19.311	133	19	16.26	0.11	0.00	0.00	0.00	0.89	0.26	0.21	0.20	0.00	0.02	0.08	0.00	0.00	0.68
Panama Central	Culebra	19.316	8	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.321	238	19	15.01	0.25	0.00	0.00	0.00	0.75	0.11	0.11	0.11	0.00	0.00	0.16	0.03	0.00	0.71
Panama Central	Culebra	19.327	102	17	15.97	0.68	0.00	0.00	0.00	0.32	0.14	0.14	0.08	0.00	0.01	0.02	0.07	0.00	0.76
Panama Central	Culebra	19.334	73	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.347	53	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.374	55	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.381	270	22	13.52	0.19	0.00	0.00	0.00	0.80	0.14	0.15	0.14	0.00	0.00	0.23	0.00	0.00	0.63
Panama Central	Culebra	19.385	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.398	150	19	16.49	0.45	0.00	0.00	0.01	0.55	0.29	0.15	0.09	0.01	0.00	0.03	0.00	0.00	0.67
Panama Central	Culebra	19.407	177	21	17.58	0.44	0.00	0.00	0.00	0.56	0.21	0.21	0.15	0.00	0.00	0.02	0.01	0.00	0.76
Panama Central	Culebra	19.409	281	22	14.09	0.37	0.00	0.00	0.00	0.63	0.11	0.10	0.08	0.01	0.00	0.10	0.10	0.01	0.70
Panama Central	Culebra	19.414	8	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.416	198	21	15.79	0.39	0.00	0.00	0.01	0.61	0.28	0.25	0.22	0.00	0.00	0.01	0.00	0.00	0.71
Panama Central	Culebra	19.425	277	25	18.11	0.51	0.00	0.00	0.00	0.49	0.28	0.25	0.20	0.00	0.00	0.03	0.00	0.00	0.69
Panama Central	Culebra	19.433	251	21	15.61	0.34	0.00	0.00	0.02	0.65	0.28	0.25	0.20	0.00	0.01	0.04	0.00	0.00	0.66
Panama Central	Culebra	19.434	313	29	20	0.47	0.00	0.00	0.02	0.51	0.26	0.27	0.23	0.00	0.00	0.01	0.01	0.00	0.70
Panama Central	Culebra	19.444	303	27	15.52	0.33	0.00	0.00	0.00	0.67	0.45	0.46	0.38	0.00	0.00	0.03	0.00	0.00	0.51
Panama Central	Culebra	19.454	285	22	14.35	0.34	0.00	0.00	0.02	0.64	0.33	0.35	0.32	0.00	0.00	0.03	0.00	0.00	0.61
Panama Central	Culebra	19.462	301	23	13.44	0.36	0.00	0.00	0.00	0.64	0.11	0.11	0.11	0.00	0.00	0.10	0.03	0.01	0.77
Panama Central	Culebra	19.462	194	17	11.73	0.28	0.00	0.00	0.01	0.71	0.30	0.30	0.26	0.01	0.00	0.01	0.00	0.00	0.68

(continued)

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N[1]	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Panama Central	Culebra	19.470	299	20	14.12	0.22	0.00	0.00	0.00	0.77	0.43	0.41	0.39	0.02	0.00	0.06	0.00	0.00	0.50
Panama Central	Culebra	19.478	313	18	12.52	0.27	0.00	0.00	0.01	0.72	0.35	0.36	0.33	0.00	0.01	0.02	0.00	0.00	0.62
Panama Central	Cucaracha	19.479	100	12	11.67	0.34	0.00	0.02	0.01	0.63	0.18	0.19	0.13	0.00	0.00	0.00	0.17	0.00	0.64
Panama Central	Cucaracha	19.480	100	6	5.76	0.21	0.00	0.00	0.00	0.79	0.06	0.06	0.00	0.00	0.00	0.00	0.11	0.00	0.83
Panama Central	Cucaracha	19.480	100	4	3.962	0.08	0.00	0.00	0.00	0.92	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.98
Panama Central	Cucaracha	19.481	100	8	7.523	0.18	0.02	0.00	0.01	0.79	0.04	0.04	0.01	0.00	0.00	0.00	0.09	0.00	0.87
Panama Central	Culebra	19.485	310	17	10.87	0.32	0.00	0.00	0.01	0.67	0.40	0.41	0.36	0.01	0.00	0.02	0.00	0.00	0.57
Panama Central	Culebra	19.493	289	19	12.65	0.26	0.00	0.00	0.00	0.74	0.50	0.49	0.46	0.00	0.00	0.03	0.01	0.00	0.46
Panama Central	Cucaracha	19.525	100	9	8.193	0.17	0.00	0.00	0.00	0.83	0.03	0.03	0.01	0.00	0.00	0.02	0.07	0.00	0.89
Panama Central	Cucaracha	19.527	100	5	4.993	0.26	0.00	0.00	0.00	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.87
Panama Central	Cucaracha	19.528	97	5	4.825	0.74	0.00	0.00	0.00	0.26	0.01	0.01	0.00	0.00	0.00	0.00	0.62	0.00	0.37

[1] Abbreviations: N = number of individuals (pollen/spore grains) counted per sample; S = number of species; S(80) = rarefied number of species at a cutoff of 80 grains; AZ = Gondwana-Amazonian; NAN = Gondwana-northern Andean; SAN = Gondwana-southern Andean; LA = Laurasian; U = Unassigned; TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest; SV = savanna; FW = freshwater marsh community; MG = mangrove swamps; MR = shallow water marine community; UK = unknown.

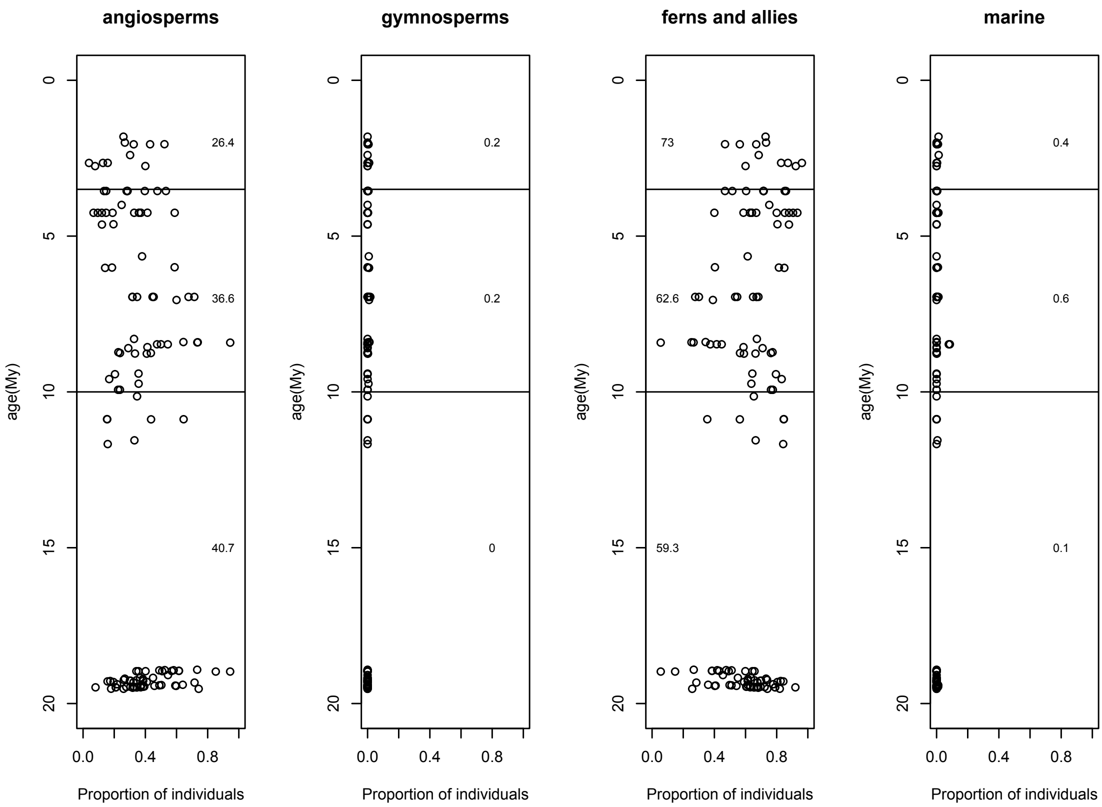

FIGURE 3. Proportion of the abundance of individuals per sample of the main groups of palynomorphs found in this study, including angiosperms, gymnosperms, fern spores and allies, and marine palynomorphs. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side.

= 1); Gondwana-northern Andean, 3.8% (SD = 4.3); Gondwana-southern Andean, 1.5% (SD = 2.4); and Laurasian, 4.2% (SD = 3.6) (Fig. 5, Table 5). However, 63% (SD = 11) of species are still unassigned to families because either the family does not have a distinct biogeographic origin (23 taxa) or the natural affinity of the species is still unknown (315 taxa). Does this proportion change when time slots are analyzed independently? Amazonian taxa are significantly more abundant prior to 3.5 Ma (> 3.5 Ma: 27.6%; < 3.5 Ma: 18.7%; $P = 0.001$, $df = 17$), Laurasian taxa do not change (> 3.5 Ma: 4.1%; < 3.5 Ma: 5.7%; $P = 0.2$, $df = 11$), and northern Andean taxa are significantly more abundant in the last 3.5 My (> 3.5 Ma: 3.6%; < 3.5 Ma: 6.4%; $P = 0.01$, $df = 14$). Amazonian taxa are more abundant > 10 Ma compared to the 10–3.5 Ma interval (19.5–10 Ma: 30.7%; 10–3.5 Ma: 24.2%; $P = 0.001$, $df = 102$), while Laurasian taxa (19.5–10 Ma: 2.9%; 10–3.5 Ma: 5.5%; $P = 0.001$, $df = 110$) and northern Andean taxa (10–3.5 Ma: 6%; 19.5–10 Ma: 1.4%; $P = 0.01$, $df = 86$) show the opposite pattern (Fig. 5).

BIOMES

Tropical rainforest (TRFO) and premontane rainforest (PMF) dominate the fossil assemblages, constituting ca. 42% of the assemblage over the entire time studied (Fig. 6, Table 5): TRFO = 20.7% (SD = 11.5), PMF = 19.1% (SD = 11). Lower montane to montane moist/wet forest (MF)

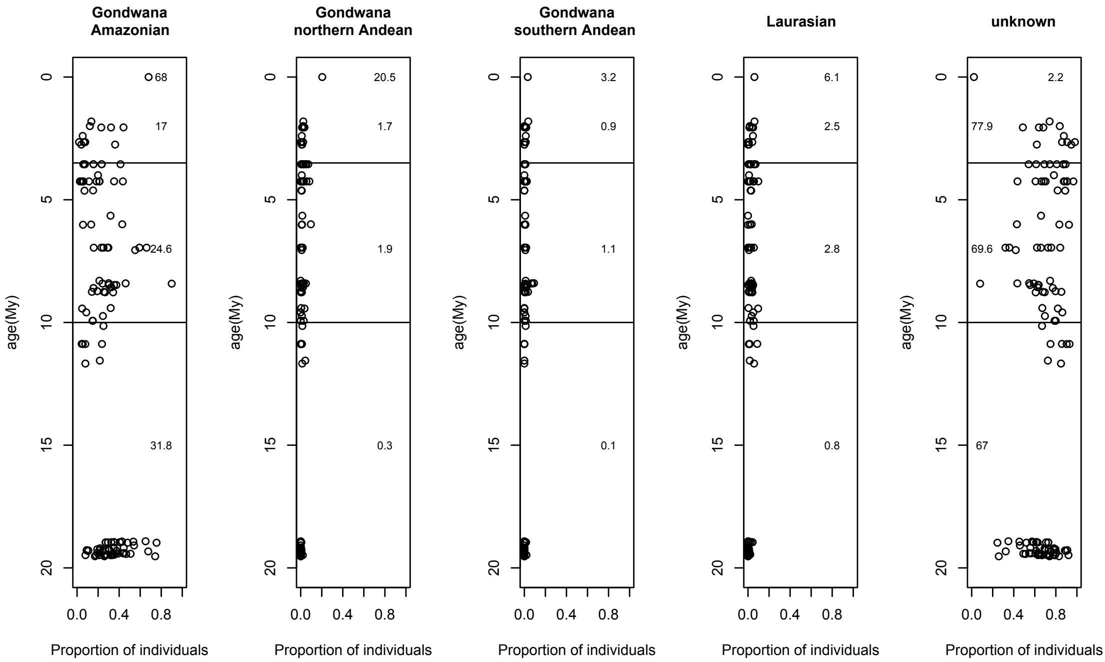

FIGURE 4. Proportion of abundance of individuals per sample that belongs to a given biogeographic affinity. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side (except for "unknown" mean abundance, given on the left-hand side).

is also important, representing 14.8% (SD = 10.1). Dry biomes represent a very small fraction of the assemblage, and they do not increase significantly over time: tropical dry forest (TDFO) = 2.0% (SD = 3.8), savanna (SV) = 0.4% (SD = 1.1). Freshwater marshes (FW) are present over the entire sequence (FW = 3.4%, SD = 6.6), as are an abundant and constant presence of both mangrove swamps (MG = 8.5%, SD = 13.1) and shallow water marine communities (MR), recognized by the presence of dinoflagellates/foram lining (MR = 0.3%, SD = 1.3) (Fig. 6). Mangroves increased significantly in the last 10 My (> 10 Ma: 4.3%; < 10 Ma: 12.3%; $P = 0.001$, $df = 104$). A large proportion of the taxa remain either unknown as to natural affinities (265 taxa = 53%) or the taxa do not have a preferred biome (104 taxa = 21%), and they correspond to a mean of 65% of the individuals counted per sample (SD = 16.4).

When biomes are analyzed by region (eastern/central/western Panama), the pattern described above does not change substantially. TRFO and PMF do not change when the three areas in Panama are analyzed independently (Fig. 7), and they dominate the assemblage in all three regions. MF is third in dominance in all three regions, but is significantly more abundant in Bocas del Toro and central Panama in the period of 3.5–10 Ma compared to Darien (Bocas del Toro & central Panama 13.9% vs. Darien 8.8%, $P = 0.001$, $df = 10$) (Fig. 7). TDFO and SV are also of very low proportion in all three areas and do not change significantly over time (Fig. 7).

DIVERSITY

There is a significant increase in diversity (rarefied to 80 grains), from an average of 14.5 species per sample in the 10–19.5 Ma interval to 21.2 in the 10–3.5 Ma interval ($P = 0.01$, $df = 110$) (Fig. 8,

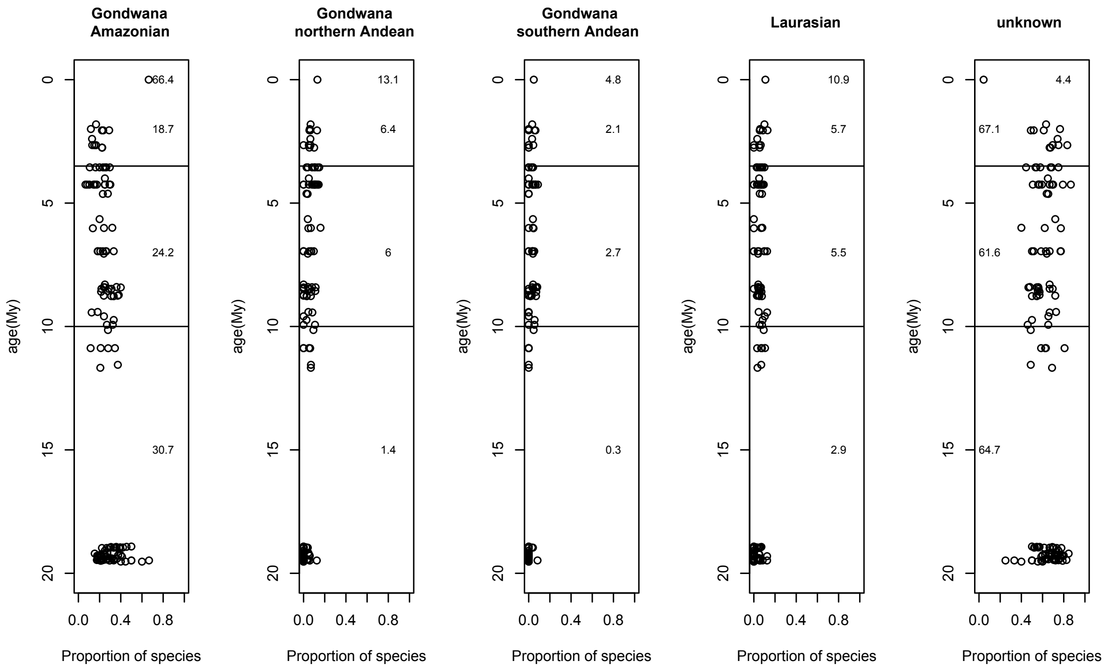

FIGURE 5. Proportion of abundance of species per sample that belongs to a given biogeographic affinity. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side (except for "unknown" mean abundance, given on the left-hand side).

Table 5). The diversity does not change from 10–3.5 Ma to the < 3.5 Ma interval (< 3.5 = 20.6, $P = 0.7$, $df = 13.1$). The species accumulation curve for each of the three time intervals (Fig. 9) shows a similar pattern, with an initial high slope of species accumulation followed by a lower slope. The 10–19.5 and 3.5–10 Ma intervals have a longer time series than the < 3.5 Ma interval, and both show an increase in the slope again, after a long hiatus of species recovery (6 My in the 10–19.5 Ma interval, and ca. 1 My in the 3.5–10 Ma interval; Fig. 9).

PLANT MACROFOSSILS

Neogene macrofossils from Panama, including wood, leaves, and fruits, were first described by Berry in 1918 and 1921. These fossils were collected during the initial excavations of the Panama Canal but since then, little attention has been given to their floristic affinities. We reexamined Berry's original specimens housed at the National Museum of Natural History (Washington, DC) and present here a revised list of macrofossil taxa from the floras of the Neogene of Panama (Table 6). From these taxa, only leaves, wood, and fruits of Arecaceae and Fabaceae of the Culebra and Gatun formations are accepted. These families were also recognized from pollen by Graham (1988b, 1991a, 1991c). The remaining fossil leaves described by Berry (1918) are poorly preserved and lack distinctive characters for their familial and generic placement. Despite the questionable affinity of the majority of the fossil leaves described by Berry, the physiognomy of these leaves and those in new collections made by the authors, i.e., entire-margined and notophyll to mesophyll in size, suggests warm and probably wet conditions during the Miocene and Pliocene of Panama.

New exposures of the early Middle Miocene Cucaracha Formation (ca. 17–19.5 Ma) from the

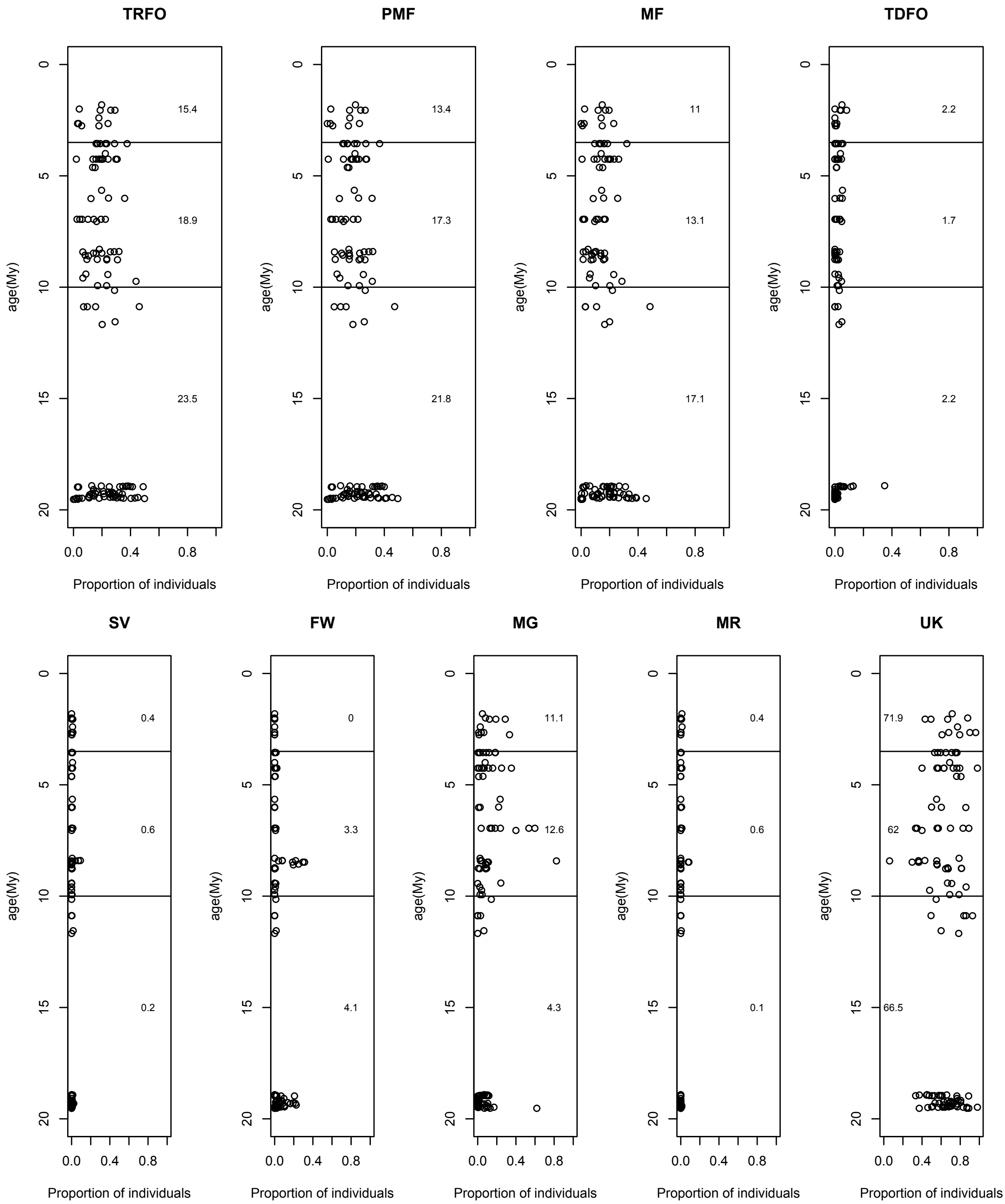

FIGURE 6. Proportion of abundance of individuals per sample that belongs to a particular biome. TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest; SV = savanna; FW = freshwater marsh community; MG = mangrove swamps; MR = shallow water marine community; UK = unassigned. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side (except for "unassigned" mean abundance, given on the left-hand side).

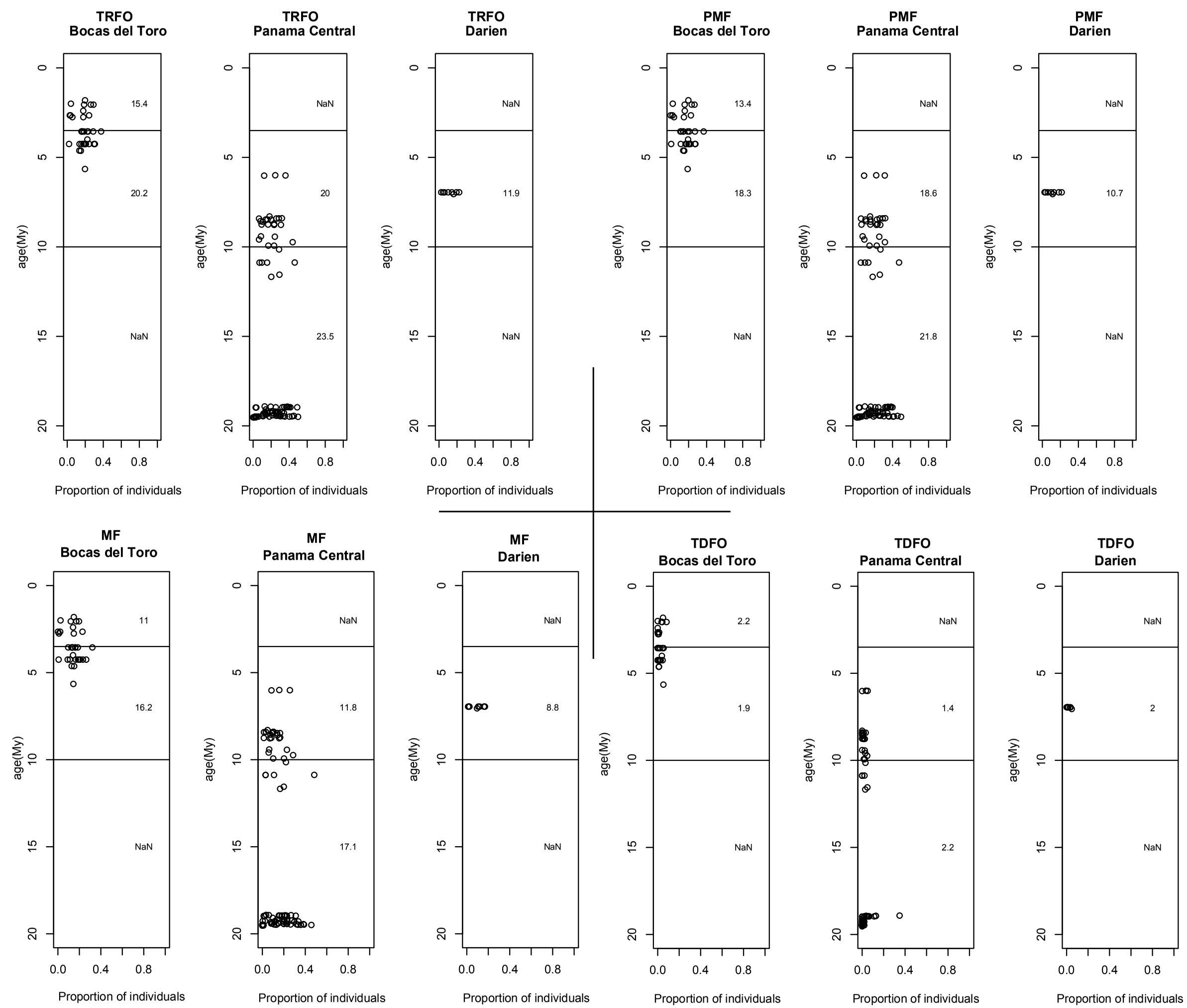

FIGURE 7. Proportion of abundance of individuals per sample that belongs to a given biome, organized by region (Bocas del Toro = western Panama; Darien = eastern Panama). TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest.

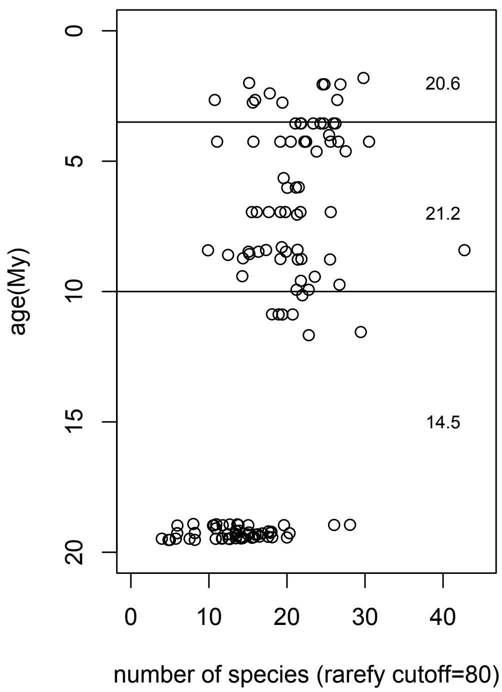

FIGURE 8. Rarefied diversity at a counting level of 80 grains per sample. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean diversity per sample is given on the right-hand side.

Panama Canal have yielded a rich deposit of well-preserved permineralized fruits and seeds (Herrera et al., 2012a; work in progress). These fossils provide additional characters of systematic significance that can facilitate accurate identification to the familial and generic levels in Panamanian macrofloras. Families and genera recognized from this carpoflora include Anacardiaceae (*Spondias* L., *Pentoperculum* Manchester), Annonaceae, Arecaceae, Cannabaceae, Chrysobalanaceae (cf. *Parinari* Aubl.), Euphorbiaceae, Fabaceae, Humiriaceae (*Sacoglottis* Mart.; Herrera et al., 2010), Icacinaceae (Phytocreneae tribe), Juglandaceae (*Oreomunnea* Oerst.), Lauraceae, Menispermaceae, Myristicaceae, Passifloraceae, and Vitaceae (*Cissus* L.). Some of these genera, e.g., *Spondias*, *Parinari*, *Sacoglottis*, and *Cissus*, are recognized for the first time in the Miocene of Panama. New collections of fruits and seeds from the Late Miocene layers of the Gatun Formation include the earliest record of *Vantanea cipaconensis* (Berry) Herrera (Humiriaceae) in Central America, and unidentified specimens of Anacardiaceae and Arecaceae.

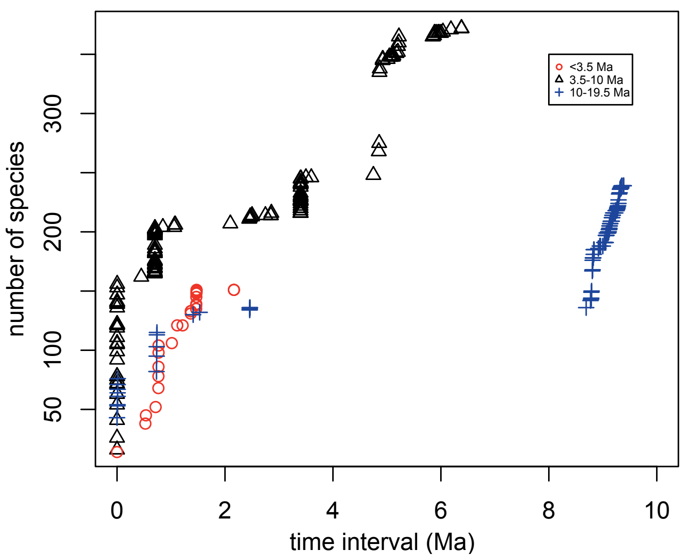

FIGURE 9. Species accumulation curve using the collector's method. There is a curve for each segment (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma). The regions of the curves with high slopes are probably due to a sampling artifact, as they are preceded by a sampling hiatus.

TABLE 6. Revised list of plant taxa of Panamanian Neogene floras described by Berry (1918, 1921*).

Taxon	Familial assignment by Berry (1918, 1921)	Current view of the familial/ generic assignment	Formation	Fossil type and comments
Palmoxylon palmacites (Sprengel) Stenzel	Arecaceae	OK	Cucaracha	stem
Iriartites vaughani Berry*	Arecaceae	family provisionally accepted	Gatun	fruit has abundant fibers as seen in modern palms; however, the specimen requires further study
Ficus culebrensis Berry	Moraceae	rejected	Culebra	fossil leaf lacks any distinctive characters
Guatteria culebrensis Berry	Annonaceae	rejected	Culebra, Caimito, and Gatun	leaves; poorly preserved specimens
Myristicophyllum panamense Berry	Myristicaceae	rejected	Culebra	leaf; poorly preserved venation and fragmented
Taenioxylon multiradiatum Felix	Fabaceae	provisionally accepted	Bohio, Culebra, and Cucaracha	wood
Inga oligocenica Berry	Fabaceae	family provisionally accepted	Culebra	the leaf shows crowded basal venation and an asymmetrical base typical of Fabaceae leaves; however, its generic assignment is highly questionable
Cassia culebrensis Berry	Fabaceae	family and genus highly questionable	Culebra	leaf; no common Fabaceae characters present
Hiraea oligocaenica Berry	Malpighiaceae	rejected	Caimito	leaf; poorly preserved venation
Banisteria praenuntia Berry	Malpighiaceae	rejected	Culebra	leaf; poorly preserved venation
Hieronymia lehmannii Engelhardt	Euphorbiaceae	rejected	Caimito	leaf; poorly preserved venation and fragmented
Schmidelia bejucensis Berry	Sapindaceae	rejected	Caimito and Culebra	leaves are entire, pinnate, and eucamptodromous; we do not see any diagnostic characters for placement in Sapindaceae or *Schmidelia* (now Boraginaceae)
Mespilodaphne culebrensis Berry	Lauraceae	rejected	Culebra	leaf; poorly preserved venation and fragmented
Calyptranthes gatunensis Berry	Myrtaceae	family and genus highly questionable	Gatun	similar venation is seen in other families such as Moraceae and Clusiaceae
Melastomites miconioides Berry	Melastomataceae	highly questionable	Culebra	leaf; tertiary veins are not well preserved; it is difficult to differentiate it from leaves in Lauraceae with similar acrodromous venation
Rondeletia goldmanii Berry	Rubiaceae	rejected	Gatun	leaf lacks any distinctive characters
Rubiacites ixoreoides Berry	Rubiaceae	rejected	Gatun	fruit; the specimen shows evidence of germination valves unlike any Rubiaceae fruits

CARBON ISOTOPES

Percentages of total nitrogen (%TN) and total organic carbon (%TOC) display different trends for the marine Culebra Formation and the terrestrial Cucaracha Formation (Fig. 10, Table 7). The %TN varies between 0.09 and 0.13 for the Culebra Formation, whereas %TN ranges between 0.02 and 0.04 for the terrestrial Cucaracha Formation. Similarly, the marine Culebra Formation displays higher TOC percentages than the Cu-

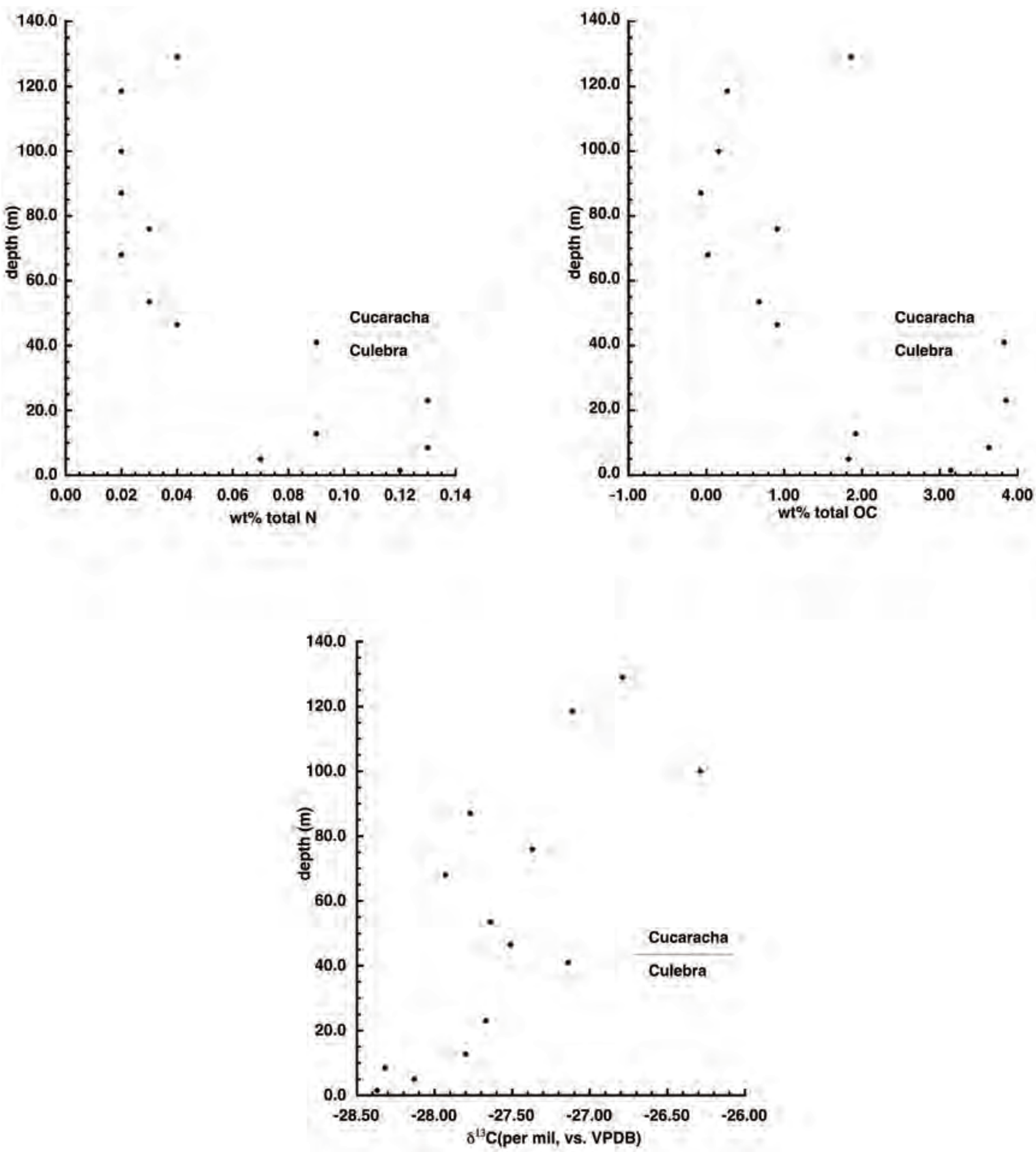

FIGURE 10. Total nitrogen, total organic carbon, and stable carbon isotope values for selected samples from the Cucaracha and Culebra formations. VPDB = Vienna Pee Dee Belemnite.

TABLE 7. Total nitrogen, total carbon (inorganic and organic fractions), and carbon isotope values for 14 selected samples from the Culebra and Cucaracha formations.

	Depth (m)	Sample ID	wt% total N	wt% total C	C/N	wt% total inorganic C	wt% total organic C	δ^{13}C (permil, vs. VPDB)
Culebra	1.5	CC010046	0.12	3.29	26.17	0.15	3.14	–28.37
	5.0	CC010048	0.07	2.24	26.14	0.41	1.83	–28.13
	8.5	CC010062	0.13	3.76	27.92	0.13	3.63	–28.32
	12.8	CC010052	0.09	2.39	21.33	0.47	1.92	–27.80
	23.0	CC010061	0.13	4.20	29.62	0.35	3.85	–27.67
	41.0	CC010078	0.09	3.86	42.56	0.03	3.83	–27.14
Cucaracha	46.5	CC010095	0.04	1.01	22.75	0.10	0.91	–27.51
	53.5	CC010001	0.03	0.75	22.67	0.07	0.68	–27.64
	68.0	CC010104	0.02	0.20	1.00	0.18	0.02	–27.93
	76.0	CC010008	0.03	0.96	30.33	0.05	0.91	–27.37
	87.0	CC010112	0.02	0.33	0.00	0.40	0.00	—
	100.0	CC010011	0.02	0.20	8.00	0.04	0.16	–26.29
	118.5	CC010012	0.02	0.33	13.50	0.06	0.27	–27.11
	129.0	CC010016	0.04	1.90	46.50	0.04	1.86	–26.79

Abbreviation: VPDB = Vienna Pee Dee Belemnite.

caracha Formation. The %TOC ranges between 1.83 and 3.85 for the Culebra Formation and between 0.00 and 1.86 for the Culebra Formation. Carbon isotope values do not display significant differences between both formations, and values range between –26.29 and –28.37.

DISCUSSION

The Isthmus of Panama represents an excellent opportunity to understand how the vegetation of a newly formed landscape in a tropical setting evolves, because most of the landscape of Panama emerged above sea level only during the last 22 Ma. It was first solely connected to a large land mass (North America) over a long period of time, from 22 to 10 Ma. It was then connected intermittently to a second large mass (South America) from 10 to 3.5 Ma, when the isthmus became permanently connected to both South America and North America. The two connections, however, are not equally balanced. While the North American connection was to a landscape dominated by temperate biomes, the South American connection was to a landscape dominated by tropical biomes.

The new landscape of Panama was formed in a tropical latitude (Montes et al., 2012a, 2012b). But were the earlier floras of Panama dominated by North American (Laurasian) families, when the connection with South America was not fully established until 3.5 Ma ago? The results presented here indicate they were not. Throughout the entire interval studied here (19.5–1.2 Ma) and in the modern flora of Barro Colorado Island, the floras are strongly dominated by Gondwana-Amazonian families, followed by Gondwana-northern Andean, when either the biogeographic affinities of individuals (Fig. 4) or species (Fig. 5) are considered. The Early Miocene macrobotanical record from Panama (Table 2) also indicates an earlier arrival for many South American lineages (e.g., Humiriaceae, Annonaceae, Euphorbiaceae). These results imply that plants were able to cross the Central American Seaway (CAS, the deep ocean gap that occurred along the tectonic boundary between the South American plate and the Panama microplate) much earlier, at least 10 Ma before other groups, mainly mammals. These results derived from the fossil record were also suggested by Graham in his multiple studies (Graham, 1988a, 1988b, 1991c, 1992, 1999, 2010, 2011), and are also supported by a recent meta-analysis of genetic data of a number of plant clades with members on both sides of the isthmus (Cody et al., 2010) that indicate migrations across CAS much earlier than the traditionally accepted 3.5 Ma final closure of the isthmus. As Cody et al. (2010) pointed out, this could reflect a higher ability of plant disseminules to travel larger distances over water and establish founder populations successfully. These long-distance dispersal events are also interpreted from Late Eocene fruits from the Azuero Peninsula in Panama (Herrera et al., 2012b).

Other recent fossil findings by our intense paleontological exploration in the Canal area have found earlier migrations (ca. 19 Ma) of turtles (Cadena et al., 2012), of snakes (Head et al., 2012), and of crocodiles (Hastings et al., 2013) from South America into Panama across CAS. Genetic evidence also indicates earlier exchanges of bees (Roubik & Camargo, 2012), tree frogs (Pinto-Sanchez et al., 2012), salamanders (Elmer et al., 2013), freshwater *Poecilia* Bloch & Schneider fishes (Alda et al., 2013), and *Amazilia* Lesson hummingbirds (Ornelas et al., 2013). Mammals, on the other hand, do not have an active exchange until much later times, starting at 10 Ma, with an acceleration at 2.7 Ma (Webb, 1976, 2006; Woodburne, 2010). The large variety of mammals found in Panama in the 22–17 Ma interval, including horses, camels, peccaries, bear-dogs, anthracotheriums, rhinocerids, geomyoid rodents, dogs, oreodonts, and protoceratids (Whitmore & Stewart, 1965; Slaughter, 1981; MacFadden & Higgins, 2004; MacFadden, 2006a, 2006b, 2009, 2010; MacFadden et al., 2012; Rincon et al., 2012, 2013), are derived from Laurasian lineages but inhabited the newly formed landscape of Panama that was dominated by a tropical rainforest of Gondwanan origin. Occasionally the same species of mammal (e.g., the rhinoceros *Floridaceras whitei* Wood) was found both in Panama and in Texas and Florida during the Early Miocene, but in contrasting biomes: a temperate forest in North America composed of Laurasian taxa, and a tropical forest in Panama composed mostly of Gondwanan taxa. How did these species interact with the tropical or temperate forest? Were there drastic changes in diet? Or were only generalist mammals able to move into the newly developed tropical forest of Panama? These questions are still open and will require more detailed analyses to be answered.

The dominance of the Gondwanan taxa in the earlier stages of Panama, when the CAS was still active, also underscores the importance of niche conservatism (Wiens & Donoghue, 2004). It was easier for tropical plants to cross the CAS and occupy the lowland tropical Panamanian landscape than for Laurasian temperate taxa to migrate south and shift to a new low-elevation tropical biome. However, some taxa, especially those adapted to montane forests, have Laurasian affinities. Niche conservatism is very strong and has been observed worldwide in a number of biomes (e.g., Crisp et al., 2009) and in the plant fossil record of South America (Jaramillo & Cardenas, 2013).

The extensive work of Graham (1988a, 1988b, 1989, 1991c) indicated that the landscape of Panama was dominated by tropical rainforest, with an associated lower montane and montane forest related to the evolution of the different volcanic arcs that are present in the isthmus (Farris et al., 2011). Graham did not find extensive presence of dry forests or savannas in any part of the sedimentary record. This view is in contrast with the view of Retallack and Kirby (2007), who, from a study of the paleosols of the Cucaracha Formation, inferred an extensive dry habitat for the Early Miocene of Panama. Our results support Graham's view that the habitats of Panama were strongly dominated by tropical rainforest and montane/lower montane forest, with minimal expansion of dry forest or savanna (Fig. 6).

The carbon isotope record of the Culebra and Cucaracha floras (Fig. 10) also supports the absence of extensive dry conditions. The ratio of total (organic) carbon to total nitrogen (TC/TN) in sediments is used as an indicator of the relative contributions of organic matter from terrestrial versus aquatic sources. Terrestrial organic matter typically possesses TC/TN values > 20, whereas algal organic matter generally displays TC/TN values from 4 to 10 (Meyers, 1994). Physiological differences between C3 and C4 plants result in different carbon isotope signatures (Tipple & Pagani, 2007). C3 plants have a wide range of isotopic values (–20 to –35‰), whereas C4 plants have a narrower range (–10 to –14‰) (Tipple & Pagani, 2007). Thus, the isotopic composition of total organic carbon reflects the relative contribution of terrestrial C3 and C4 plants to the organic matter pool (Huang et al., 1999, 2001; Filley et al., 2001). Results from the continental Cucaracha Formation indicate a dominance of C3 plants, more common to a Neotropical forest than to a tropical grassland ecosystem. Total carbon and total nitrogen values provide further evidence of the continental (i.e., Cucaracha Formation) and mostly marine (i.e., Culebra Formation) depositional environment for these two formations. The absence of extensive C4 savannas also is supported by the carbon isotopic record of mammal enamel that indicate a dominance of C3 plants during the accumulation of the Cucaracha Formation (MacFadden & Higgins, 2004).

The geochemical model used by Retallack and Kirby (2007) to infer dry conditions, the Chemical Index of Alteration without Potash (CIA-K), uses the greater mobility of base cations relative to aluminum oxides during pedogenesis to estimate paleoprecipitation in paleosols. However, this relationship has only been established for temperate climates with a mean annual precipitation (MAP) < 1500 mm and never has been tested in tropical settings. Preliminary attempts to assess this for tropical soils under a MAP > 1500 mm have indicated that there is not a significant correlation of CIA-K with precipitation when tropical soils are included, and the CIA-K should not be applied to tropical settings (Morón et al., 2011).

How did diversity of Panamanian forests fluctuate from the Early Miocene to the present day? Has plant diversity been constantly increasing? Our results indicate that plant diversity was lower in the 10–19 Ma part of the record, and then increased over the past 10 Ma (Fig. 8). However, it is not clear if this pattern is a result of taphonomic artifact. For example, we observed that the sedimentary conditions affect the proportion of pollen grains indicative of mangrove habitats. Lithofacies of the Cucaracha Formation are mostly terrestrial, while lithofacies of the younger formations (Gatún, Chagres, and Bocas del Toro and Darién regions) are shallow marine (Coates et al., 1992, 2003, 2004, 2005; Coates & Obando, 1996; Collins & Coates, 1999; Montes et al., 2012a, 2012b; Hendy, 2013; Pimiento et al., 2013a, 2013b). The taphonomic filtering for plant diversity reconstructions is suggested by the presence of mangroves that increased significantly during the last 10 My in direct association with the sedimentary deposition (Figs. 6, 7) (> 10 Ma: 4.3%; < 10 Ma: 12.3%; $P = 0.001$, $df = 104$). This taphonomic filtering alone may increase the plant diversity in marine samples because the pollen is probably derived from a larger landscape. Therefore, the observed plant diversity in the younger formations studied here would be greater, as it has been noted for modern tropical delta and shallow marine sediments (Muller, 1959; Scheihing & Pfefferkorn, 1984). To fully understand the plant diversity changes seen from the 10–19 Ma to the < 10 Ma records, we would need terrestrial environments in the entire stratigraphic sequence to rule out a possible taphonomic bias.

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APPENDIX 1. Species abundances for extant species of the Barro Colorado Island (BCI) 50-ha plot, 2005 census. —Table A. Summary of the number of individuals and species per family. Each family is assigned to a biogeographic province following Gentry's 1982 classification. —Table B. Species documented from each family and the number of individuals of each.

A. Family summary

Family	Number of individuals (BCI 50-ha plot)	Number of species	Biogeographic province or major distributional group
Acanthaceae	2	1	Gondwana-northern Andean
Achariaceae	50	1	Laurasian
Adianthaceae	—	—	unassigned
Amaranthaceae	—	—	unassigned
Anacardiaceae	154	4	Gondwana-Amazonian
Annonaceae	609	7	Gondwana-Amazonian
Anthocerotaceae	—	—	unassigned
Apocynaceae	475	4	Gondwana-Amazonian
Aquifoliaceae	—	—	Laurasian
Araceae	—	—	Gondwana-northern Andean
Araliaceae	68	1	Gondwana-northern Andean
Arecaceae	1279	5	Gondwana-Amazonian
Asteraceae	—	—	Gondwana-northern Andean
Betulaceae	—	—	Laurasian
Bignoniaceae	316	3	Gondwana-southern Andean
Blechnaceae	—	—	unassigned
Bombacoideae	801	7	Gondwana-Amazonian
Boraginaceae	628	3	Laurasian
Bromeliaceae	—	—	Gondwana-northern Andean
Burseraceae	996	6	Gondwana-Amazonian
Byttneroideae	—	—	Gondwana-Amazonian
Cabombaceae	—	—	unassigned
Caesalpinioideae	473	4	Gondwana-Amazonian
Celastraceae	19	1	Laurasian
Chloranthaceae	—	—	Laurasian
Chrysobalanaceae	786	4	Gondwana-Amazonian
Clusiaceae	214	7	Gondwana-northern Andean
Combretaceae	69	2	Gondwana-Amazonian
Connaraceae	—	—	Gondwana-Amazonian
Cucurbitaceae	—	—	unassigned
Cyatheaceae	—	—	unassigned
Cyperaceae	—	—	unassigned
Dilleniaceae	—	—	Gondwana-Amazonian
Dioscoreaceae	—	—	unassigned
Dryopteridaceae	—	—	unassigned
Ebenaceae	17	1	Gondwana-Amazonian
Elaeocarpaceae	67	1	Gondwana-Amazonian
Ericaceae	—	—	Gondwana-northern Andean
Erythroxylaceae	15	1	Dry area Gondwanan group

Family	Number of individuals (BCI 50-ha plot)	Number of species	Biogeographic province or major distributional group
Euphorbiaceae	745	12	Gondwana-Amazonian
Fabaceae	—	—	Gondwana-Amazonian
Faboideae	691	13	Gondwana-Amazonian
Fagaceae	—	—	Laurasian
Gentianaceae	—	—	Laurasian
Grewioideae	—	—	Gondwana-Amazonian
Humiriaceae	—	—	Gondwana-Amazonian
Juglandaceae	—	—	Laurasian
Labiatae	—	—	Laurasian
Lacistemataceae	31	1	Gondwana-Amazonian
Lamiaceae	—	—	unassigned
Lauraceae	603	10	Gondwana-Amazonian
Lecythidaceae	619	1	Gondwana-Amazonian
Lentibulariaceae	—	—	unassigned
Loranthaceae	—	—	Gondwana-northern Andean
Lycopodiaceae	—	—	unassigned
Lygodiaceae	—	—	unassigned
Lythraceae	4	1	Laurasian
Malpighiaceae	7	1	Gondwana-Amazonian
Malvaceae	10	1	unassigned
Malvoideae	—	—	unassigned
Marattiaceae	—	—	unassigned
Melastomataceae	85	5	Laurasian
Meliaceae	1939	6	Gondwana-Amazonian
Mimosoideae	453	18	Gondwana-Amazonian
Monimiaceae	26	2	Gondwana-northern Andean
Moraceae	1139	16	Gondwana-Amazonian
Myristicaceae	733	3	Gondwana-Amazonian
Myrtaceae	347	7	Gondwana-southern Andean
Nyctaginaceae	103	1	Gondwana-northern Andean
Nymphaeaceae	—	—	unassigned
Ochnaceae	1	1	Gondwana-Amazonian
Olacaceae	299	2	Gondwana-Amazonian
Onagraceae	—	—	Gondwana-southern Andean
Ophioglossaceae	—	—	unassigned
Phyllanthaceae	—	—	Gondwana-Amazonian
Picramniaceae	37	1	unassigned
Piperaceae	8	1	Gondwana-northern Andean
Poaceae	—	—	unassigned
Podocarpaceae	—	—	Gondwana-southern Andean
Polygalaceae	—	—	Gondwana-Amazonian
Polygonaceae	171	3	unassigned
Polypodiaceae	—	—	unassigned
Pteridaceae	—	—	unassigned
Rhamnaceae	1	1	Laurasian

Family	Number of individuals (BCI 50-ha plot)	Number of species	Biogeographic province or major distributional group
Rhizophoraceae	97	1	Gondwana-Amazonian
Rubiaceae	3395	13	Gondwana-northern Andean
Rutaceae	215	4	unassigned
Salicaceae	373	10	Laurasian
Sapindaceae	99	6	Gondwana-Amazonian
Sapotaceae	348	5	Gondwana-Amazonian
Schizaeaceae	—	—	unassigned
Selaginellaceae	—	—	unassigned
Simaroubaceae	249	2	Gondwana-Amazonian
Solanaceae	12	1	Gondwana-southern Andean
Staphyleaceae	42	1	Laurasian
Sterculiaceae	79	3	Gondwana-Amazonian
Symplocaceae	—	—	Laurasian
Tetrameristaceae	—	—	Gondwana-Amazonian
Tiliaceae	307	4	Gondwana-Amazonian
Ulmaceae	61	2	Laurasian
Urticaceae	454	4	Gondwana-northern Andean
Verbenaceae	18	1	unassigned
Violaceae	1	1	Gondwana-Amazonian
Vochysiaceae	12	1	Gondwana-Amazonian

B. Species summary

Family	Species	Number of individuals (BCI 50-ha plot)
Acanthaceae	*Trichanthera gigantea* (Bonpl.) Nees	2
Achariaceae	*Lindackeria laurina* C. Presl	50
Euphorbiaceae	*Acalypha diversifolia* Jacq.	1
Euphorbiaceae	*Acalypha macrostachya* Jacq.	2
Anacardiaceae	*Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels	21
Anacardiaceae	*Astronium graveolens* Jacq.	37
Euphorbiaceae	*Adelia triloba* (Müll. Arg.) Hemsl.	71
Anacardiaceae	*Spondias mombin* L.	32
Euphorbiaceae	*Alchornea costaricensis* Pax & K. Hoffm.	146
Euphorbiaceae	*Alchornea latifolia* Sw.	1
Anacardiaceae	*Spondias radlkoferi* Donn. Sm.	64
Annonaceae	*Annona acuminata* Saff.	1
Euphorbiaceae	*Croton billbergianus* Müll. Arg.	50
Euphorbiaceae	*Drypetes standleyi* G. L. Webster	318
Annonaceae	*Annona spraguei* Saff.	17
Euphorbiaceae	*Hieronyma alchorneoides* Allemão	40
Annonaceae	*Desmopsis panamensis* (B. L. Rob.) Saff	11
Annonaceae	*Guatteria dumetorum* R. E. Fr.	195
Euphorbiaceae	*Hura crepitans* L.	95
Annonaceae	*Mosannona garwoodii* Chatrou & Welzenis	17
Euphorbiaceae	*Margaritaria nobilis* L. f.	2

Family	Species	Number of individuals (BCI 50-ha plot)
Euphorbiaceae	*Sapium 'broadleaf'* Jacq.	2
Arecaceae	*Attalea butyracea* (Mutis ex L. f.) Wess. Boer	34
Annonaceae	*Unonopsis pittieri* Saff.	175
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	17
Annonaceae	*Xylopia macrantha* Triana & Planch.	193
Apocynaceae	*Aspidosperma spruceanum* Benth. ex Müll. Arg.	57
Apocynaceae	*Lacmellea panamensis* (Woodson) Markgr.	55
Fabaceae:Caesalpinioideae	*Prioria copaifera* Griseb.	357
Fabaceae:Caesalpinioideae	*Schizolobium parahyba* (Vell.) S. F. Blake	6
Fabaceae:Caesalpinioideae	*Senna dariensis* (Britton & Rose) H. S. Irwin & Barneby	1
Fabaceae:Caesalpinioideae	*Tachigali versicolor* Standl. & L. O. Williams	109
Fabaceae:Mimosoideae	*Abarema macradenia* (Pittier) Barneby & J. W. Grimes	1
Fabaceae:Mimosoideae	*Acacia melanoceras* Beurl.	2
Fabaceae:Mimosoideae	*Cojoba rufescens* (Benth.) Britton & Rose	1
Apocynaceae	*Tabernaemontana arborea* Rose	362
Apocynaceae	*Thevetia ahouai* (L.) A. DC.	1
Fabaceae:Mimosoideae	*Enterolobium schomburgkii* (Benth.) Benth.	4
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	68
Arecaceae	*Astrocaryum standleyanum* L. H. Bailey	160
Fabaceae:Mimosoideae	*Inga acuminata* Benth.	55
Arecaceae	*Oenocarpus mapora* H. Karst.	767
Fabaceae:Mimosoideae	*Inga cocleensis* Pittier	2
Fabaceae:Mimosoideae	*Inga goldmanii* Pittier	32
Fabaceae:Mimosoideae	*Inga laurina* (Sw.) Willd.	8
Fabaceae:Mimosoideae	*Inga marginata* Willd.	102
Fabaceae:Mimosoideae	*Inga nobilis* Willd.	71
Fabaceae:Mimosoideae	*Inga oerstediana* Benth. ex Seem.	2
Arecaceae	*Socratea exorrhiza* (Mart.) H. Wendl.	297
Fabaceae:Mimosoideae	*Inga pezizifera* Benth.	21
Bignoniaceae	*Jacaranda copaia* (Aubl.) D. Don	221
Bignoniaceae	*Tabebuia guayacan* (Seem.) Hemsl.	31
Fabaceae:Mimosoideae	*Inga punctata* Willd.	7
Fabaceae:Mimosoideae	*Inga ruiziana* G. Don	4
Fabaceae:Mimosoideae	*Inga sapindoides* Willd.	72
Fabaceae:Mimosoideae	*Inga spectabilis* (Vahl) Willd.	12
Bignoniaceae	*Tabebuia rosea* (Bertol.) DC.	64
Bombacaceae	*Cavanillesia platanifolia* (Bonpl.) Kunth	18
Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	41
Fabaceae:Mimosoideae	*Inga thibaudiana* DC.	45
Fabaceae:Mimosoideae	*Inga umbellifera* (Vahl) Steud.	12
Bombacaceae	*Ochroma pyramidale* (Cav. ex Lam.) Urb.	8
Bombacaceae	*Pachira quinata* (Jacq.) W. S. Alverson	1
Arecaceae	*Elaeis oleifera* (Kunth) Cortés	21
Bombacaceae	*Pachira sessilis* Benth.	10
Bombacaceae	*Pseudobombax septenatum* (Jacq.) Dugand	9

Family	Species	Number of individuals (BCI 50-ha plot)
Bombacaceae	*Quararibea asterolepis* Pittier	714
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	57
Boraginaceae	*Cordia bicolor* A. DC.	323
Fabaceae:Papilionoideae	*Andira inermis* (W.Wright) Kunth ex DC.	32
Boraginaceae	*Cordia lasiocalyx* Pittier	248
Burseraceae	*Protium confusum* (Rose) Pittier	1
Fabaceae:Papilionoideae	*Dipteryx oleifera* Benth.	33
Fabaceae:Papilionoideae	*Erythrina costaricensis* Micheli	18
Fabaceae:Papilionoideae	*Lonchocarpus heptaphyllus* (Poir.) DC.	105
Burseraceae	*Protium costaricense* (Rose) Engl.	111
Burseraceae	*Protium panamense* (Rose) I. M. Johnst.	39
Fabaceae:Papilionoideae	*Myrospermum frutescens* Jacq.	4
Fabaceae:Papilionoideae	*Ormosia amazonica* Ducke	1
Fabaceae:Papilionoideae	*Ormosia coccinea* (Aubl.) Jacks.	6
Burseraceae	*Protium tenuifolium* (Engl.) Engl.	406
Fabaceae:Papilionoideae	*Ormosia macrocalyx* Ducke	4
Fabaceae:Papilionoideae	*Platymiscium pinnatum* (Jacq.) Dugand	47
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	399
Burseraceae	*Trattinnickia aspera* (Standl.) Swart	40
Celastraceae	*Maytenus schippii* Lundell	19
Chrysobalanaceae	*Hirtella americana* L.	3
Chrysobalanaceae	*Hirtella triandra* Sw.	765
Chrysobalanaceae	*Licania hypoleuca* Benth.	11
Chrysobalanaceae	*Licania platypus* (Hemsl.) Fritsch	7
Fabaceae:Papilionoideae	*Platypodium elegans* Vogel	36
Fabaceae:Papilionoideae	*Pterocarpus rohrii* Vahl	53
Clusiaceae	*Calophyllum longifolium* Willd.	44
Clusiaceae	*Chrysochlamys eclipes* L. O. Williams	3
Clusiaceae	*Garcinia intermedia* (Pittier) Hammel	127
Clusiaceae	*Garcinia madruno* (Kunth) Hammel	9
Fabaceae:Papilionoideae	*Swartzia simplex* var. *grandiflora* (Raddi) R. S. Cowan	219
Fabaceae:Papilionoideae	*Swartzia simplex* var. *ochnacea* (DC.) R. S. Cowan	133
Clusiaceae	*Marila laxiflora* Rusby	9
Clusiaceae	*Symphonia globulifera* L. f.	20
Clusiaceae	*Vismia baccifera* (L.) Triana & Planch.	2
Combretaceae	*Terminalia amazonia* (J. F. Gmel.) Exell	27
Combretaceae	*Terminalia oblonga* (Ruiz & Pav.) Steud.	42
Ebenaceae	*Diospyros artanthifolia* Mart.	17
Lacistemataceae	*Lacistema aggregatum* (P. J. Bergius) Rusby	31
Lauraceae	*Beilschmiedia pendula* (Sw.) Hemsl.	270
Lauraceae	*Cinnamomum triplinerve* (Ruiz & Pav.) Kosterm.	14
Lauraceae	*Nectandra 'fuzzy'* Rol. ex Rottb.	1
Lauraceae	*Nectandra cissiflora* Mez & Rusby	31
Lauraceae	*Nectandra lineata* (Kunth) Rohwer	10
Lauraceae	*Nectandra purpurea* (Ruiz & Pav.) Mez	5

Family	Species	Number of individuals (BCI 50-ha plot)
Lauraceae	*Ocotea cernua* (Nees) Mez	26
Lauraceae	*Ocotea oblonga* (Meisn.) Mez	42
Lauraceae	*Ocotea puberula* (Rich.) Nees	21
Lauraceae	*Ocotea whitei* (Rich.) Nees	183
Lecythidaceae	*Gustavia superba* (Kunth) O. Berg	619
Lythraceae	*Lafoensia punicifolia* DC.	4
Malpighiaceae	*Spachea membranacea* Cuatrec.	7
Malvaceae	*Hampea appendiculata* (Donn. Sm.) Standl.	10
Melastomataceae	*Miconia affinis* DC.	6
Melastomataceae	*Miconia argentea* (Sw.) DC.	71
Melastomataceae	*Miconia elata* (Sw.) DC.	1
Melastomataceae	*Miconia hondurensis* Donn. Sm.	6
Melastomataceae	*Miconia prasina* (Sw.) DC.	1
Meliaceae	*Cedrela odorata* L.	2
Meliaceae	*Guarea 'fuzzy'* F. Allam. ex L.	49
Meliaceae	*Guarea grandifolia* DC.	10
Meliaceae	*Guarea guidonia* (L.) Sleumer	359
Meliaceae	*Trichilia pallida* Sw.	90
Meliaceae	*Trichilia tuberculata* (Triana & Planch.) C. DC.	1429
Monimiaceae	*Siparuna guianensis* Aubl.	10
Monimiaceae	*Siparuna pauciflora* (Beurl.) A. DC.	16
Moraceae	*Brosimum alicastrum* Sw.	205
Moraceae	*Ficus costaricana* (Liebm.) Miq.	6
Moraceae	*Ficus insipida* Willd.	1
Moraceae	*Ficus maxima* Mill.	4
Moraceae	*Ficus obtusifolia* Kunth	6
Moraceae	*Ficus popenoei* Standl.	2
Moraceae	*Ficus tonduzii* Standl.	14
Moraceae	*Ficus trigonata* L.	4
Moraceae	*Ficus yoponensis* Desv.	5
Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	1
Moraceae	*Maquira guianensis* Aubl.	153
Moraceae	*Perebea xanthochyma* H. Karst.	24
Moraceae	*Poulsenia armata* (Miq.) Standl.	630
Moraceae	*Sorocea affinis* Kunth	19
Moraceae	*Trophis caucana* (Pittier) C. C. Berg	45
Moraceae	*Trophis racemosa* (L.) Urb.	20
Myristicaceae	*Virola multiflora* (Standl.) A. C. Sm.	26
Myristicaceae	*Virola sebifera* Aubl.	559
Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	148
Myrtaceae	*Chamguava schippii* (Standl.) L. R. Landrum	6
Myrtaceae	*Eugenia coloradoensis* Standl.	81
Myrtaceae	*Eugenia galalonensis* (C. Wright ex Griseb.) Krug & Urb.	17
Myrtaceae	*Eugenia nesiotica* Standl.	51
Myrtaceae	*Eugenia oerstediana* O. Berg	187

Family	Species	Number of individuals (BCI 50-ha plot)
Myrtaceae	*Myrcia gatunensis* Standl.	1
Myrtaceae	*Psidium friedrichsthalianum* (O. Berg) Nied.	4
Nyctaginaceae	*Guapira standleyana* Woodson	103
Ochnaceae	*Cespedesia spathulata* (Ruiz & Pav.) Planch.	1
Olacaceae	*Heisteria acuminata* (Bonpl.) Engl.	7
Olacaceae	*Heisteria concinna* Standl.	292
Picramniaceae	*Picramnia latifolia* Tul.	37
Piperaceae	*Piper reticulatum* L.	8
Polygonaceae	*Coccoloba coronata* Jacq.	21
Polygonaceae	*Coccoloba manzinellensis* Beurl.	12
Polygonaceae	*Triplaris cumingiana* Fisch. & C. A. Mey.	138
Rhamnaceae	*Colubrina glandulosa* Perkins	1
Rhizophoraceae	*Cassipourea elliptica* (Sw.) Poir.	97
Rubiaceae	*Alseis blackiana* Hemsl.	1046
Rubiaceae	*Amaioua corymbosa* Kunth	2
Rubiaceae	*Chimarrhis parviflora* Standl.	2
Rubiaceae	*Coussarea curvigemmia* Dwyer	63
Rubiaceae	*Coutarea hexandra* (Jacq.) K. Schum.	1
Rubiaceae	*Faramea occidentalis* (L.) A. Rich.	1909
Rubiaceae	*Genipa americana* L.	21
Rubiaceae	*Guettarda foliacea* Standl.	63
Rubiaceae	*Macrocnemum roseum* (Ruiz & Pav.) Wedd.	24
Rubiaceae	*Posoqueria latifolia* (Rudge) Schult.	12
Rubiaceae	*Psychotria grandis* Sw.	2
Rubiaceae	*Randia armata* (Sw.) DC.	245
Rubiaceae	*Tocoyena pittieri* (Standl.) Standl.	5
Rutaceae	*Zanthoxylum acuminatum* (Sw.) Sw.	29
Rutaceae	*Zanthoxylum ekmanii* (Urb.) Alain	127
Rutaceae	*Zanthoxylum panamense* P. Wilson	58
Rutaceae	*Zanthoxylum setulosum* P. Wilson	1
Salicaceae	*Casearia aculeata* Jacq.	14
Salicaceae	*Casearia arborea* (Rich.) Urb.	75
Salicaceae	*Casearia commersoniana* Cambess.	3
Salicaceae	*Casearia guianensis* (Aubl.) Urb.	1
Salicaceae	*Casearia sylvestris* Sw.	44
Salicaceae	*Hasseltia floribunda* Kunth	182
Salicaceae	*Laetia procera* (Poepp.) Eichler	15
Salicaceae	*Laetia thamnia* L.	26
Salicaceae	*Tetrathylacium johansenii* Standl.	6
Salicaceae	*Zuelania guidonia* (Sw.) Britton & Millsp.	7
Sapindaceae	*Allophylus psilospermus* Radlk.	28
Sapindaceae	*Cupania latifolia* Kunth	12
Sapindaceae	*Cupania rufescens* Triana & Planch.	2
Sapindaceae	*Cupania seemannii* Triana & Planch.	53
Sapindaceae	*Talisia nervosa* Radlk.	1

Family	Species	Number of individuals (BCI 50-ha plot)
Sapindaceae	*Talisia princeps* Oliv.	3
Sapotaceae	*Chrysophyllum argenteum* Jacq.	75
Sapotaceae	*Chrysophyllum cainito* L.	23
Sapotaceae	*Pouteria fossicola* Cronquist	2
Sapotaceae	*Pouteria reticulata* (Engl.) Eyma	217
Sapotaceae	*Pouteria stipitata* Cronquist	31
Simaroubaceae	*Quassia amara* L.	5
Simaroubaceae	*Simarouba amara* Aubl.	244
Solanaceae	*Solanum hayesii* Fernald	12
Staphyleaceae	*Turpinia occidentalis* (Sw.) G. Don	42
Sterculiaceae	*Guazuma ulmifolia* Lam.	38
Sterculiaceae	*Sterculia apetala* (Jacq.) H. Karst.	30
Sterculiaceae	*Theobroma cacao* L.	11
Tiliaceae	*Apeiba membranacea* Spruce ex Benth.	205
Tiliaceae	*Apeiba tibourbou* Aubl.	16
Tiliaceae	*Luehea seemannii* Triana & Planch.	85
Tiliaceae	*Trichospermum galeottii* (Turcz.) Kosterm.	1
Ulmaceae	*Celtis schippii* Standl.	42
Ulmaceae	*Trema micrantha* (L.) Blume	19
Urticaceae	*Cecropia insignis* Liebm.	342
Urticaceae	*Cecropia longipes* Pittier	3
Urticaceae	*Cecropia obtusifolia* Bertol.	91
Urticaceae	*Pourouma bicolor* Mart.	18
Verbenaceae	*Aegiphila panamensis* Moldenke	18
Violaceae	*Rinorea sylvatica* (Seem.) Kuntze	1
Vochysiaceae	*Vochysia ferruginea* Mart.	12

APPENDIX 2. Description and illustration of pollen and spore morphotypes.

Morphologic characteristics of the pollen grains were compared with illustrations and descriptions from literature and summarized in Jaramillo and Rueda (2013). Major nomenclatural usages follow those in Jaramillo and Dilcher (2001). Informal species are those between quotation marks; the most important taxa are illustrated in Plates 1 to 11 and brief descriptions are given below. The taxa encountered and their counts are listed in the Supplementary Appendix (available here: <http://dx.doi.org/10.5479/data.stri.jaramillo-2014.>, as well as in Table 4, where possible natural affinities are provided. We have decided to use a nomenclature using fossil names for each taxon, even when the natural affinities are known. This approach is different from that used by Graham in all his publications, where a natural affinity is given as the name of the taxon. We feel that using a fossil taxa naming approach would be more useful when comparing to fossil floras elsewhere in the tropics, where fossil taxa have mostly been used. Also, using natural affinities as the name of a fossil taxon can bring nomenclatural problems in the future because the affinity of a given fossil species can change when further research is done, especially when using SEM and

TEM. It would be more practical to have a morphologically based fossil taxon name with a given natural affinity; that is, a hypothesis of relationship can change over time, but the name of the morphotaxon will not.

We treated 414 morphological fossil species in this appendix; we describe 241 morphologically, which correspond to informal taxa indicated by quotations marks. The other 173 are published and illustrated taxa but not described and correspond to published species. Grain descriptions follow Graham's style and organization: fern spores (trilete and monolete), followed by gymnosperms and angiosperms (monocots and eudicots). Descriptions maintain the Graham format: for pollen grains, form, ambitus, group, apertures, sculpture, exine, and size; for spores, ambitus, group, aperture, sculpture, sporodermis, and size, followed by a tentative modern botanical affinity. The illustrations (Plates 1–11, Figs. 1–399) have a graphic scale that corresponds to 1 cm = 10 µm. Exceptions are indicated directly on the corresponding picture with a special scale bar. Additionally, the slide sample number, microscope coordinate (England Finder), and geological formation are given for each illustration in the figure legend. Most of the microphotographs were taken under oil immersion (×100) using a Pixera (San Jose, California, U.S.A.) System Camera coupled to an Olympus (Tokyo, Japan) BH-2 biological scope. The palynological terminology of the original Graham descriptions has been maintained when possible, and complemented with terms proposed by Punt et al. (2007).

Abbreviations used in the text are as follows: SL = slide sample, EF = England Finder, Amb = ambitus (pollen polar and spore distal face outlines), aff. = similar to, cf. = confer with, Fm. = formation, age = expressed as million years ago (Ma), Ref: = bibliographical reference, ID = identification number that corresponds to the species ID in the public electronic database of Jaramillo and Rueda at <http://biogeodb.stri.si.edu/jaramillo/palynomorph> (Jaramillo & Rueda, 2013). Source of the authorities for extant taxa is Tropicos® (2013).

FERNS: TRILETE SPORES

Anthocerotaceae (Fig. 1). Amb circular; trilete, laesurae inconspicuous, short, thin; finely scabrate, scabrae < 1 µm long, spores displaying ca. 7 depressions fenestrae-like, fenestrae 9–10 µm in diameter; wall ca. 2.5 µm thick; 31–33 µm. Affinity: Pteridophyta, Anthocerotaceae.

Apiculatasporites obscurus. Ref: ID 10011 (Jaramillo & Rueda, 2013); fig. 7 (Graham, 1991a). Affinity: Pteridophyta, Selaginellaceae, *Selaginella* P. Beauv.

Baculatisporites "*circularis*" (Fig. 2). Amb circular; trilete, laesurae inconspicuous; baculate, baculae slightly dispersed, irregular, sometimes resembling verrucae and short echinae; wall 1 µm thick; ca. 48 µm. Affinity: Pteridophyta.

Baculatisporites "*triangularis*" (Fig. 3). Amb triangular-obtuse-concave; trilete, laesurae irregular, very thin, inconspicuous, extending to spore margin; baculate, baculae variable, ca. 1.5 µm long at proximal surface to < 1 µm at distal surface; wall < 1 µm thick; 30 µm. Affinity: Pteridophyta.

Baculatriletes "*palmiformis*" (Fig. 4). Amb circular to triangular-obtuse-convex; trilete, laesurae wide, opened, extending to spore margin; baculate, baculae conspicuous; wall variable, 3 µm thick at proximal surface and 4 µm thick at distal surface; 51 µm. Affinity: Pteridophyta.

Cicatricosisporites "*bocatorensis*" (Fig. 5). Amb triangular obtuse-convex; trilete; laesurae indistinct; cicatricose; wall 3 µm thick; 46 µm. Ref: figs. 14, 15 (Graham, 1988b). Affinity: Pteridophyta, Pteridaceae, *Ceratopteris* Brongn.

Cingulatisporites psilatus (Fig. 6). Amb triangular-obtuse-concave; trilete, laesurae extending to spore margin, thin, straight; laevigate; wall thin, < 1 µm thick, conspicuous flange present, smooth, ca. 3.5 µm thick, undulating; 26 µm. Ref: ID 10130 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Cingulatisporites "*pteriformis*" (Fig. 7). Amb triangular-obtuse-convex; trilete, laesurae extending 3/4 of the distance to spore margin, marginate, margo thick, conspicuous flange present, smooth, 7 µm wide at lateral margins and 5 µm wide at apical margins; laevigate to slightly reticulate; wall 3.5 µm thick at distal surface; 33 µm. Affinity: Pteridophyta, Pteridaceae, *Pteris* L.

Cingulatisporites "*rugulatus*." Ref: ID 10443 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Cingulatisporites "*verrutiformis*" (Fig. 8). Amb triangular-obtuse-convex; trilete, laesurae straight, extending to spore margin, spore surrounded by a smooth flange, ca. 5 µm thick; verrucate, verrucae uniform, dense; wall 1 µm thick; 38 µm. Affinity: Pteridophyta.

Concavissimisporites fossulatus (Fig. 9). Amb triangular-obtuse-concave; trilete, laesurae as wide as proximal face; reticulate, brochi variable, resembling foveolate pattern; wall thin, ca. 1 µm thick, surrounded by an irregular smooth flange; 33 µm. Ref: ID 10322 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Concavissimisporites "*kyrtomatus*" (Fig. 10). Amb triangular-obtuse-concave; trilete, laesurae marginate, extending to spore margin; laevigate at lateral margins and slightly verrucate at apical margins, displaying the kyrtomate condition; wall ca. 2 µm thick; 19 µm. Affinity: Pteridophyta.

Crassoretitriletes vanraadshoovenii (Fig. 11). Amb circular; trilete, laesurae extending 2/3 length of spore, straight; foveolate-reticulate, foveolae resembling lumina pattern, variable in shape and size, muri ca. 5 µm wide; wall 5 µm thick, irregular; ca. 74 µm. Ref: ID 10044 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Lygodiaceae, *Lygodium microphyllum* (Cav.) R. Br.

Cyatheaceae (*Alsophila*). Ref: figs. 8–11 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae, *Alsophila* R. Br.

Cyatheaceae (*Cnemidaria*). Ref: figs. 12, 13 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae, *Cnemidaria* C. Presl.

Cyatheaceae (Type 1). Ref: fig. 14 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae Type 1.

Cyatheaceae (Type 2). Ref: figs. 15–17 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae Type 2.

Cyatheacidites annulatus (Fig. 12). Amb circular; trilete; laesurae undulating, extending to spore margin, marginate, margo thin, subtle, laesurae having conspicuous torus; laevigate; wall 1–1.2 µm thick, surrounded by a smooth flange ca. 7 µm thick; 53 µm. Ref: ID 10065 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Dicksoniaceae, *Lophosoria* C. Presl.

Cyathidites "*typicus*." Ref: figs. 7–9 (Graham, 1988a). Affinity: Pteridophyta, Cyatheceae, *Cyathea* Sm.

Distaverrusporites "*usmensis*" (Fig. 13). Amb circular to slightly triangular-obtuse-convex; trilete, laesurae extending to spore margin, straight, ca. 3 µm thick; verrucate, verrucae uniform, dense, generally 3–5 µm in diameter; wall 1 µm thick; 40 µm. Ref: ID 10508 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Echinatisporis muelleri. Ref: ID 10043 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Echitriletes "*minispinosus*" (Figs. 14, 15). Amb circular to triangular-obtuse-convex; trilete, laesurae irregular, extending to spore margin; echinate, echinae < 1 µm long, uniform; wall < 1 µm thick; ca. 14 µm. Affinity: Pteridophyta.

Echitriletes "*minutuechinulatus*" (Fig. 16). Amb triangular-obtuse-straight; trilete, laesurae extending to spore margin; echinate, echinae variable, 0.5–1.9 × 0.5–1 µm, conical to cylindrical, pointed-blunted ends, densely distributed; wall 0.8 µm thick; 47 µm. Affinity: Pteridophyta.

Echitriletes "*selaginelloides*" type "*bacularis*" (Figs. 17, 18). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, thin, marginate, margo thin, inconspicuous; echinate, echinae irregular, having projections resembling baculae and clavae types, 2–5 µm long; wall 1 µm thick; 16.5 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella.*

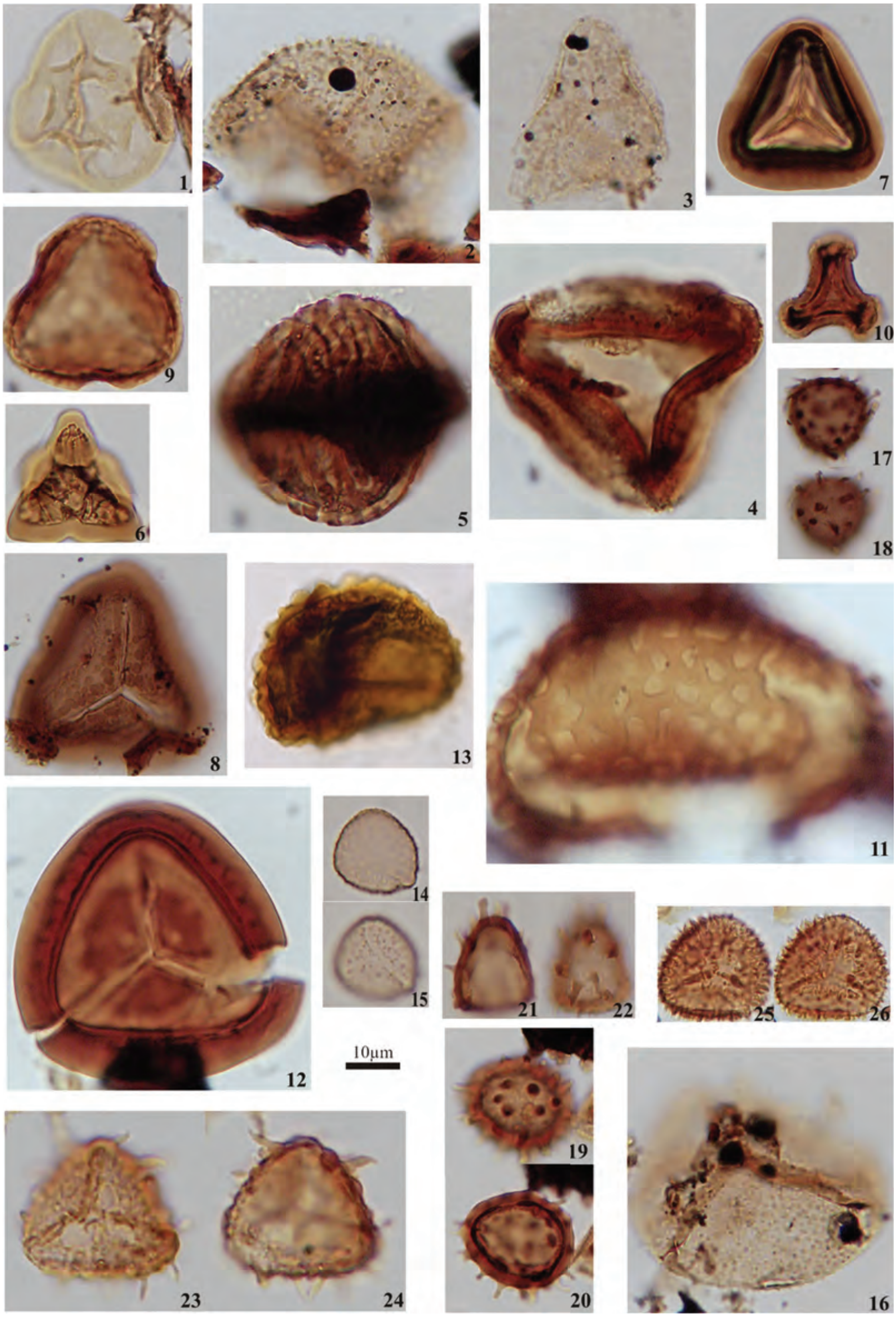
Echitriletes "*selaginelloides*" type "*bifurcatus*" (Figs. 19, 20). Amb circular; trilete, laesurae inconspicuous; baculate-echinulate, sculptural elements variable in shape and size, sometimes bifurcated; wall 2.5 µm (excluding ornamentation); ca. 23 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

Echitriletes "*selaginelloides*" type "*echiplanatus*" (Figs. 21, 22). Amb triangular-acute-convex; trilete, laesurae inconspicuous, masked by ornamentation; echinate, echinae variable in size and shape; 18 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

Echitriletes "*selaginelloides*" type "*muelleri*" (Figs. 23, 24). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, marginate, margo thin, irregular; echinate, echinae variable, 1–5 µm long, dense on proximal surface, apparently verrucate on distal surface; wall 1 µm thick; ca. 29 µm (excluding sculptural elements). Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

Echitriletes "*selaginelloides*" type "*regularis*" (Figs. 25, 26). Amb triangular-obtuse-convex; trilete, laesurae thin, inconspicuous, marginate; echinate, echinae 2 × 2 µm, conical, acute ends; wall 1.5 µm thick; 21 µm. Affinity: Selaginellaceae, *Selaginella*.

PLATE 1. Figures 1–26.
1. Anthocerotaceae SL G27/1, EF F18, Shark Hole Point Fm. –4.6 Ma.
2. *Baculatisporites* "circularis" SL 6, EF K-20/2, Chucunaque Fm. –6.95 Ma.
3. *Baculatisporites* "triangularis" SL 174, EF H-35/2, Escudo Veraguas Fm. –2.05 Ma.
4. *Baculatriletes* "palmiformis" SL 174, EF M-36/4, Escudo Veraguas Fm. –2.05 Ma.
5. *Cicatricosisporites* "bocatorensis" SL 196, EF G-28, Shark Hole Point Fm. –4.6 Ma.
6. *Cingulatisporites psilatus* SL 6, EF Y15-2, Gatun Fm. –5.6 Ma.
7. *Cingulatisporites* "pteriformis" SL G26-1, EF D-17, Gatun Fm. –10.02 Ma.
8. *Cingulatisporites* "verrutiformis" SL 18, EF U-41/2, Gatun Fm. –9.4 Ma.
9. *Concavissimisporites fossulatus* SL 68, EF V-17/4, Gatun Fm. –5.6 Ma.
10. *Concavissimisporites* "kyrtomatus" SL 307, EF L3-2, Gatun Fm. –5.6 Ma.
11. *Crassoretitriletes vanraadshoovenii* SL 6, EF G-24/3, Chucunaque Fm. –6.95 Ma.
12. *Cyatheacidites annulatus* SL G27-2, EF H-7/2, Gatun Fm. –9.4 Ma.
13. *Distaverrusporites* "usmensis" SL 75.5, EF P-12, Culebra Fm. –19.20 Ma.
14, 15. *Echitriletes* "minispinosus" SL 65, EF H-15/2-4, Cayo Agua Fm. –4.25 Ma.
16. *Echitriletes* "minutuechinulatus" SL 186, EF J-41, Gatun Fm. –9.6 Ma.
17, 18. *Echitriletes* "selaginelloides" type "bacularis" SL G27-2, EF S-47/3, Tuira Fm. –10.15 Ma.
19, 20. *Echitriletes* "selaginelloides" type "bifurcatus" SL G27-1, EF L-5/4, Gatun Fm. –8.9 Ma.
21, 22. *Echitriletes* "selaginelloides" type "echiplanatus" SL 167, EF X-22, Tuira Fm. –12.6 Ma.
23, 24. *Echitriletes* "selaginelloides" type "muelleri" SL 175, EF V-6/2-4, Gatun Fm. –8.9 Ma.
25, 26. *Echitriletes* "selaginelloides" type "regularis" SL 178, EF F-23/4=F24/3, Tuira Fm. –12.6 Ma.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Fossutriletes "*communis*" (Figs. 27, 28). Amb triangular-acute-convex; trilete, laesurae 15 µm long, almost extending to spore margin, marginate, margo 1.8 µm thick; fossulate at distal surface and laevigate at proximal surface; wall 1 µm thick; 27 µm. Affinity: Pteridophyta.

Fossutriletes "*guapissimus*" (Figs. 29, 30). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin; fossulate to foveolate at distal surface, laevigate at proximal surface; wall 2.5 µm thick; 32 µm. Affinity: Pteridophyta.

Foveotriletes "*arrugatus*" (Figs. 31, 32). Amb triangular-acute-straight; trilete, laesurae extending to spore margin; foveolate, foveolae 1 µm wide; wall 3 µm thick; 32 µm. Affinity: Pteridophyta, Ophioglossaceae, *Ophioglossum* L.

Foveotriletes "*laterodepressus*" (Fig. 33). Amb triangular-obtuse-convex; trilete, laesurae straight, almost extending to spore margin, marginate, margo irregular, undulating; foveolate, foveolae 1 µm wide; wall 2 µm thick; ca. 37 µm. Affinity: Pteridophyta.

Foveotriletes ornatus Ref: figs. 26–28 (Graham, 1991a). Affinity: Pteridophyta, trilete fern spores Type 1 & 2.

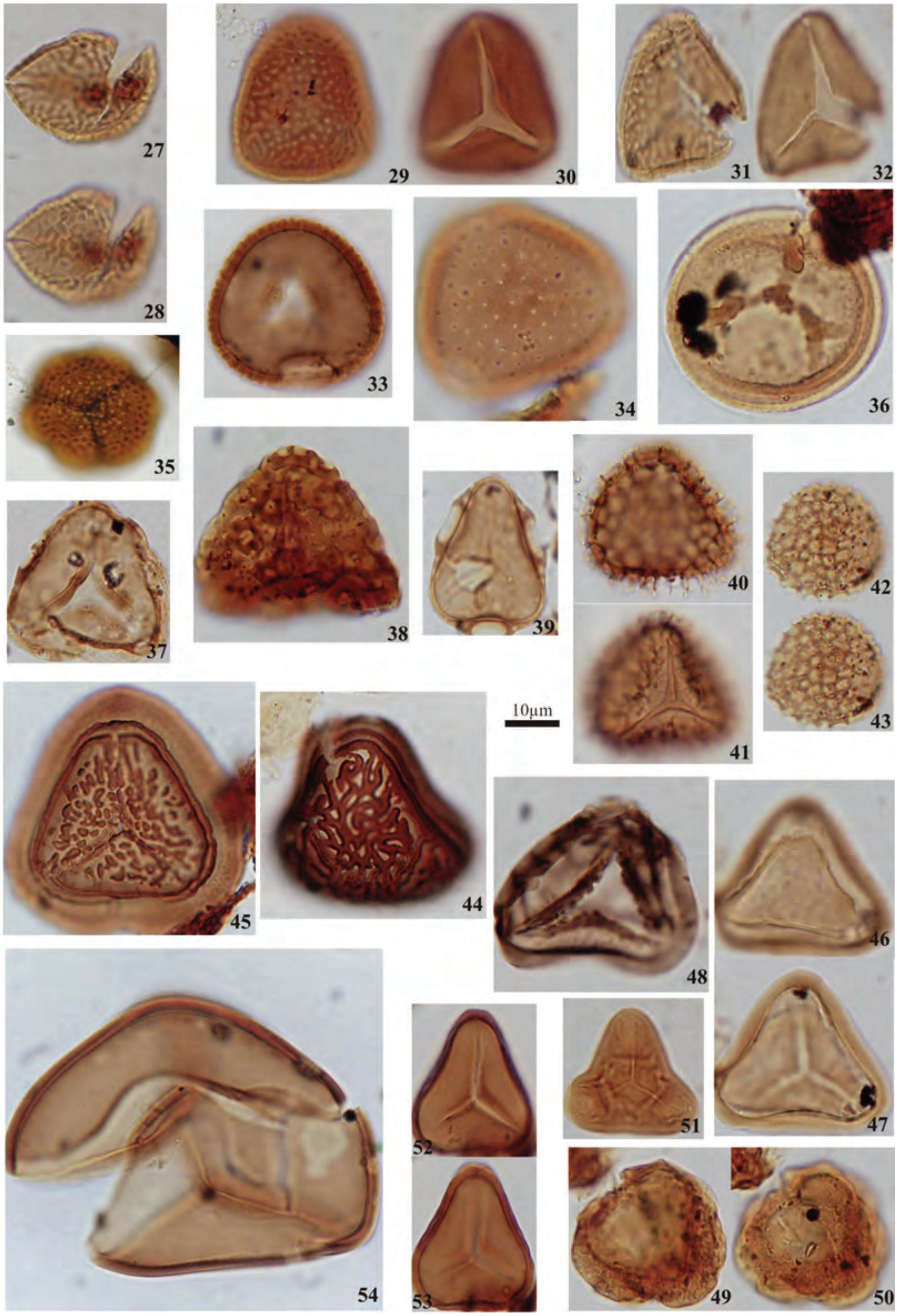
Foveotriletes aff. *ornatus* (Fig. 34). Amb triangular-obtuse-convex; trilete, laesurae straight, acute ends, marginate, margo thin, subtle; foveolate, foveolae resembling punctate pattern, perforations ca. 1 µm in diameter, dispersed; wall < 1 µm thick; 37 µm. Affinity: Pteridophyta.

Foveotriletes "*proximopsilatus*." Ref: figs. 1–3 (Graham, 1988a). Affinity: Pteridophyta, Lycopodiaceae, *Lycopodium* L.

Foveotriletes "*pseudoornatus*" (Fig. 35). Amb triangular-obtuse-concave; trilete, laesurae thin, extending to spore margin, distinct; foveolate, foveolae 1 µm wide; wall 2 µm thick; ca. 28 µm. Ref: ID 10505 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Grammitisporites "*verruminutus*" (Fig. 36). Amb circular; trilete, laesurae extending to spore margin, masked by margo, marginate, margo thick,

PLATE 2. Figures 27–54.
27, 28. *Fossutriletes* "communis" SL G26-1, EF M-11, Gatun Fm. –9.6 Ma.
29, 30. *Fossutriletes* "guapissimus" SL 184, EF E-15/4, Tuira Fm. –10.15 Ma.
31, 32. *Foveotriletes* "arrugatus" SL 370, EF T-62, Tuira Fm. –12.6 Ma.
33. *Foveotriletes* "laterodepressus" SL 2172, EF N-22, Escudo de Veraguas Fm. –2.75 Ma.
34. *Foveotriletes* aff. *ornatus* SL G27-2, EF W-7/2, Tuira Fm. –10.15 Ma.
35. *Foveotriletes* "pseudoornatus" SL Cucaracha 76, EF E-50/2, Cucaracha Fm. –18.85 Ma.
36. *Grammitisporites* "verruminutus" SL 204b, EF L-27/3, Gatun Fm. –8.47 Ma.
37. *Kuylisporites* "irregularis" SL 174, EF J-18/2, Gatun Fm. –9.6 Ma.
38. *Kuylisporites* "multiorodate" SL 187, EF V-24, Cayo Agua Fm. –4.25 Ma.
39. *Kuylisporites waterbolki* SL G26-1, EF N-19/4, Tuira Fm. –10.15 Ma.
40, 41. *Lycopodiumsporites* "clavaelongatus" SL 2172, EF Y-47, Escudo Veraguas Fm. –2.75 Ma.
42, 43. *Lycopodiumsporites* "clavatus" SL 1253, EF C-26/4=D-26/2, Tuira Fm. –6.95Ma.
44. *Nijssenosporites fossulatus* SL G27-1, EF C-16/2, Culebra Fm. –19.40 Ma.
45. *Nijssenosporites* "pteridoides" SL G27-1, EF C-15, Tuira Fm. –10.15 Ma.
46, 47. *Polypodiaceoisporites fossulatus* SL 176, EF Q-10/2, Gatun Fm. –9.6
48. *Polypodiaceoisporites* "reticulatus" SL G26-1, EF T-13/3, Tuira Fm. –12.6 Ma.
49, 50. *Psilatriletes lobatus* SL 174, EF L-15/2, Cayo Agua Fm. –3.55 Ma.
51. *Psilatriletes* sp. < 25 µm SL 27-1, EF C-9, Culebra Fm. –19.46 Ma.
52, 53. *Psilatriletes* sp. 25–50 µm SL G26-1, EF K-17, Culebra Fm. –19.46 Ma.
54. *Psilatriletes* sp. > 50 µm SL 174, EF M-9/2, Escudo Veraguas Fm. –2.5 Ma.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irregular, broken, subtle flange present, smooth; verrucate, verrucae variable; wall ca. 2 µm thick; ca. 41 µm. Ref: fig. 19 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, *Grammitis* Sw.

Kuylisporites "*irregularis*" (Fig. 37). Amb triangular-obtuse-convex; trilete, laesurae extending almost to spore margin, marginate, margo 3.5 µm thick, rounded ends; laevigate; spores displaying irregular perisporium, undulating, cribate, having dispersed and rounded perforations variable in size, ca. 4 µm wide; wall variable, 1.5–2 µm thick; 30 µm. Affinity: Pteridophyta, Cyatheaceae, *Cnemidaria*.

Kuylisporites "*multiorodate*" (Fig. 38). Amb triangular-obtuse-convex; trilete, structure complex, laesurae thin, straight, marginate, margo delimited by sculptural elements; foveolate, resembling areolate condition; wall 3.5 µm thick; 39 µm. Affinity: Pteridophyta, Cyatheaceae.

Kuylisporites waterbolki (Fig. 39). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, marginate, margo thin at ends, increasing at center; laevigate, having irregular and scarce perforations resembling fossulate pattern; spores surrounded by a conspicuous smooth flange, thin at apices, up to 5 µm thick at center, displaying ample apertures as pore-like, ca. 10 µm wide, annulate, sometimes up to three pores laterally; wall 1 µm thick; 35 µm. Ref: ID 10352 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Cyatheaceae, *Hemitelia* R. Br./*Cnemidaria* types.

Lycopodiaceae. Ref: fig. 2 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 1.

Lycopodiaceae. Ref: fig. 3 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 2.

Lycopodiaceae. Ref: figs. 4, 5 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 3.

Lycopodiaceae. Ref: fig. 6 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 4.

Lycopodiumsporites "*clavaelongatus*" (Figs. 40, 41). Amb triangular-obtuse-convex; trilete, laesurae extending almost to spore margin; reticulate, apparently perisporium present, echinate, echinae irregular; wall 1 µm thick; ca. 28 µm. Affinity: Pteridophyta.

Lycopodiumsporites "*clavatus*" (Figs. 42, 43). Amb triangular-obtuse-convex to circular; trilete, laesurae extending to spore margin; reticulate resembling the lopho-reticulate condition, apparently perisporium present, echinate, echinae irregular, thin, acute ends; 23 µm. Affinity: Pteridophyta, Lycopodiaceae, *Lycopodium clavatum* L.

Lycopodiumsporites "*morenoi.*" Ref: ID 10507 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Lycopodiaceae.

Lycopodiumsporites sp. Ref: ID 10476 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Lycopodiaceae.

Magnastriatites grandiosus. Ref: ID 10045 (Jaramillo & Rueda, 2013); fig. 20 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Ceratopteris*.

Matonisporites mullerii. Ref: ID 10363 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Nijssenosporites fossulatus (Fig. 44). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, thin, marginate, margo straight, conspicuous flange present, smooth, 4.5 µm thick, displaying external vestigial membrane; rugulate, rugulae thick, wide, sinuous, irregularly rounded at proximal surface, compressed at distal surface; wall 3 µm thick; ca. 38 µm. Ref: ID 10216 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Adianthaceae, *Pityrogramma* Link.

Nijssenosporites "*pteridoides*" (Fig. 45). Amb triangular-obtuse-convex, rounded apices; trilete, laesurae extending to spore margin, thin, subtle, irregular, undulating, conspicuous flange present, scabrate, 8 µm wide; rugulate, rugulae thick, wide, sinuous, irregularly rounded at proximal surface, compressed at distal surface; wall 3 µm thick; ca. 47 µm. Affinity: Pteridophyta, Pteridaceae, *Pityrogramma*.

Ophioglossaceae (*Ophioglossum*). Ref: fig. 18 (Graham, 1991a). Affinity: Pteridophyta, Ophioglossaceae, *Ophioglossum*.

Planisporites sp. 2. Ref: ID 10013 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Polypodiaceoisporites fossulatus (Figs. 46, 47). Amb triangular-obtuse-concave; trilete, laesurae extending to spore margin, undulating, having conspicuous and irregular verrucae around; verrucate, verrucae flat; wall ca. 1 µm thick, surrounded by smooth flange, ca. 4.5 µm thick; 30–34 µm. Affinity: Pteridophyta.

Polypodiaceoisporites? *fossulatus*. Ref: ID 10041 (Jaramillo & Rueda, 2013); fig. 21 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris* Type 1.

Polypodiaceoisporites "*reticulatus*" (Fig. 48). Amb triangular-obtuse-convex; trilete, laesurae wide, triangular, having verrucate processes on margins; laevigate, presence of perisporium on distal surface, reticulate, variable in size; wall ca. 4 µm thick; 39 µm. Affinity: Pteridophyta.

Psilatriletes "*brevilaesuratus*." Ref: ID 10503 (Jaramillo & Rueda, 2013); figs. 18, 20 (Graham, 1988a), fig. 14 (Graham, 1989). Affinity: Pteridophyta, Pteridaceae, *Antrophyum* Kaulf.

Psilatriletes "*enormis*." Ref: ID 10504 (Jaramillo & Rueda, 2013); figs. 5, 6, 11, 12, 17 (Graham, 1988a). Affinity: Pteridophyta, Lygodiaceae, *Lygodium* Sw.

Psilatriletes lobatus (Figs. 49, 50). Amb triangular-rounded; trilete, laesurae inconspicuous, thin, short, masked by flange; laevigate; flange variable in size, ca. 1–6 µm thick; wall 1.5 µm thick, surrounded by irregular, undulating, scabrate flange; 30 µm. Ref: ID 10325 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Psilatriletes peruanus. Ref: ID 10326 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Pteridaceae, *Jamesonia* Hook. & Grev., *Pteris rangiferina* Pr. & Miq.

Psilatriletes sp. < 25 µm. (Fig. 51). Amb triangular-obtuse-straight; trilete, laesurae thin, straight, extending 3/4 of the distance to spore margin; laevigate, slightly echinulate at angular areas, resembling a subtle flange; wall 1 µm thick; 22 µm. Ref: ID 10019 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Psilatriletes sp. 25–50 µm. (Figs. 52, 53). Amb triangular-obtuse-straight; trilete, laesurae thin, straight, extending to spore margin, marginate, margo thin at apex and thick at inter-radius areas; laevigate, having subtle granular perispori; wall 2.5 µm thick; 26 µm. Ref: ID 10020 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Cyatheaceae, *Cyathea*.

Psilatriletes sp. > 50 µm. (Fig. 54). Amb triangular-obtuse-convex; trilete, laesurae thin, extending to spore margin, marginate, margo 5 µm wide; laevigate; wall 2.5 µm thick; 65 × 47 µm (distal face). Ref: ID 10021 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Pteridaceae (Type 1). Ref: fig. 21 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 1.

Pteridaceae (Type 2). Ref: fig. 22 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 2.

Pteridaceae (Type 3). Ref: fig. 23 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 3.

Pteridaceae (Type 4). Ref: fig. 24 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 4.

Pteridaceae (Type 5). Ref: fig. 25 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 5.

Retitriletes sommeri. Ref: ID 10052 (Jaramillo & Rueda, 2013); figs. 15, 16 (Graham, 1988a). Affinity: Pteridophyta, Lycopodiaceae, trilete fern spores Type 3.

Rugulatisporites "*irregularis*" (Fig. 55). Amb triangular-obtuse-convex; trilete, laesurae straight, extending 2/3 of the distance to spore margin, acute ends, marginate, margo wider at vertices; laevigate, presence of subtle, irregular and persistent perisporium, rugulate; wall < 1 µm thick; 33 µm. Affinity: Pteridophyta.

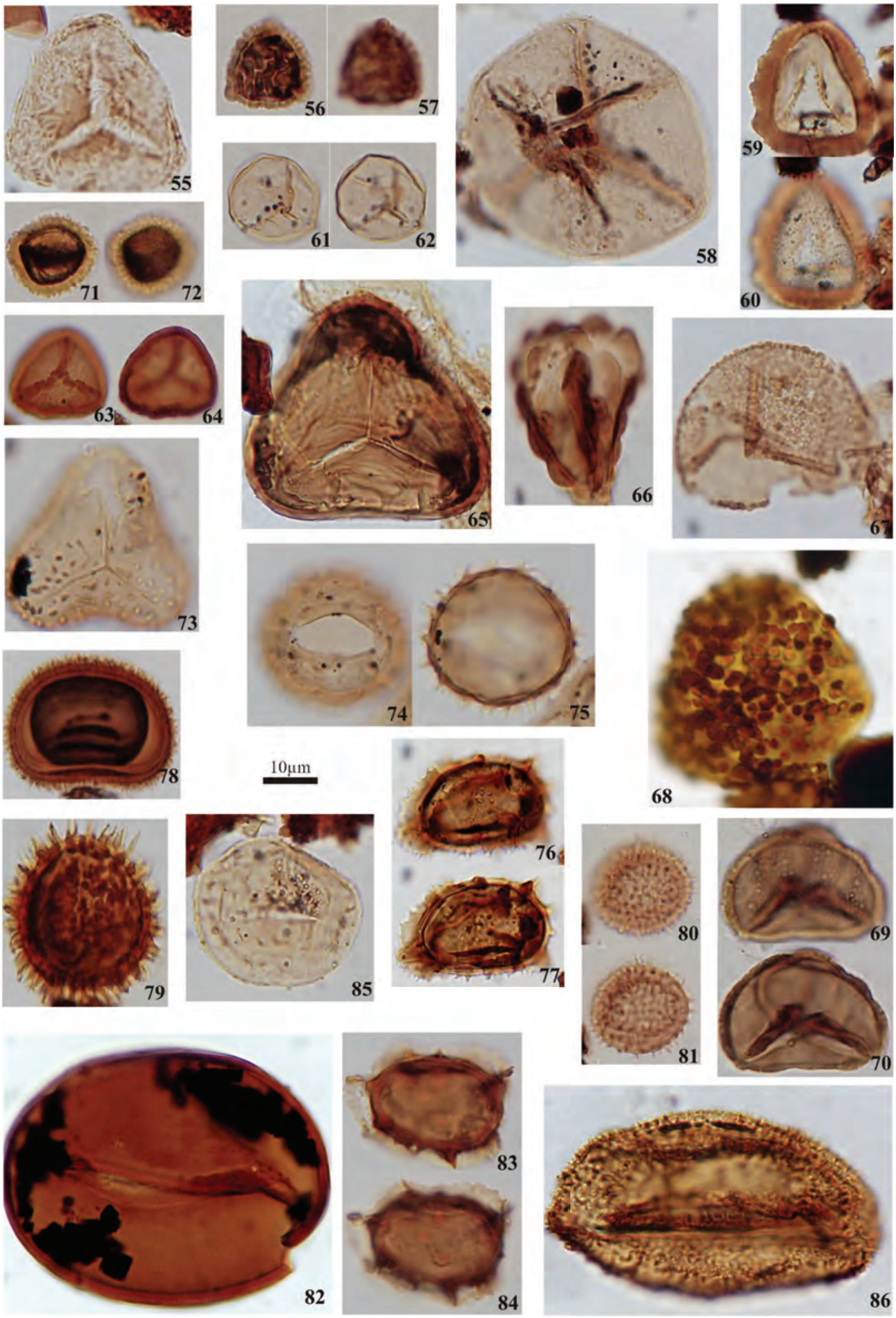
Rugulatisporites "*minutus*" (Figs. 56, 57). Amb triangular-obtuse-convex; trilete, laesurae inconspicuous; rugulate, rugulae irregular, thick, short; wall 2 µm thick; 14 µm. Affinity: Pteridophyta.

Scabratriletes "*complicatus*" (Fig. 58). Amb circular; trilete, laesurae thin, sinuous, acute ends, extending to spore margin, marginate, margo coarse; baculate, baculae small, thin, < 1 µm thick; wall < 1 µm thick; 47 µm. Affinity: Pteridophyta.

Selaginellasporites "*crestatus*" (Figs. 59, 60). Amb triangular-obtuse-convex; trilete, laesurae wide, triangular, extending 2/3 of the distance to spore margin, margins with small granules; laevigate, flange present, displaying margins irregular and serrate to baculate, ca. 4 µm thick; wall < 1 µm thick; 26 × 23 µm (distal face). Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

Selaginellasporites "*psilatus*" (Figs. 61, 62). Amb circular; trilete, laesurae irregular, thin, sinuous, extending 3/4 of the distance to spore margin; laevigate; wall 1 µm thick; 16.5 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

PLATE 3. Figures 55–86.
55. *Rugulatisporites* "irregularis" SL G27-2, EF E-19, Gatun Fm. –8.9 Ma.
56, 57. *Rugulatisporites* "minutus" SL 61, EF N-45/1=2, unnamed Fm. –2.65 Ma.
58. *Scabratriletes* "complicatus" SL G26-1, EF P-50, Gatun Fm. –8.9 Ma.
59, 60. *Selaginellasporites* "crestatus" SL 6, EF J-22/2, Gatun Fm. –9.6 Ma.
61, 62. *Selaginellasporites* "psilatus" SL 174, EF R-36/3, Gatun Fm. –9.6 Ma.
63, 64. *Selaginellasporites* "variechinatus" SL 391, EFS-20=T-20, Gatun Fm. –10.05 Ma.
65. *Striatriletes* "saccolomicites" SL 391, EF T-7/2=4, Tuira Fm. –10.15 Ma.
66. *Verrucatotriletes etayoi* SL G26-1, EF L40/4=L41/3, Tuira Fm. –10.15 Ma.
67. *Verrutriletes* "densiverrucatus" SL G27-1, EF E-17, Gatun Fm. –10.05 Ma.
68. *Verrutriletes* "magnoviruelensis" SL Culebra 12.75, EF P-39/2, Culebra Fm. –19.13 Ma.
69, 70. *Verrutriletes* "perforatus" SL 5a, EF F-7/4=G-7/2, Gatun Fm. –5.6 Ma.
71, 72. *Verrutriletes* "uniformis" SL 61, EF Q-20/4, Tuira Fm. –12.6 Ma.
73. *Verrutriletes* "variverrucatus" SL 177, EF K-22/4=K-23/3, Gatun Fm. –8.9 Ma.
74, 75. *Echinomonoletes* "amplimarginatus" SL 6, EF G-17/1, Gatun Fm. –8.4 Ma.
76, 77. *Echinomonoletes* "bifurcatus" SL 20, EF P-21/1, Gatun Fm. –10.0 Ma.
78. *Echinomonoletes* "hirsutus" SL G26-1, EF L-44, Tuira Fm. –10.15 Ma.
79. *Echinomonoletes* "megaechinatus" SL G27-1, EF C-15/4, Tuira Fm. –10.15 Ma.
80, 81. *Echinomonoletes* "sphericus" SL G27-2, EF E-36/1=D-36/3, Tuira Fm. –10.15 Ma.
82. *Laevigatosporites* "magnus" SL 1556, EF T-48/4, Tuira Fm. –6.95 Ma.
83, 84. *Perinomonoletes* "aciculiformis" SL 1253, EF Q-11/4, Tuira Fm. –12.6 Ma.
85. *Perinomonoletes* "microechinulatus" SL 193, EF L-17/2, Tuira Fm. –10.15 Ma.
86. *Perinomonoletes* "minispinosus" SL 349, EF J-15/4, Cayo Agua Fm. –4.25 Ma.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Selaginellasporites "*variechinatus*" (Figs. 63, 64). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, marginate, margo ca. 1.5 µm wide, radius 8 µm long; laevigate at proximal surface and echinate at distal surface, echinae 1 µm long, 0.5 µm apart, rounded ends, resembling small baculae; wall 1.5 µm thick; 17 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

Striatriletes "*saccolomicites*" (Fig. 65). Amb triangular-obtuse, slightly convex; trilete, laesurae extending 2/3 of the distance to spore margin, straight, thin, marginate, margo wide, straight; rugulate, rugulae variable in size; wall 2.5 µm thick; 44 µm. Affinity: Pteridophyta, Dennstaedtiaceae, *Saccoloma* Kaulf.

Trilete fern spore Type 1. Ref: fig. 26, 27 (Graham, 1991a). Affinity: Pteridophyta.

Trilete fern spore Type 2. Ref: fig. 28 (Graham, 1991a). Affinity: Pteridophyta.

Undulatisporites "*undulapolus*." Ref: ID 10202 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Verrucatotriletes etayoi (Fig. 66). Amb triangular-obtuse-convex; trilete, laesure thin, straight extending to spore margin, masked by ornamentation; verrucate, verrucae dense, variable, ca. 2–3 × 5–9 µm; wall 2.5 µm thick; 34–36 µm. Ref: ID 10323 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Verrutriletes "*densiverrucatus*" (Fig. 67). Amb circular; trilete, laesurae thin, extending to spore margin, margins bordered by conspicuous gemmae; gemmate, gemmae irregular, < 1 µm long, grouped in patches resembling "rosettes"; wall 1 µm thick; 38 µm. Affinity: Pteridophyta.

Verrutriletes "*magnoviruelensis*" (Fig. 68). Amb circular to slightly triangular-obtuse-convex; trilete, laesurae extending to spore margin, straight, ca. 2 µm thick, ends pointed, masked by sculptural elements; verrucate, verrucae variable, 3–4 µm wide, densely distributed over spore surface; wall 2 µm thick; 43 µm. Ref: ID 10330 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Verrutriletes "*perforatus*" (Figs. 69, 70). Amb circular to slightly triangular-obtuse-convex; trilete, laesurae extending to spore margin, straight, marginate; verrucate, verrucae prominent, dense, uniform, resembling the microreticulate pattern; wall 1 µm thick; 28 × 19 µm (distal face). Affinity: Pteridophyta.

Verrutriletes "*uniformis*" (Figs. 71, 72). Amb circular to triangular-obtuse-convex; trilete, laesurae thin, inconspicuous, extending almost to spore margin; probably laevigate, spores having flange, ca. 3.5 µm thick, flange gemmate, gemmae irregular, dense; wall 1 µm thick; 17 µm. Affinity: Pteridophyta.

Verrutriletes "*variverrucatus*" (Fig. 73). Amb triangular-obtuse-concave; trilete, laesurae extending to spore margin, slightly marginate, margo straight; verrucate, verrucae variable, small, elongated, scarce, disperse on spore surfaces; wall ca. 1 µm thick, becoming wider at interangular areas; 25–27 µm. Affinity: Pteridophyta.

Verrutriletes sp. Ref: fig. 19 (Graham, 1988a). Affinity: Trilete fern spore Type 4.

FERNS: MONOLETE SPORES

Dryopteridaceae (*Ctenitis*). Ref: fig. 29 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae, *Ctenitis* (C. Chr.) C. Chr.

Dryopteridaceae Type 1. Ref: fig. 29 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae Type 1.

Dryopteridaceae Type 2. Ref: fig. 30 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae Type 2.

Dryopteridaceae Type 3. Ref: fig. 31 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae Type 3.

Echinosporis "*panamensis*." Ref: ID 10290 (Jaramillo & Rueda, 2013); fig. 21 (Graham, 1988a). Affinity: Pteridophyta, Marattiaceae, *Danaea* Sm.

Echinomonoletes "*amplimarginatus*" (Figs. 74, 75). Biconvex; monolete, laesurae wide, extending 2/3 of the distance to spore margin, marginate, margo thin, inconspicuous; echinate, echinae acute, wide at base, irregular; 28 × 26 µm (proximal face). Affinity: Pteridophyta.

Echinomonoletes "*bifurcatus*" (Figs. 76, 77). Plane-convex; monolete; echinate, echinae 2–5 µm long, irregular ends, crest-like; wall 2 µm thick; 30 × 20 µm (lateral face). Affinity: Pteridophyta.

Echinomonoletes "*hirsutus*" (Fig. 78). Reniform; monolete; echinate, echinae 1.5–2 µm long, < 1 µm wide, densely distributed on surface; wall 1.5 µm thick; 33 µm. Affinity: Pteridophyta.

Echinomonoletes "*megaechinatus*" (Fig. 79). Biconvex; monolete, extending half the distance to spore margin, thin, inconspicuous; echinate, echinae 5 µm long, dense; wall 2 µm thick; 33 µm. Affinity: Pteridophyta, Polypodiaceae.

Echinomonoletes "*sphericus*" (Figs. 80, 81). Plane-convex; monolete; echinate, echinae 2 × 1 µm, acute ends; wall < 1 µm thick; 22 µm. Affinity: Pteridophyta.

Laevigatosporites catanejensis. Ref: ID 10219 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Laevigatosporites "*magnus*" (Fig. 82). Circular; monolete, laesurae extending 3/4 of the distance to spore margin, marginate, margo 3.5 µm thick; laevigate; wall 3 µm thick; 62 × 48 µm (distal face). Affinity: Pteridophyta.

Laevigatosporites tibuensis. Ref: ID 10009 (Jaramillo & Rueda, 2013); figs. 32, 33 (Graham, 1991a). Affinity: Monolete fern spores Types 1 & 2.

Monolete fern spore Type 1. Ref: fig. 32 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 2. Ref: fig. 33 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 3. Ref: fig. 34 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 4. Ref: fig. 35 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 5. Ref: fig. 36 (Graham, 1991a). Affinity: Pteridophyta.

Perinomonoletes "*aciculiformis*" (Figs. 83, 84). Reniform; monolete, laesurae inconspicuous, extending 3/4 of the distance to spore margin; laevigate, spores having perisporium, echinate, undulating, irregular, resembling a reticulate pattern; wall 1 µm thick; 20 × 30 µm (distal face). Affinity: Pteridophyta, Aspleniaceae, *Asplenium* L.

Perinomonoletes "*microechinulatus*" (Fig. 85). Biconvex; monolete, laesurae extending 2/3 of the distance to spore margin, ca. 21 × 3 µm; laevigate, spores having a thin perisporium, echinulate, translucid; wall ca.1 µm thick; 32 × 22 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*minispinosus*" (Fig. 86). Biconvex; monolete, laesurae extending to spore margin, echinate, echinae < 1 µm long, thin; wall ca.

1 µm thick; ca. 52 × 35 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*minutus*" (Fig. 87). Plane-convex; monolete, laesurae inconspicuous; laevigate, spores having perisporium, ca. 1 µm thick, irregular, sessile, resembling the striate pattern; wall 1 µm thick; 26 × 18 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*pseudoreticulatus*" (Fig. 88). Plane-convex; monolete, laesurae simple, extending 2/3 of the distance to spore margin; laevigate, spores having perisporium, irregular, sessile, echinate, echinae 2 µm long, acute ends, resembling a reticulate pattern; wall 1.8–2.4 µm thick; 20 × 14 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*reticuloacicularis*." Ref: ID 10350 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Polypodiisporites aff. *echinatus* (Fig. 89). Biconvex; monolete, laesurae extending 2/3 of the distance to spore margin, thin; laevigate; subtle flange present, echinate, echinae irregular, variable, wide, rounded ends, sometimes resembling reticulate pattern; wall ca.1 µm thick; 30 µm. Affinity: Pteridophyta.

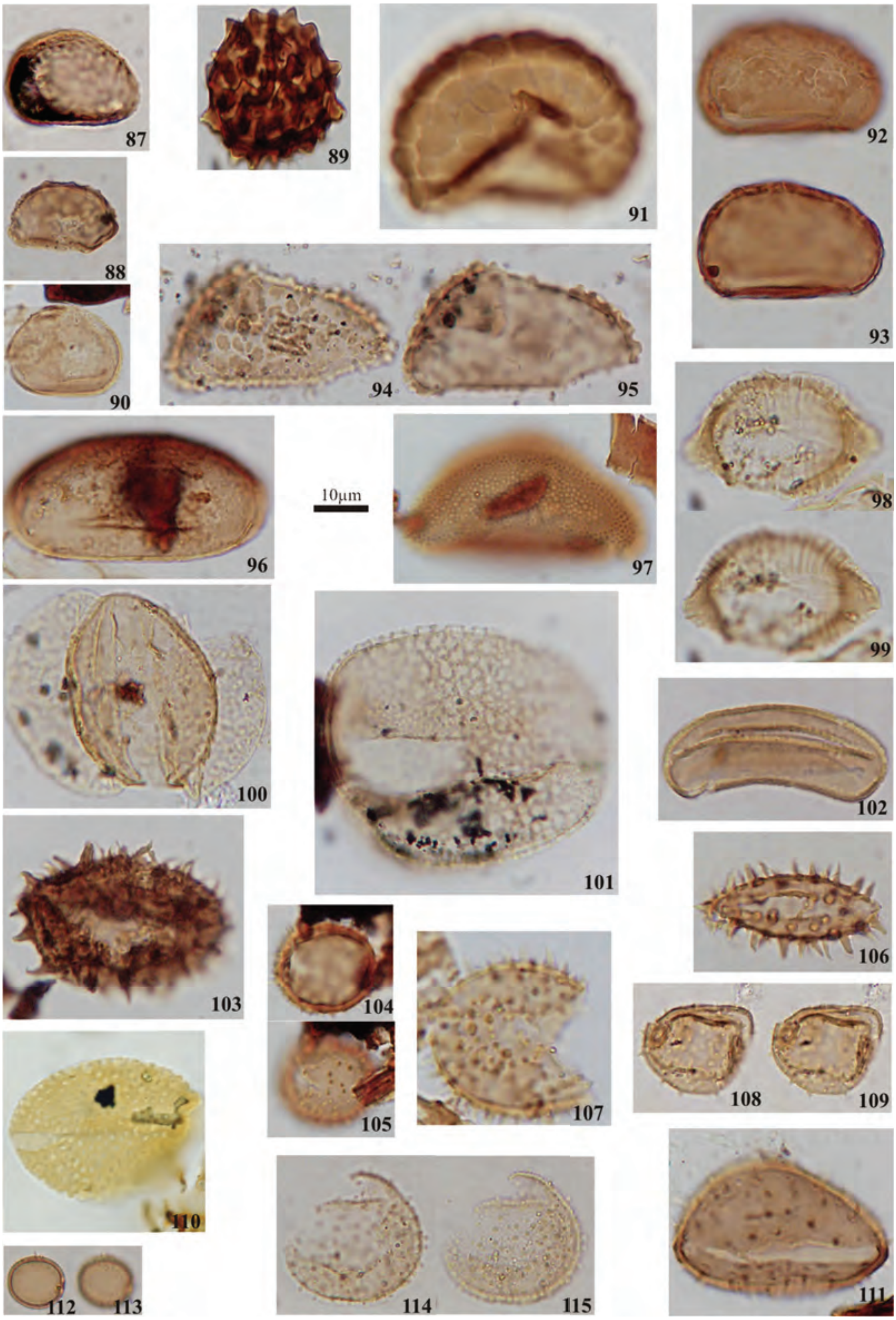
Polypodiisporites "*microverrucate*" (Fig. 90). Reniform; monolete, laesurae extending 3/4 of the distance to spore margin; verrucate at distal surface and laevigate at proximal surface, verrucae small, rounded, resembling small baculae; wall 1–1.2 µm thick; 22.5 × 18 µm. Affinity: Pteridophyta, Polypodiaceae, *Polypodium* L.

Polypodiisporites ? *planus*. Ref: ID 10449 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Polypodiisporites "*reniformis*" (Fig. 91). Reniform; monolete, laesurae extending to spore margin, marginate, margo inconspicuous; verrucate, verrucae rounded to rectangular, variable, 1.5 × 4 µm; wall 3–6 µm thick; 45 × 27 µm (distal face). Affinity: Pteridophyta, Polypodiaceae, *Polypodium*.

Polypodiisporites scabraproximatus. Ref: ID 10031 (Jaramillo & Rueda, 2013) and fig. 33 (Graham,

PLATE 4. Figures 87–115.
87. *Perinomonoletes* "minutus" SL 19, EF G-17/2=4, Gatun Fm. –10.0 Ma.
88. *Perinomonoletes* "pseudoreticulatus" SL 174, EF D-40/3, Tuira Fm. –10.15 Ma.
89. *Polypodiisporites* aff. *echinatus* SL 1241, EF G-68, Tuira Fm. –10.15 Ma.
90. *Polypodiisporites* "microverrucate" SL 174, EF D-22/3, unnamed Fm. –6.95 Ma.
91. *Polypodiisporites* "reniformis" SL 2190, EF U-22/2, Tuira Fm. –10.15 Ma.
92, 93. *Polypodiisporites* "verruplanatus" SL G27-1, EF E-13/1, Tuira Fm. –12.6 Ma.
94, 95. *Polypodiisporites* aff. sp. 2 J & D SL 174, EF F-47/3=G-47/1, Gatun Fm. –5.6 Ma.
96. *Scabramonoletes* "elongatus" SL G26-1, EF S-6/4, Gatun Fm. –8.9 Ma.
97. *Schizaea* "mosquitensis" SL G27-1, EF V-17/1, Escudo Veraguas Fm. –2.05 Ma.
98, 99. *Striatomonoletes* "incertus" SL 175, EF L-5/2=L-6/1, Escudo Veraguas Fm. –2.05 Ma.
100. *Podocarpidites* "globosus" SL Culebra 12.75, EF P-39/2, Culebra Fm. –19.3 Ma.
101. *Bromeliacidites* sp. 1. SL 5b, EF W-19/2=4, Gatun Fm. –8.9 Ma.
102. *Bromeliacidites* sp. 2. SL 65, EF J-9/4, Cayo Agua Fm. –4.25 Ma.
103. *Echimonocolpites* "dariensis" SL 5b, EF Q-21/4, Chucunaque Fm. –6.95 Ma.
104, 105. *Echimonocolpites* "mauritiformis" SL G26-1, EF N-22, Pucro Fm. –6.95 Ma.
106. *Echimonocolpites* "mosquitensis" SL 68, EF L-17, Tuira Fm. –6.95 Ma.
107. *Echimonocolpites* "panamensis" SL 174, EF D-13/1, Tuira Fm. –10.15 Ma.
108, 109. *Echiperiporites* "aquaticus" SL 1620, EF B-25/4=C-26/1, Tuira Fm. –6.95 Ma.
110. *Longapertites* "foveolatus" SL Culebra 3.5, EF Q-44/1, Culebra Fm. –19.40 Ma.
111. *Mauritiidites* "franciscoi" var. "franciscoi" SL 5a, EF J-9/1, Tuira Fm. –12.6 Ma.
112, 113. *Monoporopollenites* "minutus" SL 204, EF R-15/3, Pucro Fm. –6.95 Ma.
114, 115. *Palmapollenites* "iriartoides" SL 175, EF G-23, Tuira Fm. –12.6 Ma.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1991a). Affinity: Pteridophyta, Monolete fern spore Type 2.

Polypodiisporites aff. *speciosus*. Ref: ID 10028 (Jaramillo & Rueda, 2013) and fig. 34 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, *Stenochlaena palustris* (Burm.) Bedd.

Polypodiisporites usmensis. Ref: ID 10046 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Blechnaceae, *Stenochlaena palustris*; Dennstaedtiaceae, *Histiopteris incisa* (Thunb.) J. Sm.; Polypodiaceae, *Phlebodium aureum* (L.) J. Sm.

Polypodiisporites "*verruplanatus*" (Figs. 92, 93). Reniform; monolete, laesurae thin, extending to spore margin; verrucate, verrucae irregular in shape and size, 3–7 µm wide, decreasing toward proximal surface; wall 1 µm thick; 34 × 21 µm (distal face). Affinity: Pteridophyta.

Polypodiisporites aff. sp. 2 J & D (Figs. 94, 95). Plano-convex; monolete, laesurae thin, extending to spore margin; verrucate, verrucae irregular, 1–5 µm wide; wall 2.5 µm thick; 24 × 45.5 µm (lateral face). Ref: ID 10034 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Scabramonoletes "*elongatus*" (Fig. 96). Plane-convex; monolete, laesurae thin, straight, extending half distance to spore margin, ca. 24 µm long, marginate, margo subtle, thin; scabrate, displaying irregular and dispersed granules; wall 1 µm thick; 50 × 24 µm (distal face). Affinity: Pteridophyta.

Schizaea "*mosquitensis*" (Fig. 97). Plane-convex; monolete, laesurae masked by folded wall; cingulated, cingulum ca. 3.5 µm thick, reticulate, muri thin, lumina rounded; wall < 1 µm thick; 44 × 23 µm (distal face). Affinity: Pteridophyta, Schizaeaceae, *Schizaea* Sm.

Striatomonoletes "*incertus*" (Figs. 98, 99). Biconvex; monolete, laesurae extending to spore margin; striate, striae oriented from distal to proximal surface, dense, wide; wall 2 µm thick; 30 × 18 µm (distal face). Affinity: Pteridophyta.

GYMNOSPERMS

Podocarpidites "*globosus*" (Fig. 100). Bisaccate, inaperturate; body amb circular, psilate to finely scabrate, 20 µm, body wall 3.5 µm thick; air sacs two, hemispheric, psilate, translucid, angularly oriented; overall dimension (including air sacs) 48 µm. Ref: fig. 37 (Graham, 1991a). Affinity: Gymnospermae, Podocarpaceae, *Podocarpus* L'Hér. ex Pers.

ANGIOSPERMS: MONOCOTS

Arecipites "*perfectus*." Ref: ID 2036 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Arecipites regio. Ref: ID 34 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Bromeliacidites sp. 1 (Fig. 101). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain, margins masked by reticulum; reticulate, lumina variable, 2–4 µm wide, muri 1 µm thick, simplicolumellate; tectate, wall 2 µm thick; 57 × 47 µm. Affinity: Monocotyledoneae, Bromeliaceae.

Bromeliacidites sp. 2 (Fig. 102). Amb elliptic; monocolpate, colpus thin, extending nearly entire length of grain, margins masked by small baculae; baculate, baculae short, dense, ca. 1 µm thick; apparently intectate, wall 1.2 µm thick; 43 × 16 µm. Affinity: Monocotyledoneae, Bromeliaceae, *Catopsis* Griseb.

Cyperaceae. Ref: ID 228 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Cyperaceae.

Dioscorea/*Rajania*. Ref: ID 236 (Jaramillo & Rueda, 2013); fig. 51 (Graham, 1988a). Affinity:

Monocotyledoneae, Dioscoreaceae, *Dioscorea* L./ *Rajania* L. types.

Echimonocolpites "*dariensis*" (Fig. 103). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain; echinate-verrucate, echinae acute, irregular, wide at base, surface between echinae filled by small, dense, and variable verrucae; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 43 × 27 µm (excluding ornamentation). Affinity: Monocotyledoneae, Arecaceae.

Echimonocolpites "*mauritiformis*" (Figs. 104, 105). Amb circular, monocolpate, colpus wide, extending 2/3 length of grain; echinate, echinae acute, thin with rounded and wide base, ca. 1 µm thick; tectate, wall 1 µm thick; 21 × 17 µm. Affinity: Monocotyledoneae, Arecaceae.

Echimonocolpites "*mosquitensis*" (Fig. 106). Amb elliptic; monocolpate, colpus extending nearly entire length of grain, wide, bordered by sculptural elements; echinate, echinae irregular and dispersed, 3–6 µm long; intectate, wall 1 µm thick, nexine 1 µm thick (excluding ornamentation); 33 × 15 µm. Affinity: Monocotyledoneae, Arecaceae.

Echimonocolpites "*panamensis*" (Fig. 107). Amb circular, monocolpate, colpus extending nearly entire length of grain, thin, irregular, with margins not well defined; echinate, echinae acute, pyramidal, slightly depressed, 1.5–2.5 µm tall; tectate, wall < 1 µm thick (excluding ornamentation); 24 µm. Affinity: Monocotyledoneae, Arecaceae, cf. *Mauritia* L. f. (similar to *Mauritia*, but *Mauritia* has been reported as porate).

Echiperiporites "*aquaticus*" (Figs. 108, 109). Spherical, amb circular; periporate, pores 8, circular, 2.5 µm wide, annulate; echinate, echinae conical, sharp, wider at base, 1.5 µm long; tectate, wall 2.5 µm thick (including echinae); 25 µm. Affinity: Monocotyledoneae, Alismataceae, *Echinodorus* Rich.

Foveomonocolpites "*panamensis*." Ref: ID 2090 (Jaramillo & Rueda, 2013); figs. 33, 34 (Graham, 1988a). Affinity: Monocotyledoneae, Arecaceae, *Desmoncus* Mart. type.

Longapertites "*foveolatus*" (Fig. 110). Amb elliptic; monocolpate, colpus extending nearly entire length of grain, straight, thin; foveolate, foveolae uniform; tectate; ca. 33 µm. Ref: figs. 29–32 (Graham, 1988a); fig. 19 (Graham, 1988b). Affinity: Monocotyledoneae, Arecaceae, *Cryosophila* Blume.

Mauritiidites "*franciscoi*" var. "*franciscoi*" (Fig. 111). Amb elliptic, monocolpate, colpus wide, extending nearly entire length of grain; echinate, echinae acute, conical-based, appearing as inserted into slightly ectexine concavity, 3 µm long; tectate, wall 1.2 µm thick (excluding ornamentation); 41 × 28 µm. Ref: ID 469 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae, *Mauritia flexuosa* L. f.

Mauritiidites franciscoi var. *minutus*. Ref: ID 470 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae, *Mauritia*.

Monocolpopollenites "*canalensis*." Ref: ID 2092 (Jaramillo & Rueda, 2013); figs. 35, 36 (Graham, 1988a); figs. 28, 29 (Graham, 1989). Affinity: Monocotyledoneae, Arecaceae, *Synechanthus* H. Wendl.

Monoporopollenites annulatus. Ref: ID 487 (Jaramillo & Rueda, 2013); fig. 38 (Graham, 1991a). Affinity: Monocotyledoneae, Poaceae.

Monoporopollenites "*minutus*" (Figs. 112, 113). Spherical, amb circular; monoporate, pore circular, ca. 1 µm wide, displaying subtle annulus; psilate; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 12 µm. Affinity: Monocotyledoneae, Poaceae.

Palmae Type 1. Ref: figs. 39, 40 (Graham, 1991a). Affinity: Monocotyledoneae, Arecaceae.

Palmapollenites "*iriartoides*" (Figs. 114, 115). Amb elliptic; monocolpate, colpus inconspicuous, irregular, thin; clavate, clavae variable, 1–1.5 µm long, scarce, irregularly distributed; intectate, wall < 1 µm thick, columellae 0.5 µm tall, nexine 0.5 µm thick; 29 µm. Affinity: Arecaceae, *Iriartea deltoidea* Ruiz & Pav.

Palmapollenites "*microperforatus*." Ref: figs. 41, 42 (Graham, 1991a). Affinity: Monocotyledoneae, Arecaceae, *Oenocarpus* Mart., Palmae Type 2.

Palmapollenites "*phytelephensis*" (Fig. 116). Amb elliptic, monocolpate, colpus extending 2/3 length of grain; apparently reticulate, resembling the micropitted condition, lumina < 1 µm wide; tectate; 51 µm. Affinity: Monocotyledoneae, Arecaceae, *Phytelephas* Ruiz & Pav.

Palmapollenites "*scheeleaensis*" (Fig. 117). Amb elliptic; monocolpate, colpus irregular, thin, extending nearly entire length of grain; apparently verrucate, columellae grouping as small packages resembling verrucate pattern; tectate, wall 2 µm thick, strongly columellate, tectum 1 µm thick, sexine 1 µm thick, nexine 1 µm thick; 45 × 26 µm. Affinity: Monocotyledoneae, Arecaceae, *Scheelea zonensis* L. H. Bailey.

Psilamonocolpites amazonicus. Ref: ID 978 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae, *Euterpe* Mart.

Psilamonocolpites "*longiformis*" (Fig. 118). Amb elliptic; monocolpate, colpus thin, extending nearly entire length of grain; psilate; tectate, wall 1 µm thick; 60 × 18 µm. Affinity: Monocotyledoneae, Araceae.

Psilamonocolpites medius (Fig. 119). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain; psilate; tectate, wall 1 µm thick; 41 µm. Ref: ID 593 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Psilamonocolpites rinconii (Fig. 120). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain; reticulate, lumina < 1 µm wide, fine; tectate, wall 1 µm thick, densely columellate; 26 µm. Ref: ID 1031 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Retimonocolpites "*heteroretifossulatus*." Ref: ID 2091 (Jaramillo & Rueda, 2013); figs. 20–22 (Graham, 1988b); figs. 25–27 (Graham, 1989). Affinity: Monocotyledoneae, Arecaceae, *Manicaria* Gaertn. type.

Retimonocolpites "*palmatus*" (Figs. 121, 122). Amb circular, slightly elliptic; monocolpate, colpus wide, straight, extending nearly entire length of grain; reticulate, lumina variable, 1–1.5 µm wide, decreasing toward aperture, rounded, muri thick, simplicolumellate; tectate, wall 1 µm thick; 24 × 18 µm. Affinity: Monocotyledoneae, Arecaceae, *Cryosophila*.

Retipollenites "*minutus*" (Figs. 123, 124). Spherical, amb circular; inaperturate; reticulate, lumina 1 µm wide; tectate, wall 1 µm thick, densely columellate, columellae baculae-shaped; 12 µm. Affinity: Monocotyledoneae, Araceae.

ANGIOSPERMS: EUDICOTS

Acanthaceae aff. "*hygrophilensis*" (Fig. 125). Suboblate, amb circular; stephanocolporate, approximately 10 to 12 colpi, equatorially arranged, equidistant, thin, straight, extending nearly entire length of grain; pores inconspicuous, not seen in polar view; baculate, baculae irregular; intectate, wall 2 µm thick, sexine 1 µm thick, nexine 1 µm thick, columellae 1 µm thick, tectum absent; 21 µm. Affinity: Dicotyledonae, Acanthaceae, *Hygrophila guianensis* Nees.

Alnipollenites verus (Fig. 126). Suboblate, amb circular; stephanoporate, pores 5, vestibulate, circular, 3–4 µm wide; psilate; tectate, wall 1–2 µm thick, densely columellate; 18–20 µm. Ref: ID 15 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Betulaceae, *Alnus* Mill.

Anacardiaceae "*morenensis*" (Figs. 127, 128). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, straight, extending nearly entire length of grain, apparently having costae colpi 5–6 µm wide; pore oblongate, becoming circular, 4 µm wide; striato-reticulate, striae not well defined, thin, longitudinally oriented, lumina uniform, < 1 µm wide; tectate, wall 2 µm thick, sexine 1 µm thick, nexine 1 µm thick, tectum 1 µm thick; 26 × 18 µm wide. Affinity: Dicotyledonae, Anacardiaceae, *Spondias* L.

Annonaceae (*Cymbopetalum*). Ref: figs. 1, 2 (Graham, 1991b). Affinity: Dicotyledonae, Annonaceae, *Cymbopetalum* Benth.

Baculipollenites "*inciertus*" (Fig. 129). Suboblate, amb circular-triangular-convex, trilobate; tricolporate, equatorially arranged, equidistant, thin, acute, extending 3/4 length of grain, pores apparently endexinic, protruding; baculate, baculae < 1 µm tall; tectate, wall ca. 1.2 µm thick at intercolpium area, 2 µm at colpus area; 39 µm. Affinity: Dicotyledonae.

"Bignoniaceae" Type (Figs. 130, 131). Suboblate, amb circular-triangular-convex; tricolporate, equatorially arranged, equidistant, thin, acute, extending 3/4 length of grain, pores circular, 5 µm wide; scabrate, scabrae < 1 µm tall; tectate, wall ca. 1.5 µm thick; 22 × 24 µm. Affinity: Dicotyledonae, Bignoniaceae, *Tabebuia* Gomes ex DC.

Bombacaceae (cf. *Aguiaria*). Ref: fig. 30 (Graham, 1989); fig. 6 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae-Bombacoideae, *Aguiaria* Ducke.

Bombacacidites araracuarensis. Ref: fig. 34 (Graham, 1989); fig. 9 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Ceiba* Mill.

Bombacacidites baculatus (Fig. 132). Oblate, amb triangular-obtuse-straight; tricolporate, colpi equatorially arranged, equidistant, short, pointed ends, pores inconspicuous, circular; reticulate, lumina variable, scrobiculate at polar areas, diminishing from 2 µm (polar area) to < 0.5 µm wide at equatorial interaperture areas, muri simplicolumellate, free bacuale at apertures; semitectate, wall 1–2.5 µm thick; 50 µm (polar diameter). Ref: ID 55 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Pachira aquatica* Aubl.

Bombacacidites "*bombacopsiformis*" (Figs. 133, 134). Oblate, amb triangular-obtuse-straight; tricolporate, colpi equatorially arranged, equidistant, short, pointed ends, pores inconspicuous, apparently protruding, small; reticulate, lumina diminishing from 2 µm (polar area) to < 0.5 µm wide (equatorial interaperture areas), muri simplicolumellate; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 27 µm (polar diameter). Ref: fig. 7 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Bombacopsis* Pittier/*Bernoullia* Oliv. types.

Bombacacidites brevis (Figs. 135, 136). Oblate, amb circular; apparently tricolporate, colpi equatorially arranged, equidistant, short, rounded ends, pores inconspicuous, small, annulate, lolongate; reticulate, lumina < 1 µm wide (equatorial interaperture areas), muri simplicolumellate, columellae dense; tectate, wall < 1 µm thick; 20 µm (polar diameter). Ref: fig. 108 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 10.

Bombacacidites "*colpiechinatus*" (Fig. 137). Oblate, amb triangular-obtuse-convex; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, indistinct; pores inconspicuous, echinate, echinae short, scarcely distributed; tectate; 21 × 24 µm. Affinity: Dicotyledonae, Malvaceae–Bombacoideae.

Bombacacidites nacimientoensis. Ref: fig. 7 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Bernoullia*.

Bombacacidites "*problematicus*" (Figs. 138, 139). Oblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short; reticulate, lumina variable, mesocolpium psilate to micropitted; tectate; 20 × 28 µm. Affinity: Dicotyledonae, Malvaceae–Bombacoideae.

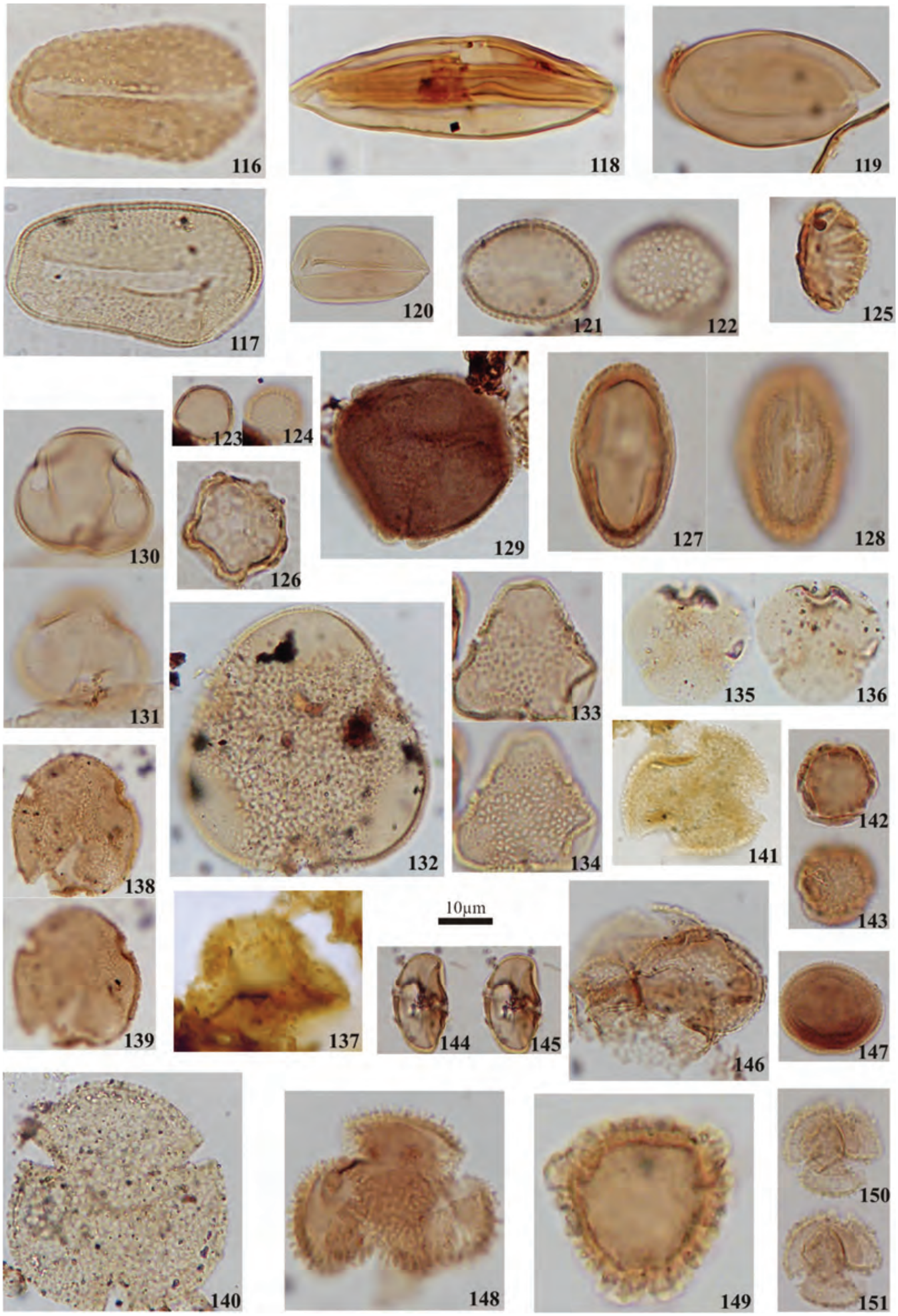
Bombacacidites "*pseudobombiformis*" (Fig. 140). Oblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, acute ends, pores inconspicuous, small; reticulate, lumina homogeneous, fine, 1 µm wide, muri simplicolumellate; tectate, wall 1.5 µm thick; 44 µm (polar diameter). Ref: fig. 8 (Graham, 1991b); fig. 35 (Graham, 1989). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Pseudobombax septenatum* (Jacq.) Dugand.

Brevitricolpites "*panamensis*" (Fig. 141). Spherical, amb circular; tricolpate, colpi equatorially arranged, equidistant, short, wide, margins straight, ends pointed, costate, margo 4 × 1 µm; baculate, baculae short, rounded; intectate, wall 1 µm thick; 27.5 µm. Affinity: Dicotyledonae.

Brevitricolpites "*triangulatus*." Ref: fig. 91 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 9.

Brevitricolpites "*scabratus*" (Figs. 142, 143). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, thin, straight, short,

PLATE 5. Figures 116–151.
116. *Palmapollenites* "phytelephensis" SL G29-2, EF O-13, Gatun Fm. –9.6 Ma.
117. *Palmapollenites* "scheeleaensis" SL 17, EF H-14/4, Tuira Fm. –6.95 Ma.
118. *Psilamonocolpites* "longiformis" SL 158, EF N-10/2=4, Gatun Fm. –8.6 Ma.
119. *Psilamonocolpites medius* SL 174, EF M-15/1, Gatun Fm. –10.0 Ma.
120. *Psilamonocolpites rinconii* SL 4, EF A-9/4, Gatun Fm. –9.6 Ma.
121, 122. *Retimonocolpites* "palmatus" SL 5a, EF J-21/2, Gatun Fm. –10.2 Ma.
123, 124. *Retipollenites* "minutus" SL 175, EF J-35/1, Gatun Fm. –9.6 Ma.
125. *Acanthaceae* aff. "hygrophilensis" SL 178, EF W-10/2, Escudo Veraguas Fm. –2.05 Ma.
126. *Alnipollenites verus* SL 210, EF X-35/2, Gatun Fm. –9.6 Ma.
127, 128. *Anacardiaceae* "morenensis" SL 2165, EF W-22/1=2, Escudo Veraguas Fm. –2.05 Ma.
129. *Baculipollenites* "inciertus" SL G26-1, EF J-18/1, Gatun Fm. –5.6 Ma.
130, 131. "Bignoniaceae" Type SL 175/6, EF U-21/4, Gatun Fm. –10.0 Ma.
132. *Bombacacidites baculatus* SL 193, EF H-15/4, Chucunaque Fm. –7.05 Ma.
133, 134. *Bombacacidites* "bombacopsiformis" SL 178, EF U-9/1, Gatun Fm. –5.6 Ma.
135, 136. *Bombacacidites brevis* SL 193, EF E-22/4, Chagres Fm. –10.0 Ma.
137. *Bombacacidites* "colpiechinatus" SL Cucaracha 56.5, EF S-47/1, Cucaracha Fm. –18.93 Ma.
138, 139. *Bombacacidites* "problematicus" SL 1620, EF H-36/1, Gatun Fm. –10.2 Ma.
140. *Bombacacidites* "pseudobombiformis" SL 193, EF Y-22/1, Gatun Fm. –5.6 Ma.
141. *Brevitricolpites* "panamensis" SL La Boca 37.5, EF E-47/2, Culebra Fm. –19.20 Ma.
142, 143. *Brevitricolpites* "scabratus" SL 168, EF C-21/4, Gatun Fm. –5.6 Ma.
144, 145. *Burseraceae* "protiumensis" SL 174, EF C-39/3, Gatun Fm. –10.2 Ma.
146. *Chelonanthus* type SL 5a, EF S-25/3, Gatun Fm. –5.6 Ma.
147. *Clavainaperturites microclavatus* SL G26-1, EF L-7/2, Gatun Fm. –10.2 Ma.
148. *Clavapollenites* "circularis" SL G27-2, EF F-19/1, Cayo Agua Fm. –4.25 Ma.
149. *Clavapollenites* "triangulatus" SL 60, EF Q-10/1, Cayo Agua Fm. –4.25 Ma.
150, 151. *Clavatricolpites* "infinitus" SL G26-1, EF N-52/4, Gatun Fm. –10.0 Ma.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inconspicuous, pores elongated, short, becoming lineal, ca. 3 µm long; verrucate-perforate, showing variable and small verrucae with small perforation betwen them resembling rugulate pattern, verrucae variable, 1–1.5 µm tall; tectate, wall 2 µm thick, tectum 1 µm thick, sexine 1 µm thick, nexine 1 µm thick; 14 µm. Affinity: Dicotyledonae, Fabaceae.

Brevitricolpites sp. Ref: fig. 96–98 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 8.

Burseraceae "*protiumensis*" (Figs. 144, 145). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, thin, extending nearly entire length of grain, straight, pore elongated-oblongate, ca. 4 × 8 µm; reticulate, muri simplicolumellate, columellae thin, dense; tectate, wall variable, 1 µm thick at polar area and 2 µm thick at aperture areas, tectum 1 µm thick, sexine 1 µm thick, nexine 1 µm thick; 19–20 × 12–16.5 µm. Affinity: Dicotyledonae, Burseraceae, *Protium* Burm. f.

Cabombaceae (*Cabomba*). Ref: fig. 38 (Graham, 1991b). Affinity: Dicotyledonae, Cabombaceae, *Cabomba* Aubl.

Chelonanthus type (Fig. 146). Lineal and crossed tetrad; individual grains oblate (compressed in tetrad), amb circular; triporate, pores adjacent at contact areas between grains, circular, 2 µm wide, annulate, annulus thin; reticulate, lumina variable, 1–2.5 µm wide, muri thin, simplibacullate; tectate, wall 1 µm thick; individual grains 26 µm, tetrad 38 µm. Affinity: Dicotyledonae, Gentianaceae, *Chelonanthus alatus* (Aubl.) Pulle.

Cichoreacidites longispinosus Ref: ID 318 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae, Liguliflorae type.

Clavainaperturites clavatus Ref: ID 152 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Clavainaperturites microclavatus (Fig. 147). Spherical, amb circular; inaperturate; clavate, clavae resembling small and fine baculae < 1 µm tall; intectate, wall 1 µm thick; 20 µm. Ref: ID 1056 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Chloranthaceae, *Hedyosmum* Sw.

Clavapollenites "*circularis*" (Fig. 148). Spherical, amb circular-trilobate; tricolpate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, wide, with margins bordered by baculae; clavate-baculate, baculae ca. 1.5 µm tall; intectate, wall ca. 2.5 µm thick, exhibiting dense and uniform baculae; 38 µm. Affinity: Dicotyledonae, Euphorbiaceae.

Clavapollenites "*triangulatus*" (Fig. 149). Amb triangular-obtuse-convex; tricolporate, colpi equatorially arranged, equidistant, short, pore indistinct; reticulate, lumina variable, 2–4 µm wide, muri curvimurate, simplicolumellate, columellae ca. 2.5 µm long; semitectate, wall 4 µm thick; 38 µm. Affinity: Dicotyledonae.

Clavatricolpites "*infinitus*" (Figs. 150, 151). Subprolate, amb circular; tricolpate, colpi equatorially arranged, equidistant, wide, deep, extending 3/4 length of grain, pores inconspicuous; clavate, having irregular and dispersed clavae not longer than 1 µm; intectate, wall 1.5 thick; 19 µm. Affinity: Dicotyledonae.

Clavatricolpites "*tectatum*." Ref: ID 915 (Jaramillo & Rueda, 2013); figs. 55–58 (Graham, 1988a). Affinity: Dicotyledonae, Euphorbiaceae, *Tetrorchidium* Poepp.

Combretaceae (cf. *Bucida*). Ref: figs. 10, 11 (Graham, 1991b). Affinity: Dicotyledonae, Combretaceae, cf. *Bucida* L.

Compositae (Mutisieae type). Ref: fig. 14 (Graham, 1991b). Affinity: Dicotyledonae, Asteraceae, Mutisieae type.

Corsinipollenites psilatus (Fig. 152). Suboblate, amb circular; triporate, pores circular, annulate, inconspicuous, protruding, coarse; scabrate; tectate, wall variable, 3 µm thick at intercolporium area to 7 µm thick at aperture; 27 µm. Ref: ID 175 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Onagraceae, *Ludwigia* L.

Crassiectoapertites columbianus (Fig. 153). Suboblate, amb circular-triangular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, straight, wide, acute ends, almost joined at apices, pore inconspicuous, probably circular; psilate; tectate, wall 4 µm thick; 47 µm. Ref: ID 180 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Fabaceae–Faboideae, *Dioclea reflexa* Hook. f.

Cricotriporites aff. *macroporus*. Ref: ID 198 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Cricotriporites "*minimus*" (Figs. 154, 155). Spherical, amb circular; triporate, pore equatorially arranged, equidistant, circular, annulate; psilate, intectate; 8 µm. Affinity: Dicotyledonae.

Crototricolpites "*euphorbiensis*" (Figs. 156, 157). Subprolate, amb circular; tricolpate, colpi equatorially arranged, equidistant, inconspicuous, masked by sculptural elements; clavate-verrucate, clavae short, resembling verrucae pattern, uniform; intectate, wall ca. 1 µm thick; 34 × 25 µm. Affinity: Dicotyledonae, Euphorbiaceae.

Crototricolpites "*pseudodaemoni*" (Figs. 158, 159). Spheroidal, amb circular; tricolpate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, inconspicuous; clavate, clavae resembling the crotonoid pattern, 1–1.5 µm high, > 1 µm wide, irregular, becoming baculae or gemmae; intectate, wall > 1 µm thick; 23 µm. Affinity: Dicotyledonae, Euphorbiaceae.

Cucurbitaceae Type (Fig. 160). Spherical, amb circular; periporate, pores 4 to 6, inconspicuous, circular, wide, annulate; baculate-echinate, baculae short, thin, echinae rounded, conical, ca. 5 × 2 µm; intectate, wall 6 µm thick; 52 µm. Affinity: Dicotyledonae, Cucurbitaceae.

Echiperiporites akanthos (Figs. 161, 162). Spherical, amb circular; periporate, 6 pores, uniformly distributed, appearing as equatorial area resembling stephanoporate condition, pores circular, 1.5 µm wide, annulate, annulus 1 µm thick; echinate, echinae conical, sharp, wide at base, short, ca. 1 µm long; tectate, wall 1.5 µm thick; ca. 23 µm. Affinity: Dicotyledonae.

Echiperiporites estelae (Fig. 163). Spherical, amb circular; periporate, > 20 pores, uniformly distributed, pores circular, 3.5 µm wide, annulate, annulus 2 µm thick; echinate-scabrate, echinae acute, ca. 5 µm long, wide at base; tectate, wall 3 µm thick; ca. 45 µm. Ref: ID 251 (Jaramillo & Rueda, 2013); fig. 36 (Graham, 1991b); figs. 59, 60 (Graham, 1988a). Affinity: Dicotyledonae, Malvaceae–Malvoideae, *Thespesia populnea* (L.) Sol. ex Corrêa, *Hibiscus tiliaceus* L., *Hampea* Schltdl./*Hibiscus* L. types; Convolvulaceae, *Ipomoea* L.

Echiperiporites "*ipomoensis*" (Figs. 164, 165). Spherical, amb circular; periporate, pores uniformly distributed, equidistant, circular, 3–4 µm wide; echinate, surface between echinae scabrate; tectate, wall 1.5–2 µm thick, columellae baculae-shaped; 35–44 µm. Affinity: Dicotyledonae, Convolvulaceae, *Ipomoea* L.

Echiperiporites "*pantagruelicus*" (Fig. 166). Spherical, amb circular; periporate, pores uniformly distributed, equidistant pores circular; echinate, echinae 15–17 µm long, uniformly arranged on surface; tectate, wall 5 µm thick, columellae 1 µm long, size increasing under the spines, tectum 0.5 µm thick, sexine 1.5 µm thick, nexine 4 µm thick; ca. 100 µm. Affinity: Dicotyledonae, Malvaceae.

Echiperiporites sp. Ref: fig. 81 (Graham, 1988b). Affinity: Dicotyledonae, Unknown 1.

Echitricolporites "*chiquitinus*" (Figs. 167–169). Prolate-spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, thin, pore indistinct, probably elongated, small; echinate, echinae acute, 2 µm tall; tectate, wall 3 µm thick (including ornamentation); 13 × 11.5 µm. Affinity: Dicotyledonae, Asteraceae.

Echitricolporites mcneillyi. Ref: ID 261 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae.

Echitricolporites "*microspinosus*" (Figs. 170, 171). Subprolate, amb circular, becoming spheroidal; tricolporate, colpi equatorially arranged, equidistant, short, wide, not well defined, having irregular margo interrupted at equator, pores elongated-oblongate; echinate, echinae short, scarce, acute, wide at base; tectate, wall 2.5 µm thick (including ornamentation); 26 × 24 µm. Affinity: Dicotyledonae, Boraginaceae, *Cordia* L.

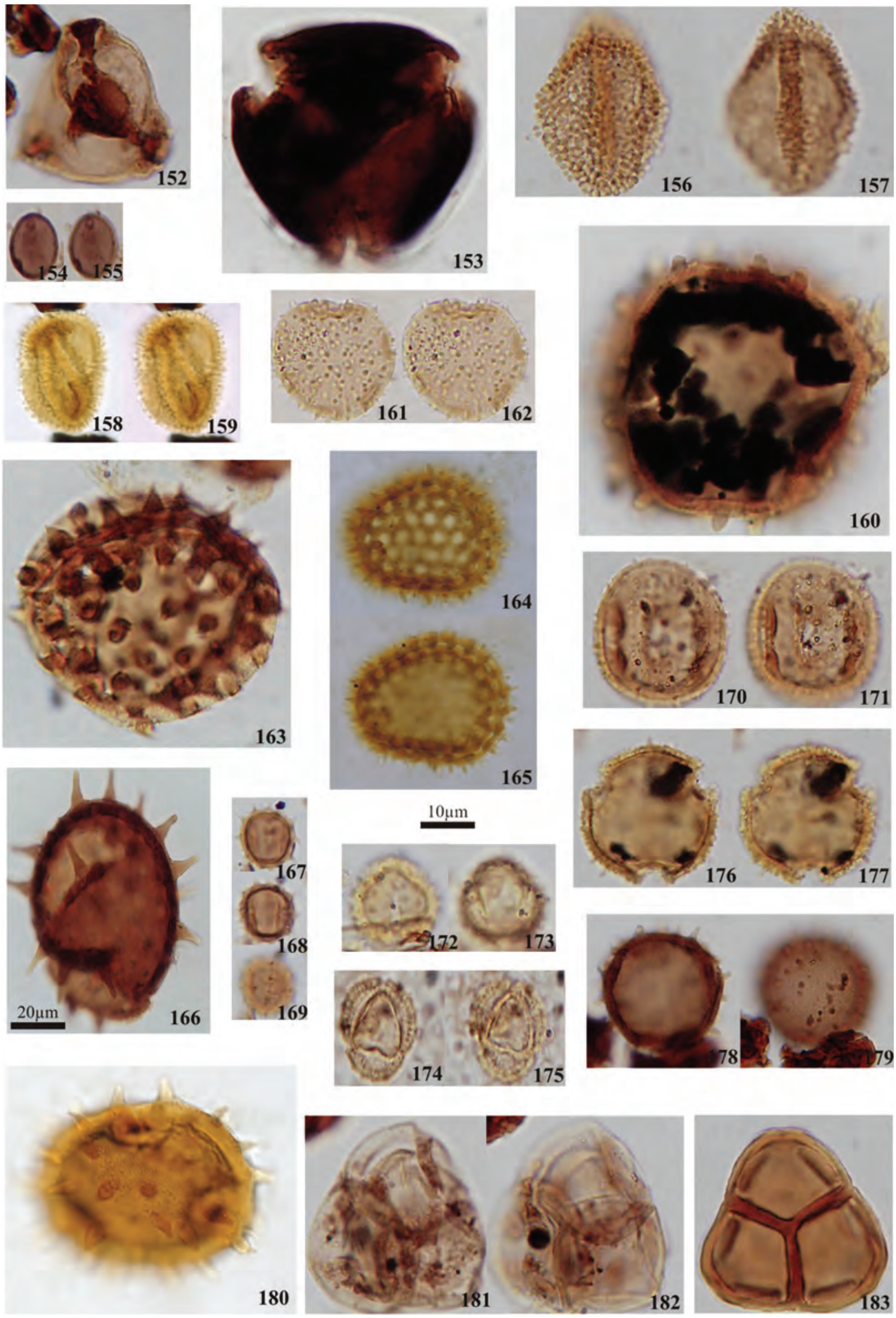
Echitricolporites spinosus (Figs. 172, 173). Spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, straight, wide, pores inconspicuous, apparently lalongate; echinate, echinae coarse, 1 µm long, wide at base, acute ends; tectate, wall 2.5 µm thick, sexine clearly separated from nexine; 15 µm. Ref: ID 263 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae, Tubiliflorae, *Espeletia* Mutis ex Bonpl., *Mikania* Willd., *Pectis* L., *Riencourtia* Cass., *Wedelia* Jacq., *Wulffia* Neck. ex Cass. types.

Echitricolporites "*spinosus*" var. "*microspinosus*" (Figs. 174, 175). Spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, pores inconspicuous; echinate, echinae thin, short, < 1 µm long, scarce, acute ends; tectate, wall 2 µm thick; 18 µm. Affinity: Dicotyledonae.

Echitricolporites "*vesiculoides*." Ref: ID 2094 (Jaramillo & Rueda, 2013). Ref: figs. 42, 43 (Graham, 1988a). Affinity: Dicotyledonae, Asteraceae.

Echitriporites "*abutiloensis*" (Figs. 176, 177). Suboblate, amb circular; triporate, pores circular, ca. 5 µm wide, bordered by dense patches of small baculae; baculate, baculae 1–2.5 µm long; intectate, wall 2.5 µm thick (excluding ornamentation);

PLATE 6. Figures 152–183.
152. *Corsinipollenites psilatus* SL 6, EF R-19/4, Gatun Fm. –9.6 Ma.
153. *Crassiectoapertites columbianus* SL 357, EF O-39/3=4, Gatun Fm. –10.05 Ma.
154, 155. *Cricotriporites* "minimus" SL 2202, EF V-33/4, Shark Hole Point Fm. –4.6 Ma.
156, 157. *Crototricolpites* "euphorbiensis" SL 307, EF S-19/3, Chagres Fm. –10.0 Ma.
158, 159. *Crototricolpites* "pseudodaemoni" SL La Boca 58.5, EF E-55, Culebra Fm. –19.24 Ma.
160. Cucurbitaceae Type SL 307, EF E-16/1, Cayo Agua Fm. –3.55 Ma.
161, 162. *Echiperiporites akanthos* SL 1617, EF U-24, Pucro Fm. –6.95 Ma.
163. *Echiperiporites estelae* SL 6, EF D-4, Gatun Fm. –9.6 Ma.
164, 165. *Echiperiporites* "ipomoensis" SL 349, EF Y-20, Cayo Agua Fm. –4.25 Ma.
166. *Echiperiporites* "pantagruelicus" SL 1152, EF Q-18, Cayo Agua Fm. –3.55 Ma.
167–169. *Echitricolporites* "chiquitinus" SL G26-1, EF L-44, Gatun Fm. –10.0 Ma.
170, 171. *Echitricolporites* "microspinosus" SL 193, EF E-22/4, Tuira Fm. –12.6 Ma.
172, 173. *Echitricolporites spinosus* SL 174, EF X-16/1, Gatun Fm. –10.2 Ma.
174, 175. *Echitricolporites* "spinosus" var. "microspinosus" SL196, EF L39/1, Cayo Agua Fm.–4.25 Ma.
176, 177. *Echitriporites* "abutiloensis" SL 177, EF R-12/4, Escudo Veraguas Fm. –2.05 Ma.
178, 179. *Echitriporites* aff. "eocenicus" SL G27-2, EF Q-14, Gatun Fm. –5.6 Ma.
180. *Echitriporites* "megaexinatus" SL Cucaracha 46.5, EF E-38/2, Cucaracha Fm. –18.48 Ma.
181, 182. *Ericipites* "baculatus" SL G26-1, EF Q-11/2, Cayo Agua Fm. –4.25 Ma.
183. *Ericipites* "psilatus" SL G27-2, EF F-20=F-21, Gatun Fm. –10.0 Ma.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27 µm. Affinity: Dicotyledonae, Malvaceae-Malvoideae, *Abutilon* Mill.

Echitriporites aff. "*eocenicus*" (Figs. 178, 179). Suboblate, amb circular; triporate, pores circular, ca. 5 µm wide, subtly bordered by dense patches of small baculae; baculate, baculae variable, irregular, large and bottle shaped, scarce, short and thin, densely distributed; intectate, wall 2 µm thick (excluding ornamentation); 24 µm. Affinity: Dicotyledonae, Theaceae.

Echitriporites "*megaexinatus*" (Fig. 180). Subprolate, amb circular; triporate, pores circular, 4–7 µm wide, costate, annulus thick; echinate, echinae 5 µm long, scarcely distributed; tectate, wall ca. 3 µm thick; 50 µm. Affinity: Dicotyledonae.

Ericaceae Type 1. Ref: fig. 18 (Graham, 1991b). Affinity: Dicotyledonae, Ericaceae Type 1.

Ericaceae Type 2. Ref: fig. 19 (Graham, 1991b). Affinity: Dicotyledonae, Ericaceae Type 2.

Ericipites "*baculatus*" (Figs. 181, 182). Tetrahedral tetrad and crossed tetrad; individual grains oblate, amb circular-trilobate; tricolporate, colpi equatorially arranged, equidistant, wide, acute, 3/4 as long as grain, having thin costae, pores probably elongated-ellipsoidal; baculate, baculae as free columellae < 1 µm long; intectate, wall 1 µm thick; tetrahedral tetrad 30–33 µm, crossed tetrad 25 × 33 µm. Affinity: Dicotyledonae, Ericaceae.

Ericipites "*psilatus*" (Fig. 183). Tetrahedral tetrad; individual grains oblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, wide, rounded ends, marginate, margo coarse, pores lalongate, displaying the "H" condition, masked by point of junction between grains; psilate to slightly scabrate; tectate, wall 2 µm thick; individual grain 24 µm, tetrad 34 µm. Ref: fig. 19 (Graham, 1991b). Affinity: Dicotyledonae, Ericaceae Type 2.

Erythrina. Ref: fig. 26 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae–Faboideae, *Erythrina* L.

Euphorbiaceae (cf. *Glycydendron*). Ref: figs. 21, 22 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, cf. *Glycydendron* Ducke.

Euphorbiaceae (cf. *Jatropha*). Ref: fig. 20 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, cf. *Jatropha* L.

Euphorbiaceae (cf. *Stillingia*). Ref: fig. 23 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, cf. *Stillingia* Garden ex L.

Fagaceae (*Quercus*). Ref: fig. 16 (Graham, 1991b). Affinity: Dicotyledonae, Fagaceae, *Quercus* L.

Fenestrites spinosus (Figs. 184, 185). Spheroidal, amb circular; lophate, ca. 20 lacunae, lacunae almost pentagonal, 6 µm wide, lacunae bridges 2 µm wide; echinate, echinae short, 1–1.5 µm long, acute ends; tectate, wall 7 µm thick, strongly columellate, columellae bifurcated; 28 µm. Ref: ID 319 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae, Liguliflorae, *Vernonia* Schreb.

Foveostephanocolpites CU488. Ref: fig. 107 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 4.

Foveotricolporites "*brevicolpatus*" (Figs. 186, 187). Spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, straight, inconspicuous; pores circular; foveolate; tectate, wall 1 µm thick; 39 × 35 µm. Affinity: Dicotyledonae.

Foveotricolporites "*cingulatum*" (Figs. 188, 189). Prolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, straight, thin, surrounded by a thick and conspicuous margo becoming wider at equator, pore elongated almost as a continuous equatorial ring (colpus equatorialis); reticulate, lumina 1 μm wide, muri simplicolumellate; tectate, wall 1.8 μm thick; 38 × 22 μm. Affinity: Dicotyledonae, Euphorbiaceae, *Sapium caudatum* Pittier.

Foveotricolporites "*colonensis*." Ref: ID 116 (Jaramillo & Rueda, 2013). Ref: figs. 46–48 (Graham, 1988a). Affinity: Dicotyledonae, Dilleniaceae, *Doliocarpus* Rol.

Foveotriporites "*bocencis*" (Figs. 190, 191). Spherical, amb circular; triporate, pores circular, 4 μm wide; foveolate, foveolae variable, 1–1.5 μm wide; tectate, wall 2–3 μm thick; 38 μm. Ref: figs. 101, 102–104 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Types 11 & 12.

Foveotriporites "*ochromensis*" (Figs. 192, 193). Spherical, amb circular; triporate, pores circular, 6 μm wide, annulate, annulus 2.5 μm thick; foveolate, foveolae variable, 1.5–4.5 μm wide; semitectate, wall scrobiculate, 2.5 μm thick; 35 μm. Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Ochroma pyramidale* (Cav. ex Lam.) Urb.

Foveotriporites "*protohammenii*" (Fig. 194). Spherical, amb circular; triporate, pores circular, 3.5 μm wide; foveolate, foveolae 1 μm wide; tectate, wall 2 μm thick; 30 μm. Ref: figs. 63, 64 (Graham, 1988a). Affinity: Dicotyledonae, Rubiaceae, *Sabicea* Aubl.

Gemmatricolporites sp. Ref: figs. 105, 106 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 6.

Gemmatriporites "*matisialis*" (Figs. 195, 196). Spherical, amb circular; triporate, pores inconspicuous, wide, annulate, surrounded by dense gemmae; gemmate, gemmae 1.5 μm tall; intectate, wall 1 μm thick; 25 μm. Affinity: Dicotyledonae, Malvaceae-Bombacoideae.

Hauya. Ref: fig. 37 (Graham, 1991b). Affinity: Dicotyledonae, Onagraceae, *Hauya* DC.

Heterocolpites "*combretoides*" (Figs. 197–199). Spherical, amb circular-hexalobate; heterocolpate, with three pseudocolpi, equatorially arranged, equidistant, colpi thin, extending nearly entire length of grain, 1.5 μm wide, pores elongated; psilate; tectate, wall 1 μm thick, tectum 0.5 μm thick, sexine 0.5 μm thick, nexine 0.5 μm thick; 12 μm. Affinity: Dicotyledonae, Combretaceae, *Combretum* Loefl.

Heterocolpites incomptus. Ref: ID 1021 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Melastomataceae, *Miconia* Ruiz & Pav.

Heterocolpites "*irregularis*" (Figs. 200, 201). Spherical, amb circular; heterocolpate, with three pseudocolpi, equatorially arranged, equidistant, colpi thin, inconspicuous, extending nearly entire length of grain, pore indistinct, circular; psilate, slightly scabrate; tectate, wall 1 μm thick, tectum 0.5 μm thick, sexine 0.5 μm thick, nexine 0.5 μm thick; 9.5 μm. Affinity: Dicotyledonae, Melastomataceae.

Heterocolpites "*melastomicus*" (Figs. 202, 203). Subprolate, amb circular-hexalobate; heterocolpate, with three pseudocolpi, equatorially arranged, equidistant, colpi thin, extending nearly entire length of grain, showing slightly "exitus digitus," pores circular to slightly ovate, 4 μm wide; psilate; tectate, wall 1 μm thick; 15 × 12.5 μm. Affinity: Dicotyledonae, Melastomataceae.

Heterocolpites "*minutus*" (Figs. 204–206). Prolate spheroidal, amb circular; heterocolpate, with three pseudocolpi, equatorially arranged, equidistant, colpi thin, inconspicuous, extending nearly entire length of grain, pores elongated, becoming almost rectangular, depressed, colpori wider than colpi; psilate; tectate, wall 1 µm thick; 9 × 8 µm. Affinity: Dicotyledonae, Melastomataceae.

Heterocolpites rotundus. Ref: ID 1022 (Jaramillo & Rueda, 2013); figs. 4, 5 (Graham, 1991b); figs. 40, 41 (Graham, 1988a). Affinity: Dicotyledonae, Combretaceae, *Combretum/Terminalia* L. types.

Ilexpollenites "*clavavariatus*." Ref: ID 2093 (Jaramillo & Rueda, 2013); fig. 3 (Graham, 1991a). Affinity: Dicotyledonae, Aquifoliaceae, *Ilex* L.

Ilexpollenites "*larguitus*" (Figs. 207, 208). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending 3/4 length of grain, slightly irregular, margins masked by sculptural elements, pore inconspicuous, apparently circular; clavate, clavae irregular, < 1 to 2.5 µm high; intectate, wall ca. 1 µm thick; 30 × 23 µm. Affinity: Dicotyledonae, Aquifoliaceae, *Ilex*.

Inaperturopollenites "*crotonoides*" (Figs. 209, 210). Spherical, amb circular; inaperturate; clavate, clavae arranged in a crotonoid pattern; intectate, wall 1.5 µm thick; 23 µm. Affinity: Dicotyledonae.

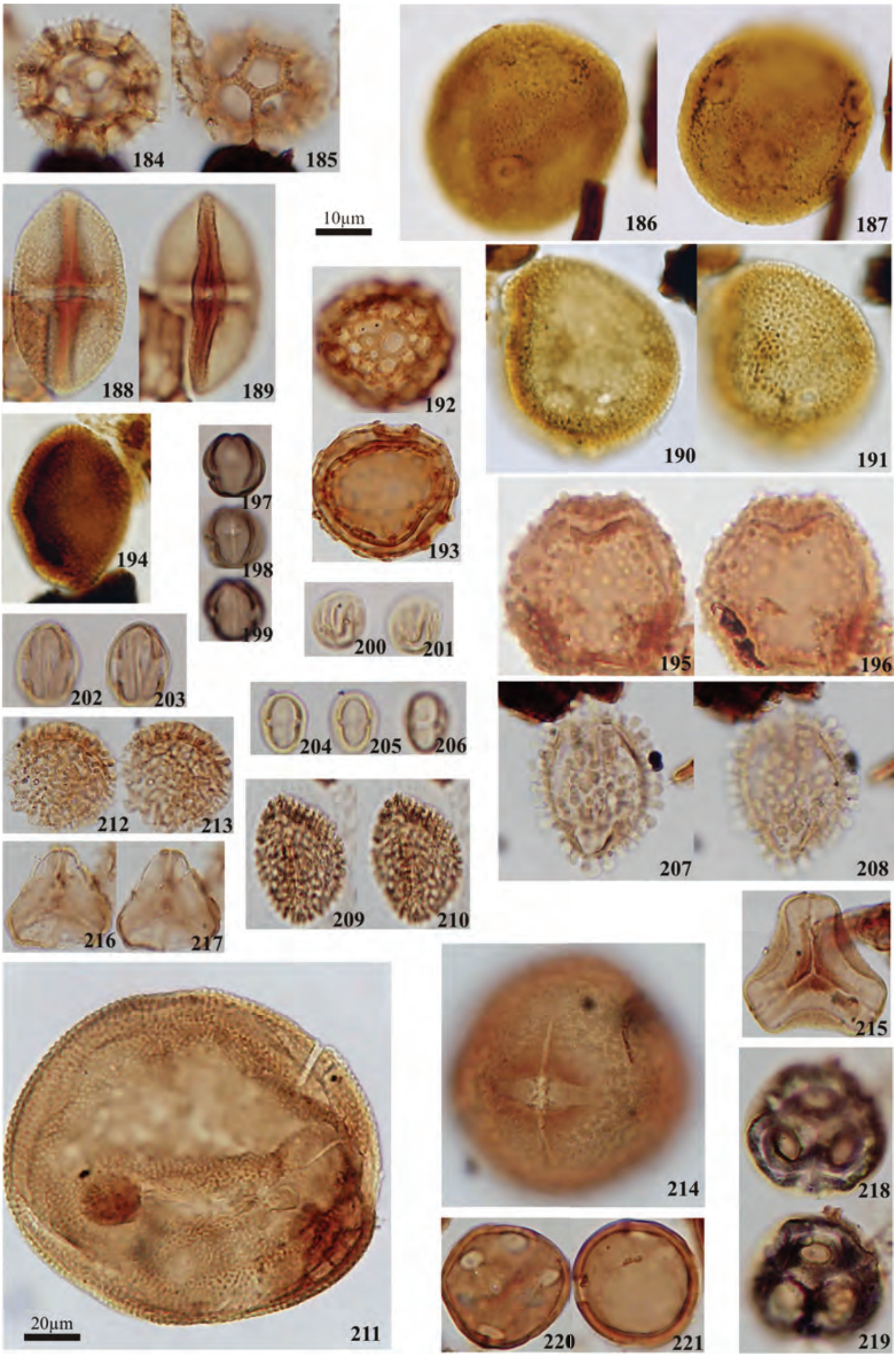
Inaperturopollenites "*grandiosus*" (Fig. 211). Spherical, amb circular; inaperturate; gemmate, gemmae ca. 1 µm tall, rounded, uniformly distributed; intectate, wall 2.5 µm thick; 122 µm. Affinity: Dicotyledonae, Annonaceae.

Inaperturopollenites "*reticulatus*" (Figs. 212, 213). Spherical, amb circular; inaperturate; reticulate, lumina variable, muri coarse, simplicolumellate, columellae clavate-shaped, ca. 1.5 µm long, rounded; tectate, tectum subtle, wall 2.5 µm thick; 19 µm. Ref: fig. 40 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Chomelia* Jacq. type.

Ladakhipollenites simplex. Ref: ID 424 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Lanagiopollis crassa (Fig. 214). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending 2/3 length of grain, costate,

PLATE 7. Figures 184–221.
184, 185. *Fenestrites spinosus* SL 175, EF Q-6/4, Escudo Veraguas Fm. –2.05 Ma.
186, 187. *Foveotricolporites* "brevicolpatus" SL Culebra 1.5, EFG-54/1, Culebra Fm. –19.18 Ma.
188, 189. *Foveotricolporites* "cingulatum" SL 178, EF Q-22/3, Tuira Fm. –12.6 Ma.
190, 191. *Foveotriporites* "bocencis" SL La Boca 67.5, EF H-45/3, Culebra Fm. –19.20 Ma.
192, 193. *Foveotriporites* "ochromensis" SL 1997, EF X-38/1, Chucunaque Fm. –6.95 Ma.
194. *Foveotriporites* "protohammenii" SL Culebra 3.5, EF V-18/4, Culebra Fm. –19.11 Ma.
195, 196. *Gemmatriporites* "matisialis" SL 18, EF J-24/1, Gatun Fm. –5.6 Ma.
197–199. *Heterocolpites* "combretoides" SL G26-1, EF N-23/3, Gatun Fm. –10.0 Ma.
200, 201. *Heterocolpites* "irregularis" SL 174, EF G-33/1, Escudo Veraguas Fm. –2.05 Ma.
202, 203. *Heterocolpites* "melastomicus" SL G26-1, EF H-17/3, Tuira Fm. –6.95 Ma.
204–206. *Heterocolpites* "minutus" SL 174, EF E-48/4, Escudo Veraguas Fm. –3.55 Ma.
207, 208. *Ilexpollenites* "larguitus" SL G26-1, EF R-8, Tuira Fm. –12.6 Ma.
209, 210. *Inaperturopollenites* "crotonoides" SL 11, EF G-7/4, Escudo Veraguas Fm. –2.75 Ma.
211. *Inaperturopollenites* "grandiosus" SL 19, EF O-19/4, Gatun Fm. –5.6 Ma.
212, 213. *Inaperturopollenites* "reticulatus" SL G27-2, EF C-6, Gatun Fm. –10.2 Ma.
214. *Lanagiopollis crassa* SL 178, EF S-7/4, Tuira Fm. –12.6 Ma.
215. *Loranthaceae* "atriensis" SL 11, EF J-10, Gatun Fm. –5.6 Ma.
216, 217. *Loranthaceae* "marginalis" SL 168, EF D-17/1, Nancy Point Fm. –5.65 Ma.
218, 219. *Loranthaceae* "oryctanthusis" SL 175, EF F-51/4, Escudo Veraguas Fm. –2.05 Ma.
220, 221. *Malpighiaceae* "bunchoensis" SL 174, EF M-25/1; SL 391, EF K-10/4, Gatun Fm. –9.6 Ma.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straight, wide, pore lalongate, ca. 7 × 23 µm; reticulate, lumina < 1 µm wide. Muri thin, pluricolumellate, columellae densely present, thin; tectate, wall 3–3.5 µm thick; 41–57 µm. Ref: ID 430 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Leguminosae. Ref: figs. 24–26 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae.

Lentibulariaceae. Ref: fig. 30 (Graham, 1991b). Affinity: Dicotyledonae, Lentibulariaceae, *Utricularia* L.

Loranthaceae "*atriensis*" (Fig. 215). Oblate, amb triangular-obtuse-concave; syncolpate, colpus thin; psilate to scabrate; tectate, wall thickest at intercolpium; 27 µm. Affinity: Dicotyledonae, Loranthaceae.

Loranthaceae "*marginalis*" (Figs. 216, 217). Oblate, amb triangular-obtuse-concave; syncolpate, colpi joined at polar areas forming small triangle (para-syncolpate condition), surrounded by thick and conspicuous margo; psilate; tectate, wall < 0.5 µm thick at intercolpium areas and 1 µm thick at aperture areas; 22 µm. Affinity: Dicotyledonae, Loranthaceae.

Loranthaceae "*oryctanthusis*" (Figs. 218, 219). Oblate, amb circular-semitriangular; tricolpate, structure complex, colpi joined at polar areas, bifurcated, forming three circular plates (aspis?) probably with pseudopori, each one 6 µm wide; psilate; tectate, wall 1 µm thick; 26 µm. Affinity: Dicotyledonae, Loranthaceae, *Oryctanthus* (Griseb.) Eichler.

Loranthaceae Type 1. Ref: fig. 31 (Graham, 1991b). Affinity: Dicotyledonae, Loranthaceae Type 1.

Loranthaceae Type 2. Ref: fig. 32 (Graham, 1991b). Affinity: Dicotyledonae, Loranthaceae Type 2.

Malpighiaceae "*bunchoensis*" (Figs. 220, 221). Spherical, amb circular; periporate, 4 to 6 pores, equidistant, pores circular, 4–5 µm wide; psilate; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 22 µm. Affinity: Dicotyledonae, Malpighiaceae.

Malpighiaceae Type 2. Ref: fig. 40 (Graham, 1989); fig. 33 (Graham, 1991b). Affinity: Dicotyledonae, Malpighiaceae Type 2.

Margocolporites "*hematoxyformis*" (Figs. 222, 223). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, wide, acute ends, pores circular, 5 µm wide, annulate; reticulate, muri simplicolumellate, lumina variable, 1.5 µm wide; tectate, wall 2 µm thick; 22 µm. Affinity: Dicotyledonae, Fabaceae–Caesalpinioideae, *Caesalpinia* L.

Margocolporites vanwijhei. Ref: ID 465 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Fabaceae, *Adipera* Raf., *Brasilettia* (DC.) Kuntze, *Haematoxylum* L., *Mezoneuron* Desf., *Poincianella* Britton & Rose, *Caesalpinia bonduc* (L.) Roxb., *C. coriaria* (Jacq.) Willd.

Melastomataceae. Ref: fig. 27 (Graham, 1991b). Affinity: Dicotyledonae, Melastomataceae.

Momipites africanus (Figs. 224, 225). Spherical, amb circular; triporate, pores equatorially arranged, equidistant, circular, 2.5 µm wide, subtly protruding, annulate, annulus thin; psilate to slightly scabrate; tectate, wall 1 µm thick; 23 µm. Ref: ID 478 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Betulaceae, *Corylus* L.

Momipites "*panamensis*." Ref: ID 2097 (Jaramillo & Rueda, 2013); fig. 30 (Graham, 1988b); fig. 33 (Graham, 1989); fig. 17 (Graham, 1991b). Affinity: Dicotyledonae, Juglandaceae, *Alfaroa* Standl./*Oreomunnea* Oerst., *Alfaroa*/*Engelhardia* Lesch. ex Blume types.

Multimarginites vanderhammenii. Ref: ID 492 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Acanthaceae, *Sanchezia klugii* Leonard & L. B. Sm.

Myrtaceae Type (Figs. 226, 227). Oblate, amb triangular-acute-straight; syncolporate, colpi equatorially arranged, equidistant, straight, thin, pores circular, ca.1.5 μm wide; psilate to slightly scabrate; tectate, wall < 1 μm thick; 20 μm. Affinity: Dicotyledonae, Myrtaceae, *Psidium* L.

Nymphaeaceae. Ref: fig. 38 (Graham, 1991b). Affinity: Dicotyledonae, Nymphaeaceae, *Cabomba*.

Ochnaceae Type (Figs. 228, 229). Suboblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, thin, inconspicuous, short, marginate, margo coarse, pores circular, 3 μm wide, annulate; reticulate, lumina homogeneous, fine, < 1 μm wide, muri thin, simplicolumellate; tectate, wall 1 μm thick; 16.5 × 18 μm. Affinity: Dicotyledonae, Ochnaceae.

Onagraceae. Ref: fig. 37 (Graham, 1991b). Affinity: Dicotyledonae, Onagraceae, *Hauya*.

Pachydermites diederixi (Fig. 230). Suboblate to spheroidal, amb circular; stephanoporate, pores equatorially arranged, equidistant, circular, 6 μm wide, margins irregular; psilate; tectate, wall 4.5–5 μm thick; 42 μm. Ref: ID 509 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Clusiaceae, *Symphonia globulifera* L. f.

Papilionoideae. Ref: fig. 26 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae–Faboideae, *Erythrina* L.

Parsonsidites "*multiporatus*" (Figs. 231, 232). Spherical, amb circular; periporate, 5 pores, circular, 3 μm wide, annulate; psilate; tectate, wall 1 μm thick; 17 μm. Affinity: Dicotyledonae.

Perisyncolporites "*gemmatus*" (Figs. 233, 234). Spherical, amb circular; perisyncolporate, pseudocolpi inconspicuous, gemmate, gemmae 3 × 2–4 μm, ends rounded, pores circular; semitectate, wall 8 μm thick, columellae 1 μm tall, tectum 3 μm thick, tectum restricted only beneath gemmae; 25 μm. Affinity: Dicotyledonae, Malpighiaceae.

Perisyncolporites pokornyi (Figs. 235, 236). Spherical, amb circular; periporate, sometimes having subtle pseudocolpi resembling the perisyncolporate condition, pores circular, 3.5 μm wide; psilate; tectate, wall 3 μm thick, columellate, columellae baculae-shaped; 27 μm. Ref: ID 532 (Jaramillo & Rueda, 2013); figs. 61, 62 (Graham, 1988a). Affinity: Dicotyledonae, Malpighiaceae, *Brachypterys* A. Juss., *Banisteroides*, *Bunchosia* Rich. ex Juss., *Hiraea* Bertero ex DC., *Mascagnia* (Bertero ex DC.) Bertero, *Stigmaphyllon* A. Juss., *Tetrapterys* Cav.

Poloretitricolpites "*centenarius*." Ref: figs. 78, 79 (Graham, 1988a). Affinity: Dicotyledonae, Sapotaceae, *Pouteria* Aubl.

Polyadopollenites mariae (Fig. 237). Sixteen-celled polyad; individual grains oblate, amb trapezoid; probably periporate, pores small, inconspicuous, restricted to point of junction of grain; psilate; tectate, wall 2.5 μm thick, thicker at distal face; individual grains ca. 18 μm, polyad 45 μm. Ref: fig. 24 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae–Mimosoideae, *Acacia* Mill.

Polyadopollenites "*minutus*" (Figs. 238, 239). Sixteen-celled polyad; individual grains oblate, amb square to polygonal; periporate, pores small, circular; scabrate; tectate, wall 1 μm thick; individual grains ca. 10 μm, polyad 27 × 21 μm. Affinity: Dicotyledonae, Fabaceae–Mimosoideae, *Acacia*.

Pouteria "*mamey*" (Figs. 240, 241). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, thin, half as long as grain, pores appearing circular, small; psilate; tectate, wall 1.5 μm thick; 20 × 18 μm. Affinity: Dicotyledonae, Sapotaceae, *Pouteria*.

Proteacidites triangulatus (Figs. 242, 243). Suboblate, amb triangular; triporate, pores equatorially arranged, equidistant, circular, 3.5 μm wide; reticulate, sometimes appearing as psilate, lumina very fine, < 0.5 μm wide, muri thin, strongly columellate; tectate, wall 1 μm thick; 22 μm. Ref: ID 562 (Jaramillo & Rueda, 2013): fig. 57 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Allophylus* L.

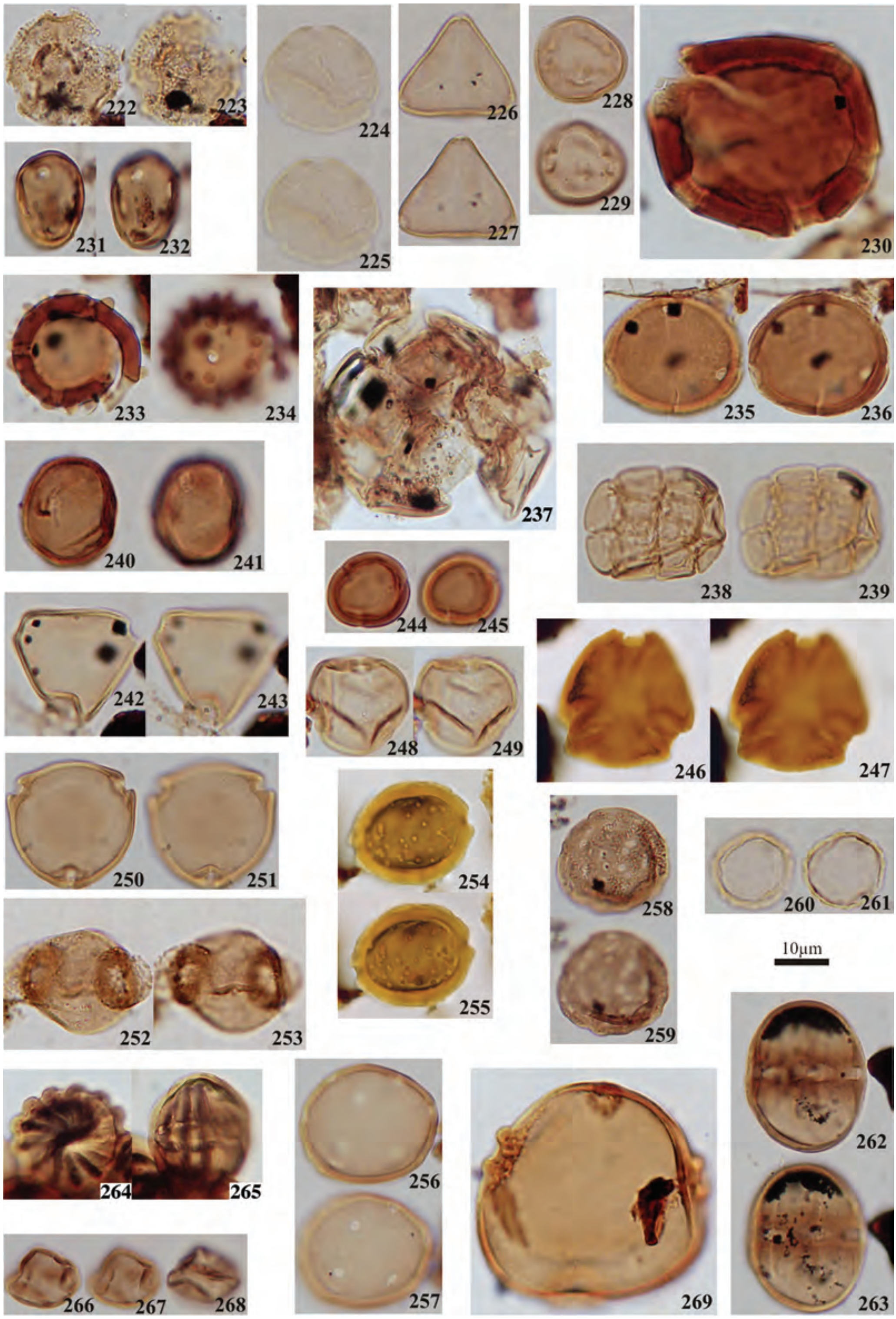
Psilabrevitricolpites aff. *flexibilis* (Figs. 244, 245). Subprolate, amb circular; tricolporate (although originally it was described as tricolpate), colpi equatorially arranged, equidistant, short, extending half the length of the grain, thin, acute ends, pores inconspicuous, apparently circular, small; psilate, sometimes resembling micropitted pattern; tectate, wall 2 μm thick; 15 μm. Ref: ID 580 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Psilabrevitricolporites devriesi. Ref: ID 637 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Humiriaceae, *Humiria* Aubl.

Psilabrevitricolporites "*magnoporatus*" (Figs. 246, 247). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, wide, pores inconspicuous, apparently circular, annulate; psilate; tectate, wall ca. 2 μm thick; 26 μm. Affinity: Dicotyledonae.

Psilabrevitricolporites aff. *rotundus* (Figs. 248, 249). Spherical, amb circular; tricolporate, sometimes appearing as triporate, colpi equatorially arranged, equidistant, subtle, very thin, inconspicuous, pores circular, 1 μm wide, annulate, annulus coarse; psilate; tectate, wall 1 μm thick; 18 μm. Affinity: Dicotyledonae.

PLATE 8. Figures 222–269.
222, 223. *Margocolporites* "hematoxyformis" SL 193, EF W-12/4, Gatun Fm. –5.6 Ma.
224, 225. *Momipites africanus* SL 174, EF D-9/4, Gatun Fm. –9.6 Ma.
226, 227. Myrtaceae Type SL 177, EF E-9/4, Gatun Fm. –9.6 Ma.
228, 229. Ochnaceae Type SL G27-2, EF E-5, Gatun Fm. –9.6 Ma.
230. *Pachydermites diederixi* SL 174, EF K-8/2, Chagres Fm. –10.0 Ma.
231, 232. *Parsonsidites* "multiporatus" SL 2174, EF V-15, Chagres Fm. –10.0 Ma.
233, 234. *Perisyncolporites* "gemmatus" SL 307, EF O-10/4, Gatun Fm. –8.9 Ma.
235, 236. *Perisyncolporites pokornyi* SL 174, EF E-22/4=E-23/3, Tuira Fm. –12.6 Ma.
237. *Polyadopollenites mariae* SL 193, EF Y-17/1=3, Tuira Fm. –6.95 Ma.
238, 239. *Polyadopollenites* "minutus" SL 176, EF C-21/3, Escudo Veraguas Fm. –2.05 Ma.
240, 241. *Pouteria* "mamey" SL G26-1, EF H-12/3, Gatun Fm. –5.6 Ma.
242, 243. *Proteacidites triangulatus* SL 178, EF M-7/4, Pucro Fm. –6.95 Ma.
244, 245. *Psilabrevitricolpites* aff. *flexibilis* SL 178, EF A-23/3, Tuira Fm. –12.6 Ma.
246, 247. *Psilabrevitricolporites* "magnoporatus" SL Culebra 15, EF X-21/2, Culebra Fm. –19.15 Ma.
248, 249. *Psilabrevitricolporites* aff. *rotundus* SL G27-2, EF E-26/2=4, Tuira Fm. –6.95 Ma.
250, 251. *Psilabrevitricolporites* "vestibulatus" SL 350, EF T-16/4, Lara Fm. –6.95 Ma.
252, 253. *Psiladiporites* "faramensis" SL 1617, EF P-18/2=4, Chucunaque Fm. –6.95 Ma.
254, 255. *Psiladiporites* "infragranulatus" SL Culebra 19, EF J-43/2, Culebra Fm. –19.1 Ma.
256, 257. *Psilaperiporites* "juglands" SL 888, EF J-9/4, Chucunaque Fm. –7.05 Ma.
258, 259. *Psilaperiporites minimus* SL 1253, EF F-44/3=4, Chagres Fm. –10.0 Ma.
260, 261. *Psilastephanocolporites* "acalyphoides" SL 176, EF Q-20/4, Cayo Agua Fm. –4.25 Ma.
262, 263. *Psilastephanocolporites* "cedreloides" SL 5a, EF M-16/1, Gatun Fm. –5.6 Ma.
264, 265. *Psilastephanocolporites fissilis* SL 307, EF D-16/4, Cayo Agua Fm. –3.55 Ma.
266–268. *Psilastephanoporites* "crassiannulatus" SL G27-1, EF K-14/4, Tuira Fm. –6.95 Ma.
269. *Psilastephanoporites herngrenii* SL 1142, EF Q-8/2, Tuira Fm. –6.95 Ma.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Psilabrevitricolporites triangularis. Ref: ID 588 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sapindaceae?

Psilabrevitricolporites "*vestibulatus*" (Figs. 250, 251). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, pores 3.5 µm wide, vestibulate, apparently annulate; psilate; tectate, wall 2–3.5 µm thick, thickness around pores; 23 µm. Affinity: Dicotyledonae.

Psiladiporites "faramensis" (Figs. 252, 253). Oblate, amb ellipsoidal; diporate, pores annulate, protruding, covered by thin membrane, circular, 4 µm wide, annulus 3.5 µm thick; psilate; tectate, wall < 1 µm thick; 19 × 27 µm. Affinity: Dicotyledonae, Rubiaceae, *Faramea* Aubl.

Psiladiporites "*infragranulatus*" (Figs. 254, 255). Oblate, amb ellipsoidal; diporate, pores circular, 3.5 µm wide; psilate; tectate, wall ca. 2 µm thick; 19 × 25 µm. Affinity: Dicotyledonae.

Psilaperiporites "*juglands*" (Figs. 256, 257). Spheroidal, amb circular; periporate, ca. 13 pores, pores slightly protruding, circular, 2.5 µm wide, annulate, annulus 1 × 4 µm; psilate; tectate, wall 2 µm thick; 27 µm. Affinity: Dicotyledonae, Juglandaceae, *Juglans* L.

Psilaperiporites minimus (Figs. 258, 259). Spheroidal, amb circular; periporate, > 40 pores, pores circular, 1µm wide, irregularly distributed; scabrate, resembling punctate pattern; tectate, wall 1.2 µm thick, strongly columellate; 21 µm. Ref: ID 594 (Jaramillo & Rueda, 2013); fig. 39 (Graham, 1988a). Affinity: Dicotyledonae, Chenopodiaceae/Amaranthaceae.

Psilastephanocolpites "*janduforius*." Ref: figs. 94, 95 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 5.

Psilastephanocolporites "*acalyphoides*" (Figs. 260, 261). Spherical, amb circular; stephanocolporate, apertures 5, colpi equatorially arranged, equidistant, inconspicuous, short, thin, pores small, circular, slighty protuberant; psilate to almost verrucate; tectate, wall ca. 1 µm thick; 15 µm. Affinity: Dicotyledonae, Euphorbiaceae, *Acalypha diversifolia* Jacq.

Psilastephanocolporites "*cedreloides*" (Figs. 262, 263). Prolate spheroidal, amb circular; stephanocolporate, apertures 5, colpi equatorially arranged, equidistant, extending 3/4 length of grain, ca. 35 × 5 µm, having a continuous equatorial costa, pores ellipsoidally lalongate, almost joining, resembling a zonorate ring; psilate; tectate, wall ca. 1.5 µm thick; 28 × 24 µm. Ref: fig. 35 (Graham, 1991b). Affinity: Dicotyledonae, Meliaceae, *Cedrela* P. Browne.

Psilastephanocolporites fissilis (Figs. 264, 265). Prolate-spheroidal to spheroidal, amb circular; stephanocolporate, apertures 13, colpi equatorially arranged, equidistant, extending nearly entire length of grain, thin, having a continuous equatorial costa, pores lalongate, almost joining, resembling a zonorate ring; psilate; tectate, wall ca. 2.5 µm thick; 23 × 21 µm. Ref: ID 604 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Polygalaceae, *Polygala* L.

Psilastephanoporites "*crassiannulatus*" (Figs. 266–268). Spherical, amb circular; stephanoporate, 4 pores, pores equatorially arranged, costate, costae 1.5 µm thick; psilate; tectate, wall 1.5 µm thick; 13 µm. Affinity: Dicotyledonae.

Psilastephanoporites herngrenii (Fig. 269). Oblate, amb circular; stephanoporate, apertures 4, pores equatorially arranged, circular, 3 µm wide, annulate, annulus 3.5 µm thick; psilate; tectate, wall ca. 1.8 µm thick; 44 µm. Ref: ID 1019 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Apocynaceae.

Psilastephanoporites "*magnus*" (Fig. 270). Spherical, amb circular; stephanoporate, pores protruding, annulate, costate, wide; psilate; tectate, wall 2.5 µm thick, tectum clearly differentiated from nexine; 71 µm. Affinity: Dicotyledonae, Apocynaceae.

Psilastephanoporites "*microcaribiensis*" (Figs. 271, 272). Spherical, amb circular; stephanoporate, pores 4, simple, circular, ca. 3 µm wide; psilate; tectate, wall 1 µm thick; 19 µm. Affinity: Dicotyledonae.

Psilastephanoporites "*punctatus*" (Fig. 273). Spherical, amb circular; stephanoporate, 4 pores, circular, 4 µm wide, costate, annulus thick; psilate; intectate; wall 1.5 µm thick; 30 µm. Affinity: Dicotyledonae.

Psilasyncolpites "*recticolpatus*" (Figs. 274, 275). Oblate, amb triangular-obtuse-straight; syncolpate, colpi continuous, joining at apices; psilate; tectate, wall 1 µm thick, decreasing toward polar areas; 23 µm. Affinity: Dicotyledonae, Myrtaceae.

Psilasyncolporites "*reticolpatus*" (Figs. 276, 277). Oblate, amb triangular-obtuse slightly concave; apparently syncolporate, colpi continuous, joining at apices, forming a small triangle (parasyncolporate condition), pore, if present, inconspicuous; psilate; tectate, wall 1 µm thick; 22 µm. Affinity: Dicotyledonae, Loranthaceae, *Struthanthus* Mart.

Psilatricolpites CU490. Ref: figs. 82–86 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 2.

Psilatricolporites "*communis*" (Figs. 278, 279). Oblate spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, wide, acute ends, pore apparently circular, becoming elongated, protruding; tectate, wall 1 µm thick; 16.5 × 18 µm. Affinity: Dicotyledonae.

Psilatricolporites costatus. Ref: ID 635 (Jaramillo & Rueda, 2013); fig. 53 (Graham, 1988a). Affinity: Dicotyledonae, Salicaceae, *Casearia* Jacq.

Psilatricolporites "*crassiexinatus*" (Figs. 280, 281). Suboblate, amb circular trilobate; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, wide, pore elongated; psilate; tectate, wall 5 µm thick; 41 µm. Affinity: Dicotyledonae.

Psilatricolporites "*faboides*" (Figs. 282, 283). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending 3/4 length of grain, thin, pores elongated, becoming circular, 3.5 µm; psilate; tectate, wall 1 µm thick; 14 × 12.5 µm. Affinity: Dicotyledonae, Fabaceae–Faboideae.

Psilatricolporites "*hornii*" (Fig. 284). Suboblate, amb circular; tricolpate, colpi equatorially arranged, equidistant, short, marginate, margo very thick, prominent; psilate; tectate, wall < 0.5 µm thick; 29 × 32 µm. Affinity: Dicotyledonae, Apocynaceae.

Psilatricolporites "*rotund*" (Fig. 285). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, costate, pores lalongate; psilate, apparently microreticulate; tectate, wall 1 µm thick, displaying short columellae; 44.5 × 35.5 µm. Affinity: Dicotyledonae.

Psilatricolporites "*sphericus*" (Figs. 286, 287). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, pores circular, wide; psilate; tectate, wall 1 µm thick; 15 µm. Affinity: Dicotyledonae.

Psilatricolporites "*vest*" (Fig. 288). Suboblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, costate, margo thick; psilate; tectate, wall 1 µm thick; 25 × 25 µm. Affinity: Dicotyledonae.

Psilatricolporites sp. Ref: ID 2385 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Psilatriporites "*lobatus*" (Figs. 289, 290). Spherical, amb triangular-obtuse-convex; triporate, pores circular, 10 µm wide, annulate, annulus 5 µm thick; psilate; tectate, wall 1.2 µm thick; 31 µm. Affinity: Dicotyledonae.

Psilatriporites "*moraceoides*" (Figs. 291, 292). Spherical, amb circular; triporate, pores circular, 1 µm wide, simple; psilate, slightly scabrate; tectate, wall 1.2 µm thick; 17 µm. Affinity: Dicotyledonae.

Psilatriporites "*ulmoides*" (Figs. 293, 294). Spherical, amb circular; triporate, pores circular, 3 µm wide, having subtle costae; psilate; tectate, wall 1.2 µm thick; 18 µm. Affinity: Dicotyledonae.

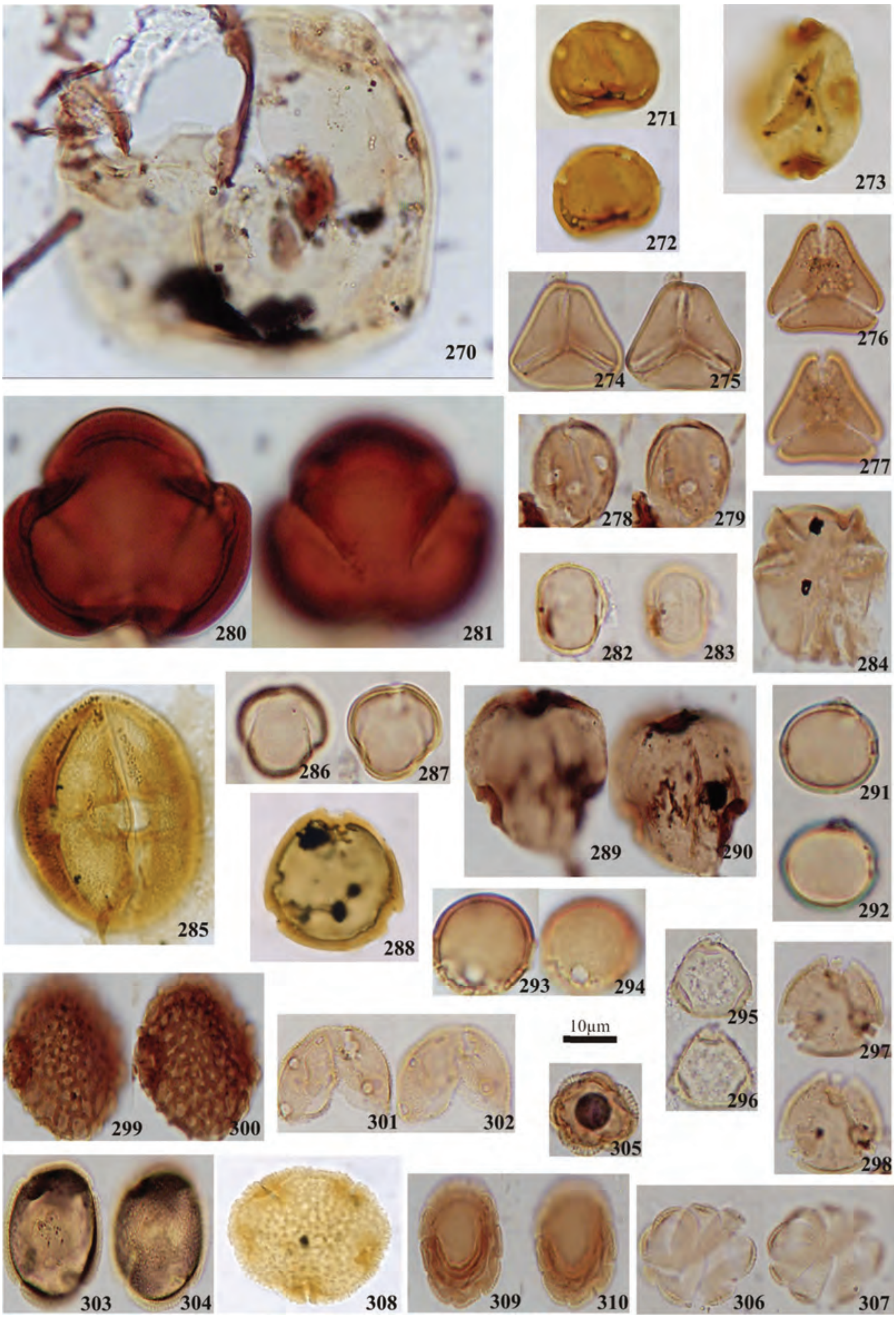
Psilatriporites "*vestibulatum*" (Figs. 295, 296). Spherical, amb triangular-rounded; triporate, pores circular-globose; psilate; tectate, wall < 1 µm at interporium area, 3 µm thick at apertural area; 15 µm. Affinity: Dicotyledonae.

Ranunculacidites operculatus (Figs. 297, 298). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, wide, short, acute ends, polar area distance between adjacent colpi 6 µm long, pores masked by conspicuous opercula, operculum thin, long, bifurcated; reticulate, lumina < 1 µm wide, muri very thin, simplicolumellate; tectate; 18 µm. Ref: ID 656 (Jaramillo & Rueda, 2013); fig. 29 (Graham, 1988b); fig. 32 (Graham, 1989); fig. 13 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, *Alchornea* Sw.

Retidiporites "*cordiaeformis*" (Figs. 299, 300). Spherical, amb circular; diporate, pores circular, 12 µm wide, protruding, annulate; reticulate, lumina decreasing toward center of grain; tectate, wall variable, ca. 1.5 thick; 32 µm. Affinity: Dicotyledonae.

Retipericolporites sp. (Figs. 301, 302). Spherical, amb circular; stephanocolpate, ca. 8 to 9 colpori,

PLATE 9. Figures 270–310.
270. *Psilastephanoporites* "magnus" SL 18, EF G-43/1, Gatun Fm. –5.6 Ma.
271, 272. *Psilastephanoporites* "microcaribiensis" SL Culebra 10.5, EF O-39/2, Culebra Fm. –19.4 Ma.
273. *Psilastephanoporites* "punctatus" SL Culebra 1.5, EF U-54/3, Culebra Fm. –19.46 Ma.
274, 275. *Psilasyncolpites* "recticolpatus" SL 177, EF G-6/4, Gatun Fm. –10.2 Ma.
276, 277. *Psilasyncolporites* "reticolpatus" SL 1188, EF J-25/3, Cayo Agua Fm. –4.25 Ma.
278, 279. *Psilatricolporites* "communis" SL 174, EF W-35/1, Gatun Fm. –10.05 Ma.
280, 281. *Psilatricolporites* "crassiexinatus" SL 168, EF K-10/1, Gatun Fm. –5.6 Ma.
282, 283. *Psilatricolporites* "faboides" SL 2165, EF N-6/2, Gatun Fm. –10.2 Ma.
284. *Psilatricolporites* "hornii" SLG23-1, EF K-20/1, Gatun Fm. –10.2 Ma.
285. *Psilatricolporites* "rotund" SL La Boca 27, EF X-14/4, Culebra Fm. –19.38 Ma.
286, 287. *Psilatricolporites* "sphericus" SL 2165, EF M-40/2, Gatun Fm. –9.6 Ma.
288. *Psilatricolporites* "vest" SL La Boca 27, EF U-46/3=4, La Boca Fm. –19.46 Ma.
289, 290. *Psilatriporites* "lobatus" SL 2222, EF M-43, Cayo Agua Fm. –4.25 Ma.
291, 292. *Psilatriporites* "moraceoides" SL 2165, EF N-6/4, Tuira Fm. –6.95 Ma.
293, 294. *Psilatriporites* "ulmoides" SL 207, EF L-15/4, Gatun F. –5.6 Ma.
295, 296. *Psilatriporites* "vestibulatum" SL G28-2, EF T-11, Gatun Fm. –5.6 Ma.
297, 298. *Ranunculacidites operculatus* SL 184, EF G-50/4, Gatun Fm. –10.2 Ma.
299, 300. *Retidiporites* "cordiaeformis" SL 2167, EF V-13/1, Gatun Fm. –9.6 Ma.
301, 302. *Retipericolporites* sp. SL 1566, EF O-6/2=4, Tuira Fm. –6.95 Ma.
303, 304. *Retistephanocolpites* "brevicolpatus" SL 370, EF R-68/1, Gatun Fm. –8.9 Ma.
305. *Retistephanocolpites* "hexalabiatus" SL 5a, EF S-25/3, Gatun Fm. –5.6 Ma.
306, 307. *Retistephanocolpites* "octolabiatus" SL 68, EF D-15/4, Gatun Fm. –9.6 Ma.
308. *Retistephanocolporites* "bombacoides" SL La Boca 8.5, EF K-54, Culebra Fm. –19.46 Ma.
309, 310. *Retistephanocolporites* "borrerioides" SL 1241, EF S-19, Gatun Fm. –8.9 Ma.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colpus very short, thin, lineal, apparently marginate, inconspicuous, pores circular, 1–1.5 µm wide; reticulate, lumina thin, homogeneous, muri simplicolumellate, columellae 0.5 µm long; tectate, wall 1 µm thick; 21 µm. Affinity: Dicotyledonae.

Retistephanocolpites "*brevicolpatus*" (Figs. 303, 304). Spherical, amb circular; stephanocolpate, 4 colpi, colpus equatorially arranged, equidistant, short, acute ends, polar area ample; reticulate, lumina 0.5 µm wide, muri 0.5 µm thick; tectate, wall 1.5 µm thick; 24 µm. Affinity: Dicotyledonae.

Retistephanocolpites "*hexalabiatus*" (Fig. 305). Spherical, amb circular hexalobate; stephanocolpate, 6 colpi, colpus equatorially arranged, equidistant, short, not well defined, pores probably present, inconspicuous; reticulate, lumina 1 µm wide, muri thin, simplibaculate; tectate, wall 1–2 µm thick, increasing toward intercolpium areas; 17 µm. Affinity: Dicotyledonae, Labiatae.

Retistephanocolpites "*octolabiatus*" (Figs. 306, 307). Spherical, amb circular to slightly ovate, octolobate; stephanocolpate, 8 colpi, colpus equatorially arranged, equidistant, extending nearly entire length of grain, deep, wide; reticulate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae dense; tectate, wall 1.8 µm thick; 22 × 19 µm. Affinity: Dicotyledonae, Labiatae.

Retistephanocolporites "*bombacoides*" (Fig. 308). Oblate, amb circular; stephanocolporate, 5 colpori, colpus equatorially arranged, equidistant, short, margins straight, ends pointed, pores indistinct, costate, annulus thick; reticulate-fossulate, lumina variable, 1–4 µm wide; semitectate, wall 1.5 µm thick; 30 µm. Affinity: Dicotyledonae.

Retistephanocolporites "*borrerioides*" (Figs. 309, 310). Oblate spheroidal, amb circular; stephanocolporate, 11 colpi, colpus equatorially arranged, equidistant, short, narrow, pores simple, inconspicuous; baculate, baculae 0.8 µm tall, densely distributed; intectate, wall 2 µm thick; 23 × 25 µm. Affinity: Dicotyledonae, Rubiaceae, *Borreria* G. Mey.

Retistephanoporites aff. *crassiannulatus* (Figs. 311, 312). Spherical, amb circular; stephanoporate, sometimes displaying triporate condition, pores circular, 6 µm wide, costate, annulus 2 µm thick, surrounded by coarse baculae processes; foveolate, foveolae regularly distributed, resembling reticulate pattern, 2.5 µm wide; tectate, wall 2.5 µm thick; 35 µm. Ref: ID 703 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Malvaceae-Bombacoideae, *Quararibea* Aubl.

Retitrescolpites "*amanoensis*" (Fig. 313). Spherical, amb circular-trilobate; tricolporate, colpus equatorially arranged, equidistant, extending 3/4 length of grain, rounded ends, pores probably circular, wide, inconspicuous; reticulate, lumina variable, 4–7 µm wide, having free baculae, muri 1 µm thick, simplicolumellate, undulating, irregular; semitectate, wall 5 µm thick; 41 µm. Affinity: Dicotyledonae, Phyllanthaceae, *Amanoa* Aubl.

Retitrescolpites? *irregularis*. Ref: ID 712 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Phyllanthaceae, *Amanoa* type, *Amanoa oblongifolia* Müll. Arg., *Pseudolachnostylis glauca* (Hiern) Hutch.

Retitrescolpites "*usualis*" (Figs. 314, 315). Subprolate, amb tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pores lalongate, 2 µm long; reticulate, lumina irregular, variable, 1.5–2.5 µm wide, muri thin, < 1 µm thick, simplicolumellate, columellae 1 µm long, baculae-shaped; tectate, wall 1.8–2 µm thick; 19 × 15 µm. Affinity: Dicotyledonae.

Retitricolpites "*generalis*" (Figs. 316, 317). Subprolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, simple; reticulate, lumina 0.7–1 µm wide; tectate, wall 1 µm thick; 34 × 29 µm. Affinity: Dicotyledonae.

Retitricolpites "*pseudosimplex*" (Figs. 318, 319). Subprolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, simple, thin; reticulate, lumina ca. 0.5 µm wide; tectate, wall 1 µm thick; 36 × 20 µm. Affinity: Dicotyledonae.

Retitricolpites simplex. Ref: ID 746 (Jaramillo & Rueda, 2013); figs. 49, 50 (Graham, 1988a). Affinity: Dicotyledonae, Euphorbiaceae, *Sapium* Jacq.

Retitricolpites "*spiraloides*." Ref: fig. 92 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 14.

Retitricolpites sp. Ref: ID 993 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, *Retitricolpites* sp. A.

Retitricolporites "*amplibrochatus*" (Figs. 320, 321). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, simple, pores wide, inconspicuous; reticulate, lumina variable, rounded, muri thick, simplicolumellate, columellae 2.5 µm long, rounded; tectate, wall 3.5 µm thick; 33 µm. Affinity: Dicotyledonae.

Retitricolporites "*colpimarginatus*" (Figs. 322, 323). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, pore lalongate, annulate; reticulate, lumina < 1 µm wide, muri thin, simplibaculate; tectate, wall 1.8 µm thick; 13 µm. Affinity: Dicotyledonae.

Retitricolporites "*communis*." Ref: figs. 44, 45 (Graham, 1988a). Affinity: Dicotyledonae, Connaraceae, *Rourea* Aubl.

Retitricolporites "*crassiannulatus*" (Figs. 324, 325). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, pore circular, 3.5 µm wide, annulate, annulus 1 µm thick; reticulate, lumina < 1 µm wide, muri sexine strongly columellate, columellae baculae-shaped; tectate, wall 2.5 µm thick; 20 µm. Affinity: Dicotyledonae, Rubiaceae, *Genipa americana* L.

Retitricolporites "*hlongorate*" (Figs. 326, 327). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, 2/3 length of grain, having thick margo broken at equator, pore circular, 2 µm wide, apertures surrounded by a psilate area resembling the "H" condition; reticulate, lumina < 1 µm wide, muri thin, strongly columellate, columellae baculae-shaped; tectate, wall 1.5 µm thick; 18 µm. Affinity: Dicotyledonae.

Retitricolporites "*minibrochatus*" (Figs. 328, 329). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, short, thin, pore probably elongated, apertures slightly aspidate; reticulate, lumina < 1 µm wide, muri thin, simplicolumellate; tectate, wall 2 µm thick; 22 µm. Affinity: Dicotyledonae.

Retitricolporites "*papilioniformis*" (Figs. 330, 331). Suboblate to oblate-spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, straight, pores lalongate, 4 × 7 µm; reticulate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae conspicuous; tectate, wall 2.5 µm thick; 16.5 × 18 µm. Affinity: Dicotyledonae, Fabaceae-Faboideae, *Machaerium* Pers.

Retitricolporites "*pluricolumellatus*." Ref: figs. 99, 100 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 7.

Retitricolporites "*poricostatus*" (Figs. 332, 333). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pores annulate, ellipsoidal; reticulate, lumina uniform, 1 μm wide, muri thin; tectate, wall 1 μm thick; 25 × 21 μm. Affinity: Dicotyledonae.

Retitricolporites "*spheroidalis*" (Figs. 334, 335). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending half the length of the grain, thin, acute ends, marginate, margo displaying costae digitatus, pore slightly elongated; reticulate, lumina < 1 μm wide, muri thin, simplicolumellate; tectate, wall 1.5–2 μm thick; 18 μm. Affinity: Dicotyledonae.

Retitricolporites "*triangularis*" (Figs. 336, 337). Spherical, amb triangular; tricolporate, colpus equatorially arranged, equidistant, extending 2/3 length of grain, thin, acute ends, pores inconspicuous; reticulate, lumina < 1 μm wide, muri thin; tectate, wall 1 μm thick; 16.5 μm. Affinity: Dicotyledonae.

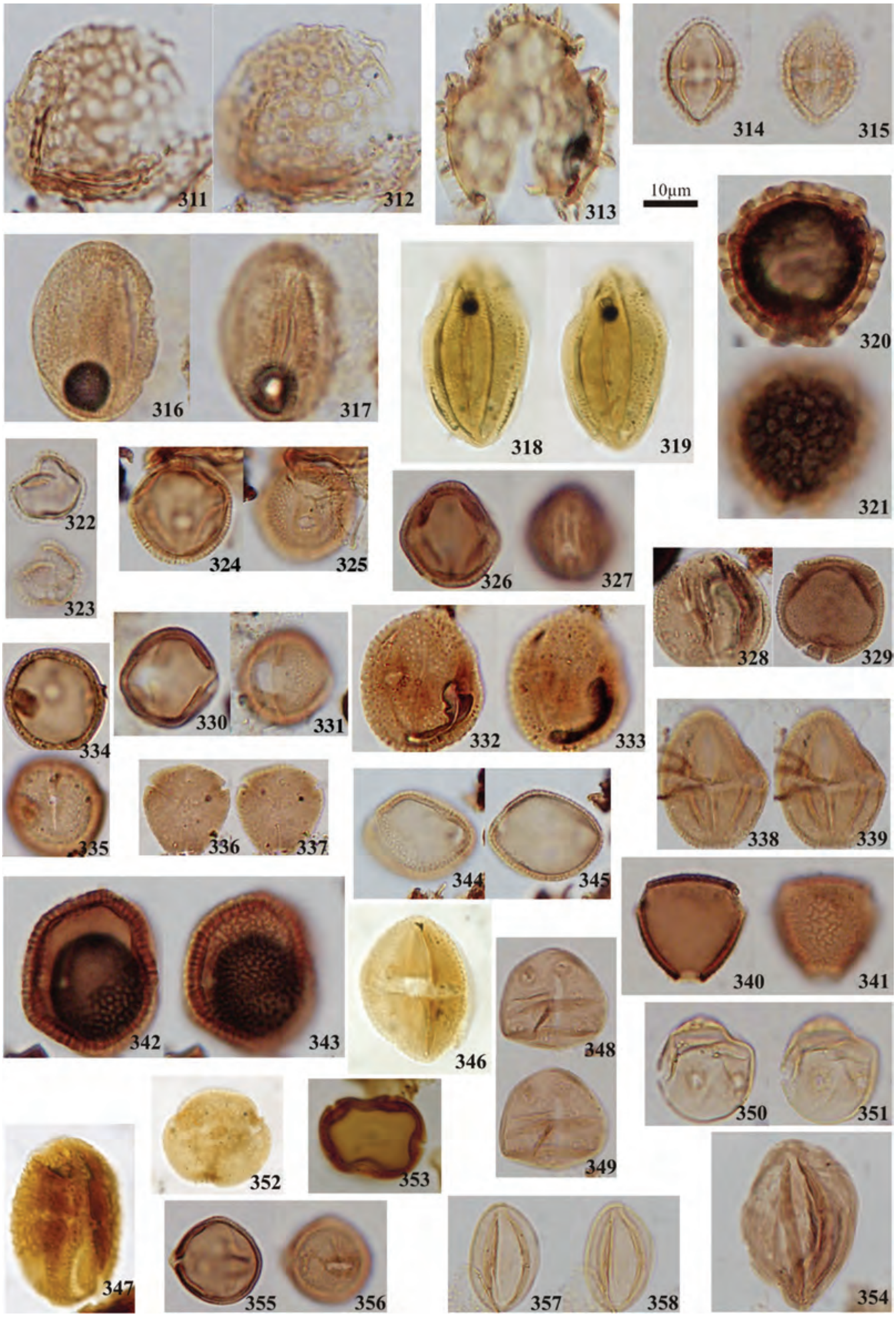
Retitricolporites "*zonoaperturatus*" (Figs. 338, 339). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, marginate, margo thick, pori elongated, joining at apices, resembling an equatorial endocingulum condition; reticulate, lumina < 1 μm wide; tectate; 26 × 23 μm. Affinity: Dicotyledonae.

Retitricolporites CU456. Ref: figs. 54, 55 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Cupania* L.

Retitricolporites CU456-2. Ref: fig. 80 (Graham, 1988a). Affinity: Dicotyledonae, Malvaceae–Byttneroideae, *Guazuma* Mill.

Retitricolporites CU57. Ref: fig. 81 (Graham, 1988a). Affinity: Dicotyledonae, Unknown Type 1.

PLATE 10. Figures 311–358.
311, 312. *Retistephanoporites* aff. *crassiannulatus* SL G27-1, EF O-48/2, Gatun Fm. –8.9 Ma.
313. *Retitrescolpites* "amanoensis" SL 193, EF F-11/4, Cayo Agua Fm. –4.25 Ma.
314, 315. *Retitrescolpites* "usualis" SL G26-1, EF H-8/2, Gatun Fm. –10.0 Ma.
316, 317. *Retitricolpites* "generalis" SL 176, EF H-14/2=4, Tuira Fm. –6.95 Ma.
318, 319. *Retitricolpites* "pseudosimplex" SL La Boca 37.5, EF P-54, Culebra Fm. –19.33 Ma.
320, 321. *Retitricolporites* "amplibrochatus" SL 38, EF H-7/2=4, Tuira Fm. –10.15 Ma.
322, 323. *Retitricolporites* "colpimarginatus" SL G27-2, EF L-39/4, Tuira Fm. –6.95 Ma.
324, 325. *Retitricolporites* "crassiannulatus" SL 175, EF L-13/2, Tuira Fm. –10.15 Ma.
326, 327. *Retitricolporites* "hlongorate" SL 63, EF V-15/2=4, Cayo Agua Fm. –4.25 Ma.
328, 329. *Retitricolporites* "minibrochatus" SL 5a, EF H-14/2, Gatun Fm. –5.6 Ma.
330, 331. *Retitricolporites* "papilioniformis" SL 18, EF Q-7/2=4, Tuira Fm. –10.15 Ma.
332, 333. *Retitricolporites* "poricostatus" SL 1617, EF Q-12/4, Chucunaque Fm. –6.95 Ma.
334, 335. *Retitricolporites* "spheroidalis" SL 19, EF R-38/1, Gatun Fm. –5.6 Ma.
336, 337. *Retitricolporites* "triangularis" SL 391, EF M-51/2, Nancy Point Fm. –5.65 Ma.
338, 339. *Retitricolporites* "zonoaperturatus" SL 1612, EF K-8, Pucro Fm. –6.95 Ma.
340, 341. *Retitriporites* "erythrinoides" SL 391, EF T-43, Tuira Fm. –12.6 Ma.
342, 343. *Retitriporites* "heterobrochatus" SL 184, EF F-22/3, Shark Hole Point Fm. –2.05 Ma.
344, 345. *Retitriporites* "vestibulatum" SL G26-1, EF S-19/1, Gatun Fm. –9.6 Ma.
346. *Rhoipites* "colpizonatus" SL La Boca 37.5, EF O-55/2, Culebra Fm. –19.46 Ma.
347. *Rousea* "cristatus" SL Culebra 15.25, EF Q-29/4, Culebra Fm. –19.12 Ma.
348, 349. *Scabraperiporites* "nothofaguiformis" SL 62, EF G-22/3, Gatun Fm. –5.6 Ma.
350, 351. *Scabrastephanoporites* "apocynaceous" SL 175, EF Q-8/4, Escudo Veraguas Fm. –2.05 Ma.
352. *Siltaria* "comunis" SL Culebra 6.75, EF O-40/2, Culebra Fm. –19.16 Ma.
353. *Stephanoporites* "scabratus" SL 2202, EF O-10/2, Shark Hole Point Fm. –4.6 Ma.
354. *Striatopollis catatumbus* SL 17, EF F-19/1, Gatun Fm. –11.55 Ma.
355, 356. *Striatricolporites* "burseriformis" SL G26-1, EF E-14/2, Tuira Fm. –6.95 Ma.
357, 358. *Striatricolporites melenae* SL 176, EF L-24/2, Cayo Agua Fm. –4.25 Ma.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Retitriporites "*erythrinoides*" (Figs. 340, 341). Suboblate, amb circular; triporate, pores equatorially arranged, equidistant, circular, 5–6 μm wide; reticulate, lumina rounded, variable, decreasing toward apertures, becoming micropitted, resembling rugulate condition; tectate, wall 1.5 μm thick; 21 μm. Affinity: Dicotyledonae, Fabaceae-Faboideae, *Erythrina* L.

Retitriporites "*heterobrochatus*" (Figs. 342, 343). Spherical, amb circular; triporate, pores equatorially arranged, equidistant, circular, 3 μm wide; reticulate, lumina variable, muri 1 μm thick, simplicolumellate, columellae baculae-shaped; tectate, wall 3.5 μm thick; 32 μm. Affinity: Dicotyledonae.

Retitriporites "*vestibulatum*" (Figs. 344, 345). Suboblate, amb circular; triporate, pores equatorially arranged, equidistant, lolongate, 3 × 2 μm, acute ends, margins irregular; reticulate, lumina <1 μm wide; tectate, wall 1.8 μm thick, muri simplicolumellate, columellae clavate-shaped; 19 × 24 μm. Affinity: Dicotyledonae, Rubiaceae.

Rhoipites aff. *cienagensis*. Ref: ID 793 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Rhoipites "*colpizonatus*" (Fig. 346). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, ca. 22 μm long, simple, margins straight, ends pointed, pores lalongate; reticulate, lumina 1μm wide; tectate, wall 1.5 μm thick; 24.7 μm. Affinity: Dicotyledonae.

Rhoipites guianensis. Ref: ID 794 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sterculiaceae, *Firmiana* Marsili, *Hildegardia* Schott & Endl., *Glossostemon* Desf., *Pterocymbium* R. Br., *Sterculia* L.

Rousea "*cristatus*" (Fig. 347). Prolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, margins straight, ends pointed, 3.5 μm wide; reticulate to micropitted, lumina 1 μm wide, angular, densely distributed; semitectate, wall thin; 29 μm. Affinity: Dicotyledonae.

Rubiaceae (*Cosmibuena*). Ref: fig. 43 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Cosmibuena* Ruiz & Pav.

Rubiaceae (*Posoqueria*). Ref: figs. 51–53 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Posoqueria* Aubl.

Rubiaceae (Type 1). Ref: fig. 41 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Faramea* Type 1.

Rubiaceae (Type 2). Ref: figs. 44, 45, 48 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Faramea* Type 2.

Rutaceae (*Casimiroa*). Ref: figs. 46, 47, 49 (Graham, 1991b). Affinity: Dicotyledonae, Rutaceae, *Casimiroa* La Llave & Lex.

Sapindaceae (*Paullinia*). Ref: fig. 50 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Paullinia* L.

Sapindaceae (*Serjania*). Ref: fig. 56 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Serjania* Mill.

Sapotaceae (cf. *Bumelia*). Ref: fig. 58 (Graham, 1991b). Affinity: Dicotyledonae, Sapotaceae, cf. *Bumelia* Sw.

Scabraperiporites "*nothofaguiformis*" (Figs. 348, 349). Spherical, amb circular; periporate, pores 6 to 7, circular, ca. 3 μm wide, slightly annulate, not well defined, appearing as pseudopori; scabrate; tectate, wall 1 μm thick; 21 μm. Affinity: Dicotyledonae, Fagaceae, *Nothofagus dombeyi* (Mirb.) Oerst.

Scabrastephanoporites "*apocynaceous*" (Figs. 350, 351). Spherical, amb circular; stephanoporate, pores equatorially arranged, circular, ca. 1.5 µm wide, annulate, annulus < 1 µm wide; scabrate; tectate, wall 1 µm thick; 18 µm. Affinity: Dicotyledonae, Apocynaceae.

Siltaria "*comunis*" (Fig. 352). Spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, short, margins straight, ends pointed, pores circular, costate; micropitted; tectate, wall 1 µm thick; 19 µm. Affinity: Dicotyledonae.

Siltaria dilcheri. Ref: ID 2075 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Stephanoporites "*scabratus*" (Fig. 353). Suboblate, amb circular; stephanoporate, pores 5, circular, vestibulate; reticulate, lumina < 1 µm wide, muri thin; tectate, wall 2.5–3 µm thick; 17 × 22 µm. Affinity: Dicotyledonae.

Striatopollis catatumbus (Fig. 354). Subprolate, amb probably circular; tricolpate, colpus equatorially arranged, equidistant, extending 3/4 length of grain, wide, costate, irregular; striate, striae dense, longitudinally oriented, 1 µm wide; tectate, wall 1.5 µm thick; 32 × 22 µm. Ref: ID 2075 (Jaramillo & Rueda, 2013); fig. 31 (Graham, 1988b); figs. 37, 38 (Graham, 1989); fig. 25 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae, *Crudia* Schreb., *Anthonotha* P. Beauv., *Isoberlinia* Craib & Stapf ex Holland, *Macrolobium bifolium* (Aubl.) Pers.

Striatricolporites "*burseriformis*" (Figs. 355, 356). Oblate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pori lalongate, 1 × 4 µm, slightly protruding, costate, annulus inconspicuous; reticulate-striate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae baculae-shaped, striae longitudinally oriented; tectate, wall 1.8 µm thick; 15 × 16.5 µm. Ref: fig. 12 (Graham, 1991b). Affinity: Dicotyledonae, Burseraceae, *Bursera simaruba* (L.) Sarg.

Striatricolporites digitatus. Ref: ID 883 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Striatricolporites melenae (Figs. 357, 358). Prolate, amb probably circular; tricolporate, colpus equatorially arranged, equidistant, extending 2/3 length of grain, thin, pori circular, 2 µm wide, slightly protruding, costate, annulus inconspicuous; reticulate-striate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae baculae-shaped, striae longitudinally oriented; tectate, wall 1.8 µm thick; 22 × 14 µm. Ref: ID 883 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Anacardiaceae?

Striatricolporites tenuissimus. Ref: ID 888 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Symplocaceae (*Symplocos*). Ref: fig. 59 (Graham, 1991b). Affinity: Dicotyledonae, Symplocaceae, *Symplocos* Jacq. Type 1.

Syncolporites "*paraisus*." Ref: ID 2095 (Jaramillo & Rueda, 2013); fig. 77 (Graham, 1988a). Affinity: Dicotyledonae, Sapindaceae, *Matayba* Aubl.

Syncolporites poricostatus. Ref: ID 900 (Jaramillo & Rueda, 2013); figs. 65, 66 (Graham, 1988a); fig. 32 (Graham, 1988b); fig. 28 (Graham, 1991b). Affinity: Dicotyledonae, Myrtaceae, *Eugenia* L./*Myrcia* DC. types.

Tetracolpites "*rectangularis*" (Figs. 359, 360). Oblate, amb rectangular; stephanocolpate, colpi 4, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, irregular; perforate; tectate, wall 1.5 µm thick; 22 µm. Affinity: Dicotyledonae.

Tetracolporites "*guareaensis*" (Figs. 361–363). Oblate, amb rectangular; stephanocolpate, colpori 4, colpus equatorially arranged, equidistant, short, very thin, pore slightly oval, having subtle costae, annulus thin; psilate; tectate, wall 1 µm thick; 18 µm. Ref: figs. 39, 42 (Graham, 1991b). Affinity: Dicotyledonae, Meliaceae, *Guarea* F. Allam. ex L.

Tetracolporites "*trichiliensis*" (Figs. 364–366). Subprolate, amb circular; stephanocolporate, colpori 4, colpus equatorially arranged, equidistant, colpus 2/3 length of grain, thin, pores lalongate-ellipsoidal, 2 × 8 µm, costate, costae ca. 2 µm thick; reticulate, lumina < 1 µm wide, muri simplicolumellate; tectate, wall 1 µm thick at intercolpium area and 2.5 µm at apertural area; 20 × 16.5 µm. Affinity: Dicotyledonae, Meliaceae, *Trichilia* P. Browne.

Tetracolporites "*vestibulatum*" (Figs. 367, 368). Spherical, amb circular; stephanocolporate, colpori 4, colpus equatorially arranged, equidistant, short, 4–5 µm long, pores circular, 2.5–3 µm wide, annulate, vestibulate; psilate, slightly scabrate; tectate, wall 1.5 µm thick; 26 µm. Affinity: Dicotyledoneae.

Tetracolporopollenites maculosus. Ref: ID 909 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sapotaceae, *Chrysophyllum argenteum* Jacq.

Tetracolporopollenites aff. *spongiosus*. Ref: ID 912 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Tetracolporopollenites transversalis. Ref: ID 913 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sapotaceae, subtype VII-A of Harley (1991), *Micropholis* (Griseb.) Pierre.

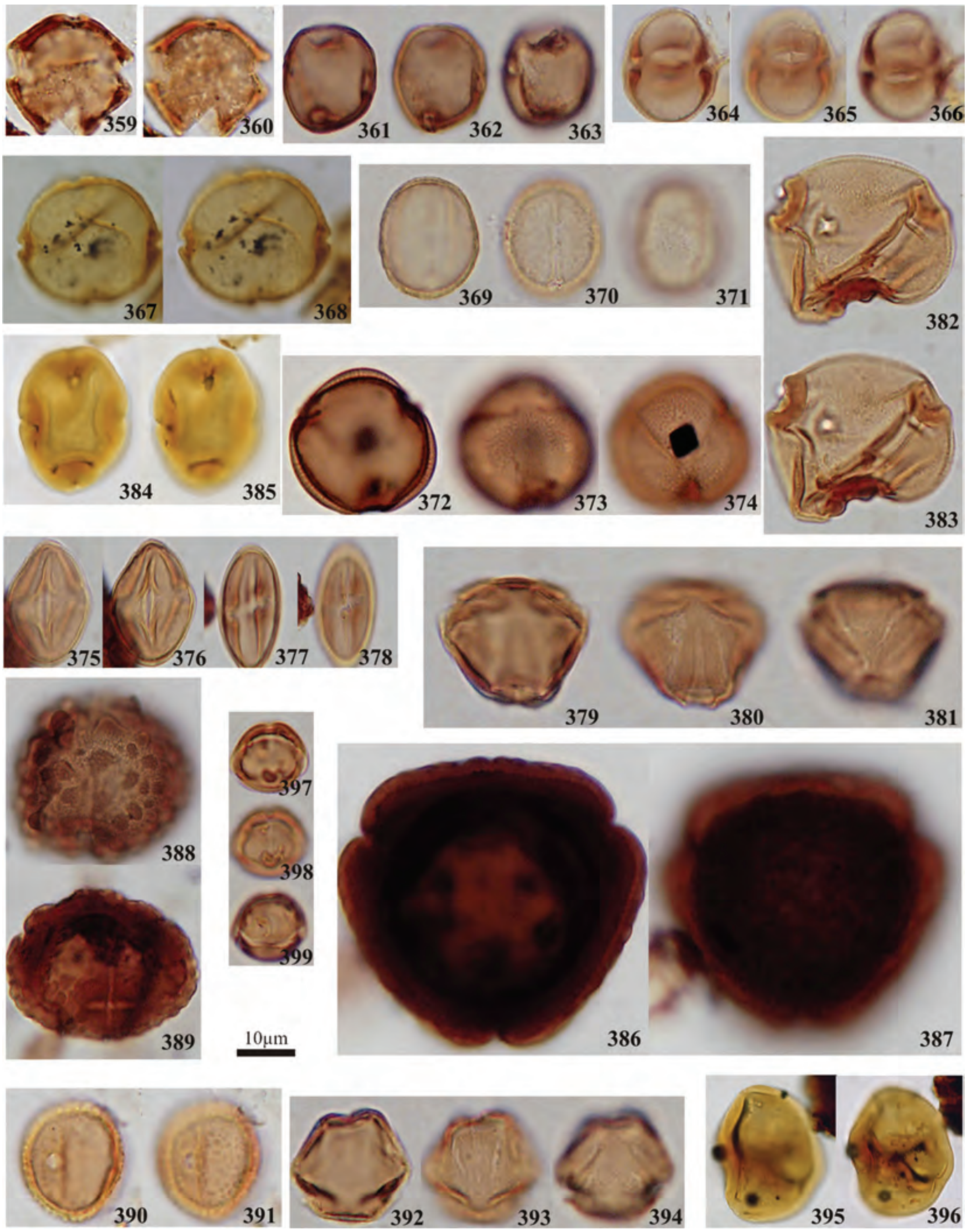
Tiliaceae (*Mortoniodendron*). Ref: fig. 61 (Graham, 1991b). Affinity: Dicotyledonae, Tiliaceae, *Mortoniodendron* Standl. & Steyerm.

Tricolpites "*minutibacularis*" (Figs. 369–371). Subprolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, marginate, margo surrounded by small baculae; baculate; intectate, wall 1.2 µm thick; 20 × 17 µm. Affinity: Dicotyledonae.

Tricolpites "*punctatus*." Ref: figs. 87–90 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 3.

Tricolporites "*annulatus*" (Figs. 372–374). Spherical, amb triangular to circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, pore annulate; retic-

PLATE 11. Figures 359–399.
359, 360. *Tetracolpites* "rectangularis" SL 1553, EF P-5/4, Tuira Fm. –6.95 Ma.
361–363. *Tetracolporites* "guareaensis" SL 5b, EF N-12/2=4, Gatun Fm. –5.6 Ma.
364–366. *Tetracolporites* "trichiliensis" SL G27-2, EF T-6/1, Tuira Fm. –10.15 Ma.
367, 368. *Tetracolporites* "vestibulatum" SL 11, EF C-18/4=D-18/2, Gatun Fm. –5.6 Ma.
369–371. *Tricolpites* "minutibacularis" SL 68, EF K-22, unnamed Fm. –3.55 Ma.
372–374. *Tricolporites* "annulatus" SL 2179, EF E-48, Cayo Agua Fm. –4.25 Ma.
375–378. *Tricolporites* "colpidigitatus" SL G26-1, EF V-6, Gatun Fm. –9.6 Ma.
379–381. *Tricolporites* "ericipitiformis" SL G28-1, EF H-45/4, Tuira Fm. –6.95 Ma.
382, 383. *Tricolporites* "megaporatus" SL 177, EF O-26/3, Cayo Agua Fm. –4.25 Ma.
384, 385. *Venezuelites* "centroamericanus" SL La Boca 8.5, EF X-38/2, Culebra Fm. –19.49 Ma.
386, 387. *Verrutricolporites* "desmodiensis" SL 65, EF L-21/1, Cayo Agua Fm. –4.25 Ma.
388, 389. *Verrutricolporites* "faboides" SL 169, EF H-46/1, Tuira Fm. –6.95 Ma.
390, 391. *Verrutricolporites* "poricircularis" SL 1553, EF D-13/2, Tuira Fm. –6.95 Ma.
392–394. *Vochysia* Type SL 174, EF E-21/4, Gatun Fm. –11.55 Ma.
395, 396. *Zonocostites* "elongatus" SL Culebra 1.5, EFS-43, Culebra Fm. –19.18 Ma.
397–399. *Zonocostites ramonae* SL 174, EF D-19/3, Tuira Fm. –12.6 Ma.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ulate, lumina < 1 μm wide, appearing almost psilate; tectate, wall variable, 1 μm thick at apertural area, cavate at intercolpium area, cavea 1 μm long; 24 μm. Affinity: Dicotyledonae.

Tricolporites "*colpidigitatus*" (Figs. 375–378). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, thin, 1 μm wide, marginate, margo bifurcated at equator (exitus digitus), pore elongated, not well defined; apparently clavate, resembling reticulate pattern; tectate, wall 2–2.5 μm thick, sexine 1.5 μm thick, strongly columellate, columellae baculae-like, thin, nexine < 1 μm thick; 20 × 19 μm. Affinity: Dicotyledonae.

Tricolporites "*ericipitiformis*" (Figs. 379–381). Suboblate, amb circular-triangular; tricolporate, colpus equatorially arranged, equidistant, 22 × 2.5 μm, marginate, margo 2.5 μm thick, almost joining at polar area, pores elongated, surrounded by a psilate area resembling the "H" condition; psilate; tectate, wall 2 μm thick; 19 × 22 μm. Affinity: Dicotyledonae, Ericaceae.

Tricolporites "*megaporatus*" (Figs. 382, 383). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, subtle, wide, acute ends, pores circular, 5 μm wide, annulate, annulus 2.5 μm thick; baculate, baculae < 1 μm long, dense; intectate, wall 1 μm thick; 32 μm. Affinity: Dicotyledonae.

Unknown 1. Ref: figs. 65, 66 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 1.

Unknown 2. Ref: figs. 67, 68 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 2.

Unknown 4. Ref: fig. 71 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 4.

Unknown 6. Ref: fig. 73 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 6.

Unknown 7. Ref: figs. 74–77 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 7.

Unknown 8. Ref: fig. 78 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 8.

Unknown 9. Ref: figs. 79, 80 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 9.

Unknown 10. Ref: fig. 81 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 10.

Unknown 11. Ref: fig. 82 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 11.

Unknown 12. Ref: fig. 83 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 12.

Unknown 13. Ref: fig. 84 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 13.

Unknown 14. Ref: fig. 85 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 14.

Unknown 15. Ref: fig. 86 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 15.

Unknown 16. Ref: fig. 92 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 16.

Unknown 17. Ref: fig. 91 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 17.

Unknown 18. Ref: figs. 87, 88 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 18.

Unknown 19. Ref: figs. 97, 98 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 19.

Unknown 20. Ref: figs. 89, 90 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 20.

Unknown 21. Ref: fig. 95 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 21.

Unknown 22. Ref: fig. 94 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 22.

Unknown 23. Ref: fig. 96 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 23.

Unknown 24. Ref: fig. 93 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 24.

Unknown 25. Ref: figs. 100, 101 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 25.

Unknown 26. Ref: figs. 102, 103 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 26.

Unknown 27. Ref: fig. 99 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 27.

Utricularia. Ref: ID 950 (Jaramillo & Rueda, 2013); fig. 30 (Graham, 1991b); fig. 36 (Graham, 1989). Affinity: Dicotyledonae, Lentibulariaceae, *Utricularia* L.

Venezuelites "*centroamericanus*" (Figs. 384, 385). Oblate, amb circular; stephanoporate, pores 4, circular, 1 μm wide, costate, annulus thick; psilate; wall 3 μm thick; 25 μm. Affinity: Dicotyledonae.

Verbenaceae (*Aegiphila*). Ref: figs. 62, 63 (Graham, 1991b). Affinity: Dicotyledonae, Verbenaceae, *Aegiphila* Jacq.

Verbenaceae (*Petrea*). Ref: fig. 64 (Graham, 1991b). Affinity: Dicotyledonae, Verbenaceae, *Petrea* L.

Verrutricolporites "*desmodiensis*" (Figs. 386, 387). Suboblate, amb circular, slightly angular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, pores inconspicuous, masked by ornamentation; verrucate, verrucae flat, wide, 2 μm long; tectate, wall 6 μm thick; 48 μm. Affinity: Dicotyledonae, Fabaceae–Faboideae, *Desmodium* Desv.

Verrutricolporites "*faboides*" (Figs. 388, 389). Oblate, amb circular; tricolporate, colpus equatorially arranged, equidistant, short, 12 × 1 μm, surrounded by dense patches of verrucae resembling a thick margo, pore lineal-elongated, 1 × 8 μm; verrucate, verrucae variable in shape and size; tectate, wall > 3 μm thick, masked by sculpture; 18 × 31 μm. Affinity: Dicotyledonae, Fabaceae-Faboideae.

Verrutricolporites "*poricircularis*" (Figs. 390, 391). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, 3/4 length of grain, inconspicuous, pores circular, 2 μm wide; verrucate, verrucae flat, variable in size; tectate, wall 1–1.5 μm thick; 18 × 17 μm. Affinity: Dicotyledonae.

Vochysia Type (Figs. 392–394). Suboblate, amb circular-hexagonal, concave; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain × 1.5 μm wide, rounded ends, pores elongated, surrounded by a psilate area resembling the "H" condition; psilate; tectate, wall > 3 μm thick, masked by sculpture, densely columellate; 18–19 μm. Affinity: Dicotyledonae,Vochysiaceae, *Vochysia* Aubl.

Zonocostites "*elongatus*" (Figs. 395, 396). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, simple, pores apparently lalongate, inconspicuous; psilate to micropitted; tectate, wall 1 μm thick; 26.5 × 22 μm. Affinity: Dicotyledonae.

Zonocostites ramonae (Figs. 397–399). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pores lalongate, joining at apices, displaying a continuous equatorial ring, costate, costae slightly protruding; psilate; tectate, wall 1.8 μm thick; 12 × 11 μm. Ref: ID 975 (Jaramillo & Rueda, 2013); figs. 67–70 (Graham, 1988a); figs. 33, 34 (Graham, 1988b); fig. 47 (Graham, 1989), fig. 29 (Graham, 1991b). Affinity: Dicotyledonae, Rhizophoraceae, *Rhizophora* L., *Bruguiera* Lam., *Ceriops* Arn., *Carallia* Roxb. types.

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APPENDIX 3. Code for the analysis used in this paper using the R Project for Statistical Computing syntaxis (R Development Core Team, 2012).

```
library(permute)
library(vegan)
count.temp<-read.delim("count_data.txt", header = FALSE, sep = "\t",na.strings = "NA")#count data
count.temp=as.matrix(count.temp)
age=count.temp[1,]
count.graham=count.temp[2:nrow(count.temp),]
count.graham[is.na(count.graham)] = 0

origin<-read.delim("origin.txt", header = TRUE, sep = "\t",na.strings = "NA")#family origin
locality=read.delim("sample_area.txt", header = TRUE, sep = "\t",na.strings = "NA")# samples site

BCI.temp<-read.delim("BCI.txt", header = TRUE, sep = "\t",na.strings = "NA")#BCI data
BCI.count=as.matrix(BCI.temp[,1:2])
BCI.per=prop.table(BCI.count, 2)#BCI table in percentages


##abundances in absolute counts
totalcount=apply(count.graham,2, sum)#counts per sample
angiosperms=apply(count.graham[which(origin[,3]=="Angiosperm"),],2, sum)##sum angiosperms
```

```
gymnosperms=count.graham[which(origin[,3]=="Gymnosperm"),]#only one gymnosperm
ferns=apply(count.graham[which(origin[,3]=="Spore"),],2, sum)#
marine=apply(count.graham[which(origin[,3]=="Marine"),],2, sum)#


#abundances in percentages
perc.graham=prop.table(count.graham, 2)#table in percentages

age.80=age[which(totalcount>80)]##ages for samples >80

##ONLY SAMPLES WITH COUNTS LARGER THAN 80 grains
angiosperms.per=apply(perc.graham[which(origin[,3]=="Angiosperm"),which(totalcount>80)],2,
sum)##sum angiosperms
gymnosperms.per=perc.graham[which(origin[,3]=="Gymnosperm"),which(totalcount>80)]#only one
gymnosperm
ferns.per=apply(perc.graham[which(origin[,3]=="Spore"),which(totalcount>80)],2, sum)#
marine.per=apply(perc.graham[which(origin[,3]=="Marine"),which(totalcount>80)],2, sum)#

par(mfrow = c(1, 4))##FIGURE ANGIOSPERMS OVER TIME
plot(angiosperms.per,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1),xlab="Proportion of indi-
viduals", ylab="age(My)", main="angiosperms")
abline(h=3.5)#
abline(h=10)#
text(0.9, 2, round(mean(100*angiosperms.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.9, 7, round(mean(100*angiosperms.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.9, 15, round(mean(100*angiosperms.per[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(gymnosperms.per,age[which(totalcount>80)], xlim=c(0,1),ylim=c(20,0),xlab="Proportion of in-
dividuals", ylab="age(My)",main="gymnosperms")
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*gymnosperms.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*gymnosperms.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),
1),cex = .75)
text(0.8, 15, round(mean(100*gymnosperms.per[which(age.80>10)],na.rm = TRUE),3),cex = .75)
plot(ferns.per,age[which(totalcount>80)], xlim=c(0,1),ylim=c(20,0),xlab="Proportion of individuals",
ylab="age(My)",main="ferns and allies")
abline(h=3.5)#
abline(h=10)
text(0.1, 2, round(mean(100*ferns.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*ferns.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 15, round(mean(100*ferns.per[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(marine.per,age[which(totalcount>80)], xlim=c(0,1),ylim=c(20,0),xlab="Proportion of individu-
als", ylab="age(My)", main="marine")
```

```
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*marine.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*marine.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*marine.per[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END FIGURE

t.test(angiosperms.per[which(age.80>10)],angiosperms.per[which(age.80<10 & age.80>3.5)])#>10 0.40, 10-3.5 0.36, p 0.2, df 109; angiosperms proportion do not differ from the 3.5 to 19.5 My interval
t.test(angiosperms.per[which(age.80<10 & age.80>3.5)],angiosperms.per[which(age.80<3.5)])#10-3.5 0.36, <3.5 0.26, p 0.07, df 17.

t.test(ferns.per[which(age.80>10)],ferns.per[which(age.80<10 & age.80>3.5)])#>10 0.59, 10-3.5 0.62, p 0.3, DF 108 ferns proportion do not differ from the 3.5 to 19.5 My interval
t.test(ferns.per[which(age.80<10 & age.80>3.5)],ferns.per[which(age.80<3.5)])#10-3.5 0.62, >10 0.73, p 0.009, dF 17


#INDIVIDUAL ANALYSIS abundances in percentages per origin, counts larger than 80 grains
Amazonian.or=apply(perc.graham[which(origin[,2]==“Gondwana-Amazonian centered”),which(totalcount>80)],2, sum)##sum angiosperms
Andean.or=apply(perc.graham[which(origin[,2]==“Gondwana-Northern Andean centered”),which (totalcount>80)],2, sum)#only one gymnosperm
Southern.or=apply(perc.graham[which(origin[,2]==“Gondwana-Southern Andean centered”),which (totalcount>80)],2, sum)#
Laurasia.or=apply(perc.graham[which(origin[,2]==“Laurasia”),which(totalcount>80)],2, sum)#


BCI.Az=sum(BCI.per[which(BCI.temp[,3]==“Gondwana-Amazonian centered”),1])##data %indiv for BCI
BCI.Andes=sum(BCI.per[which(BCI.temp[,3]==“Gondwana-Northern Andean centered”),1])
BCI.SouthAndes=sum(BCI.per[which(BCI.temp[,3]==“Gondwana-Southern Andean centered”),1])
BCI.Laur=sum(BCI.per[which(BCI.temp[,3]==“Laurasia”),1])
BCI.Unk=sum(BCI.per[which(BCI.temp[,3]==“Unassigned”),1])

unknown.or=1-(Amazonian.or+Andean.or+Southern.or+Laurasia.or)#percentage of unknown abundance of species per sample
plot(unknown.or,age[which(totalcount>80)], ylim=c(20,0),xlab=“Proportion of individuals”, ylab= “age(My)”, main=“Proportion of individuals with unknown natural affinities”)##FIGURE unknown SP
length(which(is.na(origin$Origin)==FALSE))##how many unknown taxa
```

```
par(mfrow = c(1, 5))##FIGURE ORIGIN OVER TIME, % of individuals in assemblage
plot(Amazonian.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of indi-
viduals”, ylab=“age(My)”, main=“Gondwana\nAmazonian centered”,cex.main=1)
points(BCI.Az,0)
text(0.8, 0, round(mean(100*BCI.Az),1),cex = .75)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*Amazonian.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Amazonian.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.8, 15, round(mean(100*Amazonian.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Andean.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab=“Proportion of individu-
als”, ylab=“age(My)”,main=“Gondwana\nNorthern Andean centered”,cex.main=1)
points(BCI.Andes,0)
text(0.8, 0, round(mean(100*BCI.Andes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Andean.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Andean.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.8, 15, round(mean(100*Andean.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Southern.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab=“Proportion of individu-
als”, ylab=“age(My)”,main=“Gondwana\nSouthern Andean centered”,cex.main=1)
points(BCI.SouthAndes,0)
text(0.8, 0, round(mean(100*BCI.SouthAndes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Southern.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Southern.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.8, 15, round(mean(100*Southern.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Laurasia.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab=“Proportion of individu-
als”, ylab=“age(My)”, main=“Laurasia”,cex.main=1)
points(BCI.Laur,0)
text(0.8, 0, round(mean(100*BCI.Laur),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Laurasia.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Laurasia.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.8, 15, round(mean(100*Laurasia.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(unknown.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab=“Proportion of individu-
als”, ylab=“age(My)”, main=“Unknown”,cex.main=1)
points(BCI.Unk,0)
```

```
text(0.8, 0, round(mean(100*BCI.Unk),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.1, 2, round(mean(100*unknown.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*unknown.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.1, 15, round(mean(100*unknown.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END OF FIGURE

t.test(Amazonian.or[which(age.80>3.5)],Amazonian.or[which(age.80<3.5)])#
t.test(Laurasia.or[which(age.80>3.5)],Laurasia.or[which(age.80<3.5)])#
t.test(Andean.or[which(age.80>3.5)],Andean.or[which(age.80<3.5)])#
t.test(Amazonian.or[which(age.80<10 & age.80>3.5)],Amazonian.or[which(age.80>10)])#
t.test(Laurasia.or[which(age.80<10 & age.80>3.5)],Laurasia.or[which(age.80>10)])#

summary (Amazonian.or)##summary data Amazonian centered, # of individuals
summary (Andean.or)
summary (Southern.or)
summary (Laurasia.or)
summary(unknown.or)
sd(unknown.or)

##SPECIES ANALYSIS
pa.graham=perc.graham##presence absence table
pa.graham[(pa.graham>0)]=1## only presence/absence
paper.graham=prop.table(pa.graham, 2)#presence/absence in percentages

Amazonian.sp=apply(paper.graham[which(origin[,2]=="Gondwana-Amazonian centered"),which
(totalcount>80)],2, sum)##sum angiosperms
Andean.sp=apply(paper.graham[which(origin[,2]=="Gondwana-Northern Andean centered"),which
(totalcount>80)],2, sum)#only one gymnosperm
Southern.sp=apply(paper.graham[which(origin[,2]=="Gondwana-Southern Andean centered"),which
(totalcount>80)],2, sum)#
Laurasia.sp=apply(paper.graham[which(origin[,2]=="Laurasia"),which(totalcount>80)],2, sum)#

BCIsp.Az=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Amazonian centered"),2])##data %sp for
BCI
BCIsp.Andes=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Northern Andean centered"),2])
BCIsp.SouthAndes=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Southern Andean centered"),2])
BCIsp.Laur=sum(BCI.per[which(BCI.temp[,3]=="Laurasia"),2])
BCIsp.Unk=sum(BCI.per[which(BCI.temp[,3]=="Unassigned"),2])

unknown.sp=1-(Amazonian.sp+Andean.sp+Southern.sp+Laurasia.sp)#percentage of unknown species
per sample
```

```
plot(unknown.sp,age[which(totalcount>80)], ylim=c(20,0),xlab="Proportion of species", ylab= "age(My)", main="Proportion of species with unknown origin")##


par(mfrow = c(1, 5))##FIGURE ORIGIN OVER TIME, % of species in assemblage
plot(Amazonian.sp,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of species", ylab="age(My)", main="Gondwana\nAmazonian centered",cex.main=1)
points(BCIsp.Az,0)
text(0.8, 0, round(mean(100*BCIsp.Az),1),cex = .75)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*Amazonian.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Amazonian.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Amazonian.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Andean.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species", ylab="age(My)",main="Gondwana\nNorthern Andean centered",cex.main=1)
points(BCIsp.Andes,0)
text(0.8, 0, round(mean(100*BCIsp.Andes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Andean.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Andean.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Andean.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Southern.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species", ylab="age(My)",main="Gondwana\nSouthern Andean centered",cex.main=1)
points(BCIsp.SouthAndes,0)
text(0.8, 0, round(mean(100*BCIsp.SouthAndes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Southern.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Southern.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Southern.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Laurasia.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species", ylab="age(My)", main="Laurasia",cex.main=1)
points(BCIsp.Laur,0)
text(0.8, 0, round(mean(100*BCIsp.Laur),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Laurasia.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Laurasia.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
```

```
text(0.8, 15, round(mean(100*Laurasia.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(unknown.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species",
ylab="age(My)", main="Unknown",cex.main=1)
points(BCIsp.Unk,0)
text(0.8, 0, round(mean(100*BCIsp.Unk),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.1, 2, round(mean(100*unknown.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*unknown.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.1, 15, round(mean(100*unknown.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END OF FIGURE

t.test(Amazonian.sp[which(age.80>3.5)],Amazonian.sp[which(age.80<3.5)])#
t.test(Laurasia.sp[which(age.80>3.5)],Laurasia.sp[which(age.80<3.5)])#
t.test(Andean.sp[which(age.80>3.5)],Andean.sp[which(age.80<3.5)])#
t.test(Amazonian.sp[which(age.80<10 & age.80>3.5)],Amazonian.sp[which(age.80>10)])#
t.test(Laurasia.sp[which(age.80<10 & age.80>3.5)],Laurasia.sp[which(age.80>10)])#

mean (Amazonian.sp)##summary data Amazonian centered, # of species
sd (Amazonian.sp)
mean (Andean.sp)
sd (Andean.sp)
mean (Southern.sp)
sd (Southern.sp)
mean (Laurasia.sp)
sd (Laurasia.sp)
mean(unknown.sp)
sd(unknown.sp)

##ECOLOGICAL ANALYSES
ecol<-read.delim("ecology.txt", header = TRUE, sep = "\t",na.strings = "NA")#count data
ecol[is.na(ecol)] = 0
Uk.temp=apply(ecol,1, sum)#species that do have any ecology

#proportion individuals
TRFO.or=apply(perc.graham[which(ecol$TRFO==1),which(totalcount>80)],2, sum)##sum TRFO
PMF.or=apply(perc.graham[which(ecol$PMF==1),which(totalcount>80)],2, sum)##sum
MF.or=apply(perc.graham[which(ecol$MF==1),which(totalcount>80)],2, sum)##sum
TDFO.or=apply(perc.graham[which(ecol$TDFO==1),which(totalcount>80)],2, sum)##sum
SV.or=apply(perc.graham[which(ecol$SV==1),which(totalcount>80)],2, sum)##sum
FW.or=apply(perc.graham[which(ecol$FW==1),which(totalcount>80)],2, sum)##sum
MG.or=apply(perc.graham[which(ecol$MG==1),which(totalcount>80)],2, sum)##sum
MR.or=apply(perc.graham[which(ecol$MR==1),which(totalcount>80)],2, sum)##sum
```

```
UK.or=apply(perc.graham[which(Uk.temp==0),which(totalcount>80)],2, sum)##sum

par(mfrow = c(1, 4))##Ecology ORIGIN OVER TIME PART A, % of individuals in assemblage
plot(TRFO.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“TRFO”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(PMF.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“PMF”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*PMF.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(MF.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“MF”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MF.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(TDFO.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“TDFO”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END FIGURE
```

```
par(mfrow = c(1, 5))##Ecology ORIGIN OVER TIME PART B, % of individuals in assemblage
plot(SV.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“SV”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*SV.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*SV.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*SV.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
```

```
plot(FW.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“FW”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*FW.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*FW.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*FW.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(MG.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“MG”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MG.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MG.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MG.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(MR.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“MR”)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MR.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MR.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MR.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(UK.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“UK”)
abline(h=3.5)#
abline(h=10)#
text(0.1, 2, round(mean(100*UK.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*UK.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 15, round(mean(100*UK.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END FIGURE

round(100*sd(TRFO.or,na.rm = TRUE),2)
round(100*sd(PMF.or,na.rm = TRUE),2)
round(100*sd(MF.or,na.rm = TRUE),2)
round(100*sd(TDFO.or,na.rm = TRUE),2)
round(100*sd(SV.or,na.rm = TRUE),2)
round(100*sd(FW.or,na.rm = TRUE),2)
round(100*sd(MG.or,na.rm = TRUE),2)
round(100*sd(MR.or,na.rm = TRUE),2)
round(100*sd(UK.or,na.rm = TRUE),2)

t.test(MF.or[which(age.80>10)],MF.or[which(age.80<10)])#

famgen<-read.delim(“family_genus.txt”, header = TRUE, sep = “\t”)#family/genus
```

```
length(which(famgen[,1]!="Unknown" & Uk.temp==0)) number of taxa that have a family assignment but not an ecological preference

##SAMPLE AREAS
area<-read.delim("sample_area.txt", header = TRUE, sep = "\t")#family/genus sample_area.txt

#proportion individuals per region
TRFO.pc=apply(perc.graham[which(ecol$TRFO==1), which(totalcount>80 & area[,1]=="Panama Central")],2, sum)##sum TRFO pc
age.pc=age[totalcount>80 & area[,1]=="Panama Central"]
TRFO.d=apply(perc.graham[which(ecol$TRFO==1), which(totalcount>80 & area[,1]=="Darien")],2, sum)##sum TRFO d
age.d=age[totalcount>80 & area[,1]=="Darien"]
TRFO.b=apply(perc.graham[which(ecol$TRFO==1), which(totalcount>80 & area[,1]=="Bocas del Toro")],2, sum)##sum TRFO bocas
age.b=age[totalcount>80 & area[,1]=="Bocas del Toro"]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals in assemblage by AREA TRF
plot(TRFO.b,age.b, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TRFO\nBocas del Toro",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.b[which(age.b<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.b[which(age.b<10 & age.b>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.b[which(age.b>10)],na.rm = TRUE),1),cex = .75)
plot(TRFO.pc,age.pc, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TRFO\nPanama Central",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.pc[which(age.pc<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.pc[which(age.pc<10 & age.pc>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.pc[which(age.pc>10)],na.rm = TRUE),1),cex = .75)
plot(TRFO.d,age.d, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TRFO\nDarien",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.d[which(age.d<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.d[which(age.d<10 & age.d>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.d[which(age.d>10)],na.rm = TRUE),1),cex = .75)
##END

PMF.pc=apply(perc.graham[which(ecol$PMF==1), which(totalcount>80 & area[,1]=="Panama Central")],2, sum)##sum PMF pc
```

```
age.pcPMF=age[totalcount>80 & area[,1]==“Panama Central”]
PMF.d=apply(perc.graham[which(ecol$PMF==1), which(totalcount>80 & area[,1]==“Darien”)],2, sum)##sum PMF darien
age.dPMF=age[totalcount>80 & area[,1]==“Darien”]
PMF.b=apply(perc.graham[which(ecol$PMF==1), which(totalcount>80 & area[,1]==“Bocas del Toro”)],2, sum)##sum PMF bocas
age.bPMF=age[totalcount>80 & area[,1]==“Bocas del Toro”]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals in assemblage by AREA PMF
plot(PMF.b,age.bPMF, ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“PMF\nBocas del Toro”,cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.b[which(age.bPMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.b[which(age.bPMF<10 & age.bPMF>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*PMF.b[which(age.bPMF>10)],na.rm = TRUE),1),cex = .75)
plot(PMF.pc,age.pcPMF, ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“PMF\nPanama Central”,cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.pc[which(age.pcPMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.pc[which(age.pcPMF<10 & age.pcPMF>3.5)],na.rm = TRUE), 1),cex = .75)
text(0.8, 15, round(mean(100*PMF.pc[which(age.pcPMF>10)],na.rm = TRUE),1),cex = .75)
plot(PMF.d,age.dPMF, ylim=c(20,0), xlim=c(0,1), xlab=“Proportion of individuals”, ylab=“age(My)”, main=“PMF\nDarien”,cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.d[which(age.dPMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.d[which(age.dPMF<10 & age.dPMF>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*PMF.d[which(age.dPMF>10)],na.rm = TRUE),1),cex = .75)
##END

MF.pc=apply(perc.graham[which(ecol$MF==1), which(totalcount>80 & area[,1]==“Panama Central”)],2, sum)##sum PMF pc
age.pcMF=age[totalcount>80 & area[,1]==“Panama Central”]
MF.d=apply(perc.graham[which(ecol$MF==1), which(totalcount>80 & area[,1]==“Darien”)],2, sum)##sum PMF darien
age.dMF=age[totalcount>80 & area[,1]==“Darien”]
MF.b=apply(perc.graham[which(ecol$MF==1), which(totalcount>80 & area[,1]==“Bocas del Toro”)], 2, sum)##sum PMF bocas
```

```
age.bMF=age[totalcount>80 & area[,1]=="Bocas del Toro"]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals by AREA MF
plot(MF.b,age.bMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="MF\nBocas del Toro",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.b[which(age.bMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.b[which(age.bMF<10 & age.bMF>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MF.b[which(age.bMF>10)],na.rm = TRUE),1),cex = .75)
plot(MF.pc,age.pcMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="MF\nPanama Central",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.pc[which(age.pcMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.pc[which(age.pcMF<10 & age.pcMF>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MF.pc[which(age.pcMF>10)],na.rm = TRUE),1),cex = .75)
plot(MF.d,age.dMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="MF\nDarien",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.d[which(age.dMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.d[which(age.dMF<10 & age.dMF>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MF.d[which(age.dMF>10)],na.rm = TRUE),1),cex = .75)
##END

TDFO.pc=apply(perc.graham[which(ecol$TDFO==1), which(totalcount>80 & area[,1]=="Panama Central")],2, sum)##sum PMF pc
age.pcTDFO=age[totalcount>80 & area[,1]=="Panama Central"]
TDFO.d=apply(perc.graham[which(ecol$TDFO==1),which(totalcount>80&area[,1]=="Darien")],2, sum)##sum PMF darien
age.dTDFO=age[totalcount>80 & area[,1]=="Darien"]
TDFO.b=apply(perc.graham[which(ecol$TDFO==1), which(totalcount>80 & area[,1]=="Bocas del Toro")],2, sum)##sum PMF bocas
age.bTDFO=age[totalcount>80 & area[,1]=="Bocas del Toro"]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals by AREA TDFO
plot(TDFO.b,age.bTDFO, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab= "age(My)", main="TDFO\nBocas del Toro",cex.main=1)
abline(h=3.5)#
```

```
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.b[which(age.bTDFO<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.b[which(age.bTDFO<10 & age.bTDFO>3.5)],na.rm = TRUE),
1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.b[which(age.bTDFO>10)],na.rm = TRUE),1),cex = .75)
plot(TDFO.pc,age.pcTDFO, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab=
"age(My)", main="TDFO\nPanama Central",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.pc[which(age.pcTDFO<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.pc[which(age.pcTDFO<10 & age.pcTDFO>3.5)],na.rm =
TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.pc[which(age.pcTDFO>10)],na.rm = TRUE),1),cex = .75)
plot(TDFO.d,age.dTDFO, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab=
"age(My)", main="TDFO\nDarien",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.d[which(age.dTDFO<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.d[which(age.dTDFO<10 & age.dTDFO>3.5)],na.rm = TRUE),
1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.d[which(age.dTDFO>10)],na.rm = TRUE),1),cex = .75)
##END

t.test(c(MF.pc[which(age.pcMF >3.5 & age.pcMF<10)],MF.b[which(age.bMF >3.5 & age.bMF<10)]),
MF.d[which(age.dMF >3.5 & age.dMF<10)])

##diversity
diversity.35 <- specaccum(t(count.graham[,which(age<3.5 & totalcount>80)]))
diversity.1035 <- specaccum(t(count.graham[,which(age<10 & age>3.5 & totalcount>80)]))
diversity.2010 <- specaccum(t(count.graham[,which(age>10 & totalcount>80)]))

plot(diversity.1035,col="red", lwd=2, ci.lty=0, ci.col="red", xlim=c(0,60), xlab="samples", ylab="num-
ber of species")##FIGURE SPECIES ACCUMULATION CURVE
plot(diversity.35,col="purple", add=TRUE)
plot(diversity.1035,col="red", add=TRUE)
plot(diversity.2010,col="blue", add=TRUE)
legend(0, 350, c("<3.5 Ma","3.5-10 Ma", "10-19.5 Ma"), cex=0.8,
   col=c("purple","red","blue"), lty=1)
   ##END

diverColl.1035 <- specaccum(divetemp[which(divetemp[,1]<10 & divetemp[,1]>3.5),2:ncol(dive-
temp)], method = 'collector')
diverColl.35 <- specaccum(divetemp[which(divetemp[,1]<3.5),2:ncol(divetemp)], method = 'collector')
diverColl.10 <- specaccum(divetemp[which(divetemp[,1]>10),2:ncol(divetemp)], method = 'collector')
```

```
plot(divetemp[which(divetemp[,1]<10 & divetemp[,1]>3.5),1]+6.59204-10.14304,diverColl.1035$
richness, xlab="Time Interval (Ma)",ylab="number of species",xlim=c(0,10), pch=2)##FIGURE A
COLLECTORS CURVE
points(divetemp[which(divetemp[,1]<3.5),1]+8.85804-10.14304,diverColl.35$richness,col="red")
points(divetemp[which(divetemp[,1]>10),1]-10.14304,diverColl.10$richness, col="blue", pch=3)
legend(8, 350, c("<3.5 Ma","3.5-10 Ma", "10-19.5 Ma"), cex=0.5, pch=c(1,2,3),
   col=c("red","black","blue"))
   ##ENDS

library(vegan)
data(BCI)
sp1 <- specaccum(BCI)
plot(sp1$sites,sp1$richness) #the plot assuming equal time bins
times <- c(1:5, 8, 22, 23, 25, 26:46, 56:65, 81:90)
plot(times,sp1$richness) #the plot with different time bins


##rarefaction
richness.80=rarefy(t(count.graham[,which(totalcount>80)]),80)
age.rar=age[which(totalcount>80)]
plot(richness.80,age.rar, ylim=c(20,0), xlim=c(0,45), xlab="number of species (rarefy cutoff=80)",
ylab="age(My)")##FIGURE RAREFACTION
abline(h=3.5)#
abline(h=10)#
text(40, 2, round(mean(richness.80[which(age.rar<3.5)],na.rm = TRUE),1),cex = .75)
text(40, 7, round(mean(richness.80[which(age.rar<10 & age.rar>3.5)],na.rm = TRUE),1),cex = .75)
text(40, 15, round(mean(richness.80[which(age.rar>10)],na.rm = TRUE),1),cex = .75)
##ENDS

t.test(richness.80[which(age.rar<10 & age.rar>3.5)],richness.80[which(age.rar>10)])
```