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The Pliocene–Pleistocene palynology of the Negro River, Brazil

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ABSTRACT

Palynological studies in central Amazonia are scarce, especially those concerned with resolving the age of sedimentary deposits. A recent opportunity allowed the stratigraphical and palynological study of a sedimentary unit below the Negro River’s current channel. Age was constrained by the basal occurrence of *Alnipollenites verus*, and the top occurrence of *Grimsdalea magnaclavata* and *Paleosantalaceaeapites cingulatus*, as late Pliocene to early Pleistocene. Here, we provide additional details on the palynostratigraphy and biodiversity of this deposit. Samples yielded 95 palynomorphs that included 58 pollen and 26 spore species, of which we identified botanical affinities with 26 angiosperm, one gymnosperm and four pteridophyte families. Twenty-five new taxa are erected, from which we recognise five angiosperm genera, namely *Pacourina/Vernonia* (Asteraceae), *Myrsine?* (Myrsinaceae), *Symmeria* (Polygonaceae), *Faramea* (Rubiaceae) and *Schefflera* (Araliaceae), plus a possible Marcgraviaceae pollen. These taxa, along with the majority of the recovered assemblage, are indicative of Amazonian lowland floras.

KEYWORDS

Negro River; Pliocene; Pleistocene; palynology; Amazonia; Brazil

1. Introduction

Applying palynology to stratigraphical studies in Central Amazonia continues to be problematic because only a few studies have used pollen and spores to date Neogene (Dino et al. 2012; Guimarães et al. 2015; Soares et al. 2015, 2017) and Cretaceous (Daemon 1975; Dino et al. 1999) sedimentary deposits. Ages are largely dependent on correlation with palynological zonations of other areas in northern South America, for instance from the Brazilian coast (Regali et al. 1974), Venezuela (Germeraad et al. 1968; Lorente 1986; Mueller et al. 1987; Pocknall et al. 2001), Colombia (Jaramillo et al. 2011) and western Amazonia (Horn 1993). The lack of both data and reliable biostratigraphical markers in Central Amazonia (e.g. Caputo 2011; Guimarães et al. 2015) has hampered the understanding of the regional stratigraphy and basin evolution.

In a recent study Soares et al. (2017) described a unit underneath the channel of the Negro River and, using palynology, dated it as late Pliocene to early Pleistocene. This was the first section of this age from Central Amazonia and, indeed, from most of the basin. Here, we describe and illustrate the palynological record of this deposit to improve our understanding of the late Neogene depositional history of Amazonia.

1.1. Geological setting

In Central Amazonia (Figure 1) sedimentary deposits are dominated by the Alter do Chão Formation red beds of Aptian/Cenomanian age (Dino et al. 1999) and the Neogene Novo Remanso

unit so far mapped from Manacapuru to east of Itacoatiara in the Uatumã River area (Figure 1; Dino et al. 2012; Soares et al. 2015, 2016; Caputo and Soares 2016). These units are unconformably topped by middle to Upper Pleistocene sands and fine-grained sediments of river terraces (Soares et al. 2010; Gonçalves et al. 2016). Several cores from the Negro Bridge construction, near Manaus where the Negro and Solimões rivers meet (Figure 1), were studied (Soares et al. 2017). These cores revealed a centimetre-thick unit composed of sands and secondary muds in unconformable contact with both the underlying Miocene and the overlying Recent deposits. This new unit was traced along all sections over ~1.8 km (Figure 1).

1.1.1. Age and significance

The palynological record of the thin unit was well preserved and included some key species, such as *Alnipollenites verus* (Potonié 1931) ex. Potonié 1934, *Grimsdalea magnaclavata* Germeraad et al. (1968) and *Paleosantalaceaeapites cingulatus* Jaramillo et al. (2011) (Soares et al. 2017). On the basis of the first appearance datum (FAD) of *A. verus* and the last appearance datum (LAD) of *G. magnaclavata* and *P. cingulatus*, we propose an age for the deposits that ranges from late Pliocene (Piacenzian) to early Pleistocene (Gelasian), ~3.6 to ~1.9 Ma (Soares et al. 2017). These ages have been calibrated using calcareous nannofossils (Figure 2).

The lateral continuity over ~1.8 km of the channel deposits indicates that by the late Pliocene to early Pleistocene, large-scale fluvial activity was already in place at the Negro–Solimões confluence area. The occurrence of Andean taxa (*A. verus*)

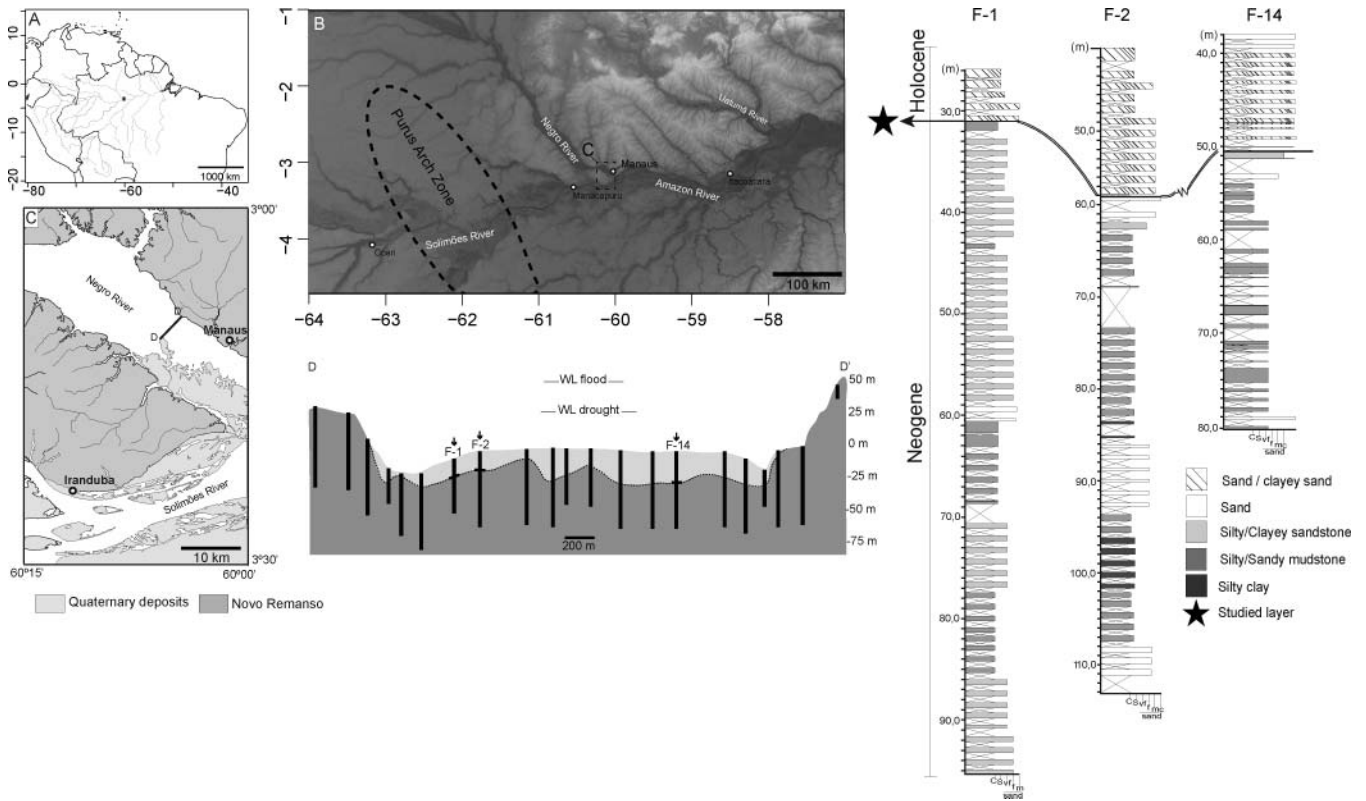


Figure 1. A, Map of northern South America with Amazonian drainage; B, drainage in central Amazonia around the region of Manaus; the Purus structural high is indicated, as well as towns (white circles); C, geological cover around the Negro–Solimões confluence and the Negro River bridge section D–D'. Sections used to reconstruct the Negro River’s channel are shown as black bars. Three cores (F1, F2, F14) where the entire stratigraphy was recovered are pointed out to show the position of the studied sediments (star) between the Neogene and the Quaternary sedimentary covers. Figure adapted from Soares et al. (2017). Digital Elevation Model (DEM) derived from ETOPO 1 (Amante & Eakins 2009). WL: water level.

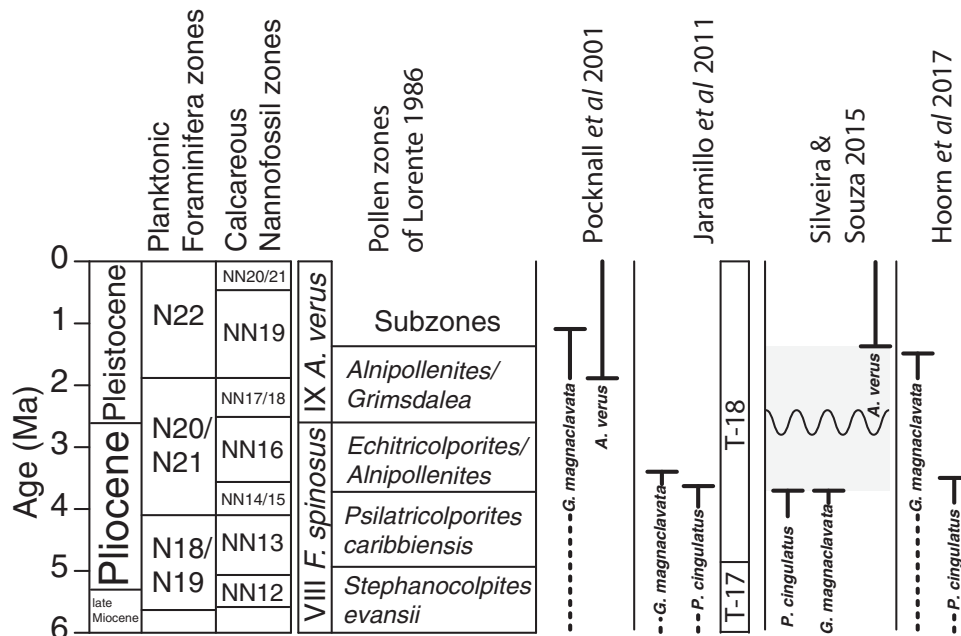


Figure 2. Comparison of ranges for *Alnipollenites verus*, *Grimsdalea magnaclavata* and *Paleosantalaceapites cingulatus* and palynological zonation schemes in Venezuela (Lorente 1986; Pocknall et al. 2001), Colombia (Jaramillo et al. 2011), Foz do Amazonas (Hoorn et al. 2017), and the Coari section (Nogueira et al. 2013; Silveira and Souza 2015). T-17 and T-18 are pollen zones for the Llanos zonation (Jaramillo et al. 2011). Foraminiferal and nannoplankton zones compared with the geological time scale of Hilgen et al. (2012). Adapted from Soares et al. (2017).

indicates that the water flow coming from the Andes was not impeded from reaching Central Amazonia by any topographical barriers such as the Purus arch (Figure 1).

2. Materials and methods

Using the palynological methods described by Wood et al. (1996), we processed pelitic samples from the Negro Bridge unit described by Soares et al. (2017). Pollen was recovered from four samples (Table 1). We described the pollen and spores and compared them to taxa published from South America and stored in the online database of Jaramillo & Rueda (2017). Terminology used for descriptions followed Punt et al. (2007), with some additions from Jaramillo & Dilcher (2001). For spores, TLI refers to the trilete index, which is the [radius length/(spore diameter/2)]; MLI refers to the Monolete index, which is [laesura length/spore length]. For pollen, CPI is calculated in equatorial view, being [colpi length/polar diameter]; CEI was calculated in polar view, being [colpi length/equatorial diameter]. All grains are located using the England Finder coordinate system (EF), and slides are stored at the Geosciences department in the University of Mato Grosso (UFMT), Brazil, where specimens are curated at the Paleontology Museum.

We gathered botanical affinities for the identified taxa from the lists of Jaramillo et al. (2010, 2014), Jaramillo & Rueda (2017), Salamanca et al. (2016) and Hoorn et al. (2017). Botanical affinities for newly described taxa were derived from Absy (1979), Colinvaux et al. (1999) and Roubik & Moreno (1991) and from comparison with extant reference collections from the National Institute for Amazon Research (INPA, Manaus) and the Alan Graham pollen collection stored at the Smithsonian Tropical Research Institute (STRI, Panama).

3. Results and discussion

These four samples yielded 545 specimens and 95 species, including two freshwater algae, 58 pollen and 26 spore species (Table 1). Nine of the palynomorphs had been reworked. Eight new species are described (Table 1). The palynological assemblage is fully continental and representative of the tropical lowlands. Except for an extra-Amazonia taxon (*A. verus*), all of the listed families and genera are typical of extant floodplain and *terra firme* (unfloodable rainforest) plant communities of Amazonia.

3.1. Regional correlations

Only one locality in central Amazonia has a palynological assemblage comparable to the one studied herein. Nogueira et al. (2013) and Silveira & Souza (2015) studied the region of Coari, west of the Purus Arch (Figure 1), and dated sections with the top Solimões Formation as late Miocene to Pliocene and the overlying unconformable Içá Formation as Pleistocene (Figures 2 and 3). In Coari, the presence of *Cyatheacidites annulatus* and *Stephanocolpites evansii* further constrains the top of the Solimões Formation to an age not older than latest Miocene given their FADs of ~7.1 and ~6.2 Ma, respectively (Jaramillo et al. 2011). Moreover, the Solimões Formation at Coari contains *G. magnaclavata* and *P. cingulatus*, whose LADs are ~3.4 and ~3.7 Ma, respectively (Jaramillo et al. 2011), or ~1 and ~3.7 Ma, respectively (Hoorn et al. 2017)

(Figure 2), indicating that the top of the Solimões is not younger than lower Pliocene (Zanclean). None of these taxa is recorded in the overlying Içá Formation, which has a Pleistocene age based on the occurrence of *A. verus* (Figure 2). The Negro Bridge channel deposits, in comparison, contain a mixture of all aforementioned taxa (Figure 2), and therefore cannot be placed in either the *A. verus* Pleistocene zone or in the *F. spinosus* Pliocene zone of Lorente (1986). This assemblage could, however, be found in the *Alnipollenites/Grimsdalea* Concurrent Range Zone of Lorente (1986), dated as Pliocene/Pleistocene (Figure 2), which also agrees with the stratigraphical ranges of Pocknall et al. (2001), Jaramillo et al. (2011) and Hoorn et al. (2017). In summary, the Negro strata were deposited during the time that encompasses the unconformity between the Solimões and Içá Formations in Coari (Figure 3; Nogueira et al. 2013; Silveira and Souza 2015).

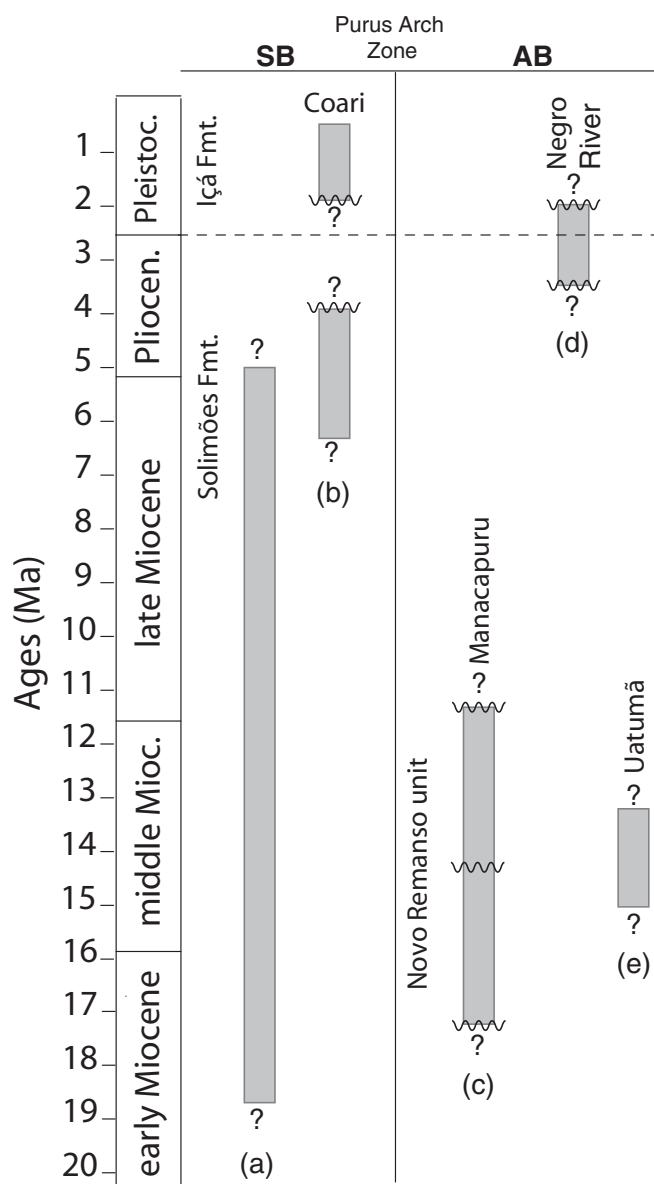


Figure 3. Correlation of sections discussed in the text. From left to right: (a) Solimões Formation cores in the upper Solimões River (Hoorn et al. 1993; Silva Caminha et al. 2010; Kachniasz & Silva-Caminha et al. 2016; Leite et al. 2017; Jaramillo et al. 2017); (b) Coari section (Nogueira et al. 2013; Silveira & Souza 2015); (c) Manacapuru sections (Dino et al. 2012; Guimarães et al. 2015); (d) Negro River bridge palaeochannel (Soares et al. 2017; this study) and (e) Uatumã sections (Soares et al. 2016). SB = Solimões Basin, AB = Amazonas Basin, wiggly line = unconformities.

Table 1. Pollen raw counts of samples from the Negro River deposit, Manaus, Brazil. RW = reworked. Sample sp-68 = borehole 5; sample ap-47 = borehole F-9; samples ap-48-3 and ap-48-2 = borehole F-10.

Category	Family	Genus	Taxa	sp-68	ap-47	ap-48-3	ap-48-2
			<i>Botryococcus</i> spp.	1			
			<i>Pediastrum</i> spp.			3	
RW			<i>Afropollis jardinus</i>	1			
Pollen	Betulaceae	<i>Alnus</i>	<i>Alnipollenites verus</i>	20	5		
Pollen			Angiosperm indet.			2	
Pollen	Arecaceae		<i>Arecipites regio</i>		1		
Pollen	Malvaceae (Bombacoideae)		<i>Bombacacidites ciriloensis</i>	1	3		
Pollen	Asteraceae		cf. <i>Echitricolporites mcneillyi</i>	1			
Pollen	Asteraceae		<i>Cichoreacidites longispinosus</i>		3		
RW			<i>Classopollis classoides</i>				1
Pollen	Chloranthaceae	<i>Hedyosmum</i>	<i>Clavainaperturites microclavatus</i>	8	7	1	
Pollen	Arecaceae	<i>Iriarteia(?)</i>	<i>Clavamonocolpites lorentei</i>	2	2		
RW			<i>Cretacaeiporites polygonalis</i>	1			
Pollen			<i>Crototricolpites finitus</i>	1			
Pollen	Alismataceae	<i>Sagittaria/Echinodorus</i>	<i>Echiperiporites akanthos</i>	1	11		
Pollen	Convolvulaceae?		<i>Echiperiporites lophatus</i>		2		
Pollen	Asteraceae		<i>Echitricolporites spinosus</i>	13	17	1	
RW			<i>Equisetosporites</i> sp.				1
Pollen	Ericaceae		<i>Ericipites</i> cf. <i>annulatus</i>	2	2		
Pollen	Asteraceae	<i>Pacourina/Vernonia</i>	<i>Cichoreacidites igapoensis</i> sp. nov.		2		
Pollen	Asteraceae		<i>Fenestrites spinosus</i>	2			
Pollen			<i>Foveotricolporites ponticus</i> sp. nov.	1			
Pollen	Arecaceae	Extinct	<i>Grimsdalea magnaclavata</i>	1			
Pollen	Aquifoliaceae	<i>Ilex</i>	<i>Ilexpollenites tropicalis</i>	11	13		
Pollen	Marcgraviaceae?		<i>Ladakhpollenites? porolenticularis</i> sp. nov.		1		
Pollen	Polygonaceae	<i>Symmeria</i>	<i>Ladakhpollenites? lolongatus</i> sp. nov.	3	3		
Pollen			<i>Ladakhpollenites? densicolumellatus</i> sp. nov.		1		
Pollen			<i>Malvacipollis minutispinulosa</i> sp. nov.		1		
Pollen	Malvaceae	<i>Abutilon?</i>	<i>Malvacipolloides</i> aff. <i>maristellae</i>	1			
Pollen			<i>Margocolporites</i> aff. <i>fastigiatus</i>	1			
Pollen			<i>Margocolporites</i> spp.	1			
Pollen	Arecaceae	<i>Mauritia</i>	<i>Mauritiidites franciscoi</i> var. <i>franciscoi</i>	13	17	1	
Pollen	Arecaceae	<i>Mauritia</i>	<i>Mauritiidites franciscoi</i> var. <i>minutus</i>	1			
Pollen	Arecaceae	<i>Mauritia</i>	<i>Mauritiidites franciscoi</i> var. <i>pachyexinatus</i>		1		
Pollen	Poaceae		<i>Monoporopollenites annulatus</i>	22	55	6	
Pollen			<i>Paleosantalaceaeipites cingulatus</i>	1	1		
Pollen			<i>Parsonidites? brenacii</i>	1			
Pollen			<i>Perisyncolporites pokorny</i>	1	3		
Pollen	Malpighiaceae		<i>Podocarpites</i> spp.	1			
Pollen	Podocarpaceae	<i>Podocarpus</i>	<i>Proteacidites triangulatus</i>	1	1		
Pollen	Sapindaceae/Proteaceae	<i>Allophylus?</i>	<i>Psilabrevitricolporites devriesii</i>	1			
RW			<i>Psilabrevitricolporites niger</i> sp. nov.		1		
Pollen			<i>Psilastephanocolporites</i> aff. <i>marinamensis</i>	1			
Pollen	Myrsinaceae?	<i>Myrsine?</i>	<i>Psilastephanocolporites brevissimus</i> sp. nov.		1		
Pollen	Sapotaceae	<i>Pouteria</i>	<i>Psilatricolporites labiatus</i>	3			
Pollen	Euphorbiaceae	<i>Alchornea/Aparisthmium</i>	<i>Psilatricolporites operculatus</i>	2			
Pollen	Burseraeae/Sapotaceae		<i>Psilatricolporites silvaticus</i>	5	4		
Pollen			<i>Psilatricolporites</i> spp.	8	11		
Pollen	Rubiaceae	<i>Faramea</i>	<i>Psilatriporites aspidatus</i> sp. nov.		1		
Pollen			<i>Retimonocolpites ordinarius</i> sp. nov.	1			
Pollen			<i>Retistephanocolpites quadraticus</i> sp. nov.		1		
Pollen			<i>Retistephanocolporites centrimaculatus</i> sp. nov.		1		
Pollen			<i>Retistephanoporites amazonicus</i> sp. nov.		1		
Pollen	Phyllanthaceae	<i>Amanoa</i>	<i>Retitrescolpites? irregularis</i>	4	3		
Pollen			<i>Retitricolporites</i> spp.	9	6	6	
Pollen			<i>Rhoipites basicus</i> sp. nov.	1			
Pollen	Araliaceae	<i>Schefflera</i>	<i>Rhoipites manausensis</i> sp. nov.		3		
Pollen			<i>Rhoipites minuticirculatus</i> sp. nov.	1			
Pollen			<i>Rhoipites negroensis</i> sp. nov.		2		
Pollen			<i>Siltaria</i> cf. <i>dilcheri</i>	1			
Pollen	Passifloraceae/Bignoniaceae/Fabaceae		<i>Spirosyncolpites spiralis</i>	1	2		
Pollen	Rubiaceae	<i>Spermacoce</i>	<i>Stephanocolpites evansii</i>		2		
Pollen	Fabaceae	<i>Crudia/Macrolobium</i>	<i>Striatopollis catatumbus?</i>	1			
Pollen			<i>Striatricolporites</i> spp.			1	
Pollen	Sapindaceae?		<i>Syncolporites</i> aff. <i>anibalii</i>	1			
Spore			<i>Camarozonosporites</i> cf. <i>crassus</i>		1		
Spore			cf. <i>Neoraistrickia</i>	1			
Spore			<i>Cingulatisporis oligodistalis</i> sp. nov.		1		
Spore			<i>Concavissimisporites varzeanus</i> sp. nov.	1			
RW	Schizaceae	<i>Lygodium</i>	<i>Crossoretitriletes vanraadshoovenii</i>	1			
Spore	Cyatheaceae	<i>Lophosoria</i>	<i>Cyatheacidites annulatus</i>	1			
Spore			<i>Echinatisporis parviechinatus</i> sp. nov.	1			
Spore			<i>Echinatisporis</i> spp.	1			

(continued)

Table 1. (Continued)

Category	Family	Genus	Taxa	sp-68	ap-47	ap-48-3	ap-48-2
RW	Spore		<i>Echinosporis conicus</i> sp. nov.			1	
	Spore		<i>Foveotrilites ornatus</i>	1	1		
	Spore	Cyatheaceae	<i>Hemitelia/Cnemidaria</i>	1			
	Spore		<i>Kuylisporites waterbolkii</i>				
	Spore		<i>Laevigatosporites tibuensis</i>	12	16	3	
	Spore	Pteridaceae	<i>Ceratopteris</i>		2		
	Spore		<i>Matonisporites muelleri</i>		1		
	Spore		<i>Polypodiaceoisporites amazonensis</i>				1
	Spore	Polypodiaceae	<i>Polypodiisporites</i> aff. <i>speciosus</i>		18		
	Spore	Polypodiaceae	<i>Polypodiisporites</i> cf. <i>scabraproximatus</i>		13		
	Spore	Polypodiaceae	<i>Polypodiisporites timidus</i> sp. nov.	1			
	Spore	Polypodiaceae	<i>Polypodiisporites serratus</i> sp. nov.	1			
	Spore	Polypodiaceae	<i>Polypodiisporites</i> spp.	11	13		
	Spore		<i>Psilatrieltes lobatus</i>	1			
	Spore		<i>Psilatriletes</i> > 50 μm		6		
	Spore		<i>Psilatriletes</i> 25–50 μm	25	27	2	1
	Spore		Spore indet.	1			
	Spore		<i>Verrucatotrilites etayoi</i>	3			
	Spore		<i>Verrucatotrilites tortus</i> sp. nov.	1			
	Spore		<i>Verrucatotrilites laesuraverrucatus</i> sp. nov.		2		
	Spore		<i>Verrutrilites</i> spp.		2		
RW	Spore		<i>Waltzisporea?</i>		1		

Additional localities in central Amazonia with biostratigraphical data include Manacapuru (Dino et al. 2012) and Uatumã (Soares et al. 2015), where the Novo Remanso unit was studied. Both sites have Miocene pollen assemblages dated as middle Miocene age by the authors. Taxa used for this age assignment have long ranges (e.g. *G. magnaclavata*, ~16 to 3.4 Ma according to Jaramillo et al. 2011) and should not be regarded as middle Miocene markers on their own (see Guimarães et al. 2015). However, no late Miocene or Pliocene markers were reported. Furthermore, regional stratigraphical contexts (e.g. lateritic crusts, traceable discontinuities) are correlated with middle Miocene ages elsewhere in the basin (Dino et al. 2012). A better understanding of the stratigraphical positions of these and other sections – with potential implications in palaeogeographical reconstructions – will be achieved only with extensive mapping and dating, which is still ongoing in Central Amazonia.

4. Systematic palaeontology

4.1. Spores

4.1.1. Monoletes

Genus *Echinosporis* Krutzsch 1967

Type species. *Echinosporis echinatus* Krutzsch 1967

Echinosporis conicus sp. nov.

Holotype. Plate 1, figures 1–2, sample ap48, EF E-18.

Description. Spores single, symmetry radial, reniform; mono-lete, laesura characteristics not visible, 30 μm long, MLI 0.63, intexine 2 μm , echinate. Echinae densely and evenly distributed over the entire surface of the spore, conical shaped, 2 μm tall, 2 μm wide at base and 1 μm spaced.

Dimensions. Equatorial diameter 30 μm ; polar diameter 47 μm ; equatorial/polar diameter 0.63, number measured (nm) = 1, number observed (no) = 1.

Comparisons. *Echinosporis* sp. Raine 1981 is smaller and spines are sparser.

Derivation of name. After the conical spines.

Genus *Polypodiisporites* Potonié 1956

Type species. *Polypodiisporites favus* Potonié 1956

Polypodiisporites cf. *P. scabraproximatus* Silva-Caminha et al. 2010

Specimen. Plate 1, figure 5, sample ap47, EF H-10.

Description. Spores single, symmetry radial, elliptic; mono-lete, curvature absent, laesura characteristics not visible, intexine 1.5–2 μm , verrucate. Verrucae short, rounded, < 0.5 μm tall, 2–3 μm wide and 1–2 μm spaced.

Dimensions. Equatorial diameter 25–33 μm ; polar diameter 49–50 μm ; equatorial/polar diameter 0.59–0.66, nm = 2, no = 2.

Comparisons. *P. scabraproximatus* Silva-Caminha et al. 2010 is scabrate proximally, a feature not well distinguishable in the present specimen.

Polypodiisporites serratus sp. nov.

Holotype. Plate 1, figures 6–7, sample sp68, EF C-8-4.

Description. Spores single, symmetry radial, oval; mono-lete, curvature absent, laesura 25 μm long, MLI 0.55, margo absent or indistinct, commissure indistinct, intexine 1 μm , verrucate. Verrucae densely and evenly distributed over the entire surface of the spore, 2 μm tall, 2–3 μm wide and 1 μm spaced. Verrucae circular but many have an unusual irregular serrate outline in plain view.

Dimensions. Equatorial diameter 30 μm ; polar diameter 45 μm ; equatorial/polar diameter 0.66, nm = 1, no = 1.

Comparisons. This represents the only species of *Polypodiisporites* to have verrucae of irregular/serrate outline.

Derivation of name. After serrate outline of verrucae.

Polypodiisporites timidus sp. nov.

Holotype. Plate 1, figures 8–9, sample sp68, EF K-25-1.

Description. Spores single, symmetry radial, reniform; mono-lete, curvature absent, laesura 36 μm long, MLI 0.7, margo distinct, very thin, 1 μm wide, commissure distinct, straight,

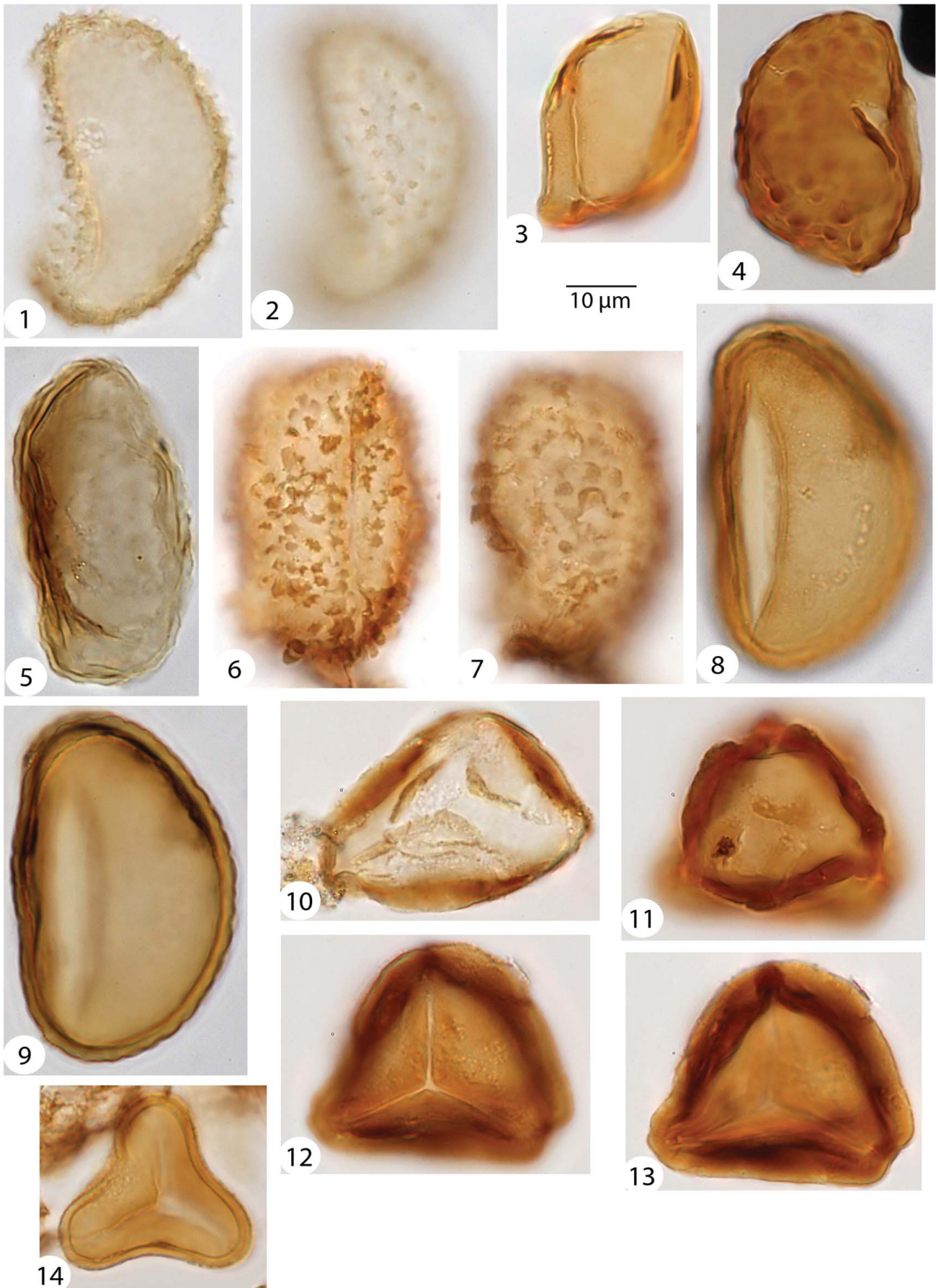


Plate 1. 1–2. *Echinosporis conicus* sp. nov.; 3. *Laevigatosporites tibuensis*; 4. *Polypodiisporites* aff. *speciosus*; 5. *Polypodiisporites* cf. *scabraproximatus*; 6–7. *Polypodiisporites serratus* sp. nov.; 8–9. *Polypodiisporites timidus* sp. nov.; 10. *Camarozonosporites* cf. *crassus*; 11–13. *Cingulatisporites oligodistalis* sp. nov.; 14. *Concavissimisporites varzeanus* sp. nov.

tapering; intexine 2 μm , verrucate. Verrucae very short, flat, densely and evenly distributed over the entire surface, closely spaced and of constant height, < 0.5 μm tall, 3–5 μm wide and 1 μm spaced.

Dimensions. Equatorial diameter 33 μm ; polar diameter 51 μm ; equatorial/polar diameter 0.64, nm = 1, no = 1.

Comparisons. *Polypodiisporites* aff. *speciosus* Sah 1967 is laevigate on the proximal face and has larger irregular verrucae. *P. scrabraproximatus* Silva-Caminha et al. 2010 is scabrate proximally and the distal verrucae form a negative reticulum.

Derivation of name. After being discretely verrucate, i.e. having short and flat verrucae.

4.1.2. *Triletes*

Genus *Camarozonosporites* Pant ex. Potonié 1954, emend. Klaus 1960

Type species. *Camarozonosporites cretaceous* (Weyland & Krieger 1953) Potonié 1956

Camarozonosporites cf. *C. crassus* Silva-Caminha et al. 2010

Specimen. Plate 1, figure 10, sample ap47, EF L-15-1/3.

Description. Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii long 10 μm long, TLI 1, margo distinct, 1.5 μm wide, commissure distinct, straight, ends pointed, intexine 1–2 μm , increasing 5 μm to towards interradsial region, which has interradsial crassitude. Laevigate.

Dimensions. Equatorial diameter length 40 μm ; equatorial diameter width 31 μm ; polar diameter view length/width (P/dv) 1.3, nm = 1, no = 1.

Comparisons. *C. crassus* Silva-Caminha et al. 2010 is verrucate.

Genus *Cingulatisporites* Thomson in Thomson & Pflug 1953

Type species. *Cingulatisporites levispeciosus* Pflug 1953, in Thomson & Pflug 1953

Cingulatisporites oligodistalis sp. nov.

Holotype. Plate 1, figures 11–13, sample ap47, EF V-20-3.

Description. Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii long, 17 μm long, TLI 0.85, margo distinct, 3–4 μm wide, commissure distinct, straight, intexine 1.5 μm , cingulate, cingulum 4 μm thick. Verrucate on distal face, verrucae few, sparse, large and elongate, 3–4 μm wide. Proximal face laevigate.

Dimensions. Equatorial diameter length 40 μm ; equatorial diameter width 35 μm ; P/dv length/width 1.15, nm = 1, no = 1.

Comparisons. *C. verrucatus* Regali et al. 1974 has a circular outline of the inner body of spore, simple laesura and dense circular verrucae. *C. laevigatus* Silva-Caminha et al. 2010 has a triangular projection in distal face.

Derivation of name. After the low number of distal verrucae.

Genus *Concavissimisporites* Delcourt & Sprumont 1955

Type species. *Concavissimisporites verrucosus* Delcourt & Sprumont 1955

Concavissimisporites varzeanus sp. nov.

Holotype. Plate 1, figure 14, sample sp68, EF P-40-3.

Description. Spores single, symmetry radial, triangular-obtuse-concave; trilete, curvatura absent, laesura distinct, radii 14 μm long, reaching the equator, TLI 1.12, margo absent, commissure straight; intexine 1.3 μm . Laevigate. Interradsial area concave.

Dimensions. Equatorial diameter length 25 μm ; equatorial diameter width 30 μm ; P/dv length/width 1.2, nm = 1, no = 1.

Comparisons. *Psilatriteles martinensis* Sarmiento 1992 does not have concave sides and its laesurae are shorter. *Psilatriteles lobatus* Hoorn 1994 has interradsial crassitude. *Polypodiaceoisporites pseudopsilatus* Lorente 1986 has a thick cingulum. *Concavissimisporites juriensis* Balme 1957 has kyrtome and kyrtome-like thickenings on the distal surface. *Concavissimisporites lamontis* Habib 1969 is kyrtomate. *Concavissimisporites baldurnensis* Delcourt and Sprumont 1955 has much more concave sides and shorter laesura. Other *Concavissimisporites/Concavissimisporites* species are not laevigate.

Derivation of name. After the flooded forests of Amazonia called várzea.

Genus *Echinatisporis* Krutzsch 1959

Type species. *Echinatisporis longechinus* Krutzsch 1959

Echinatisporis parviechinatus sp. nov.

Holotype. Plate 2, figures 3–4, sample sp68, EF J-20-4.

Description. Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii long, 27 μm long, TLI 1.3, margo absent, commissure distinct, straight; intexine 2.5 μm . Echinulate. Spines very sparse, present all over the surface; 1.5 μm wide at base, 2 μm tall.

Dimensions. Equatorial diameter length 41 μm ; equatorial diameter width 41 μm ; P/dv length/width 1, nm = 1, no = 1.

Comparisons. *E. brevispinosus* Jaramillo and Dilcher 2001, *E. muelleri* (Regali et al. 1974) Silva-Caminha et al. 2010 and *E. circularis* Silva-Caminha et al. 2010 differ in spine shape and having a denser coverage of spines.

Derivation of name. After the low number of spines.

Genus *Verrucatotriteles* Van Hoeken-Klinkenberg 1964

Type species. *Verrucatotriteles bullatus* Van Hoeken-Klinkenberg 1964

Verrucatotriteles laesuraverrucatus sp. nov.

Holotype. Plate 3, figures 5–6, sample ap47, EF T-38-3.

Description. Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, slightly irregular, radii middle sized, 15–20 μm long, TLI 0.75–0.66, margo absent, commissure indistinct; intexine 1–1.5 μm . Verrucate. Verrucae present over the entire surface of the grain. Verrucae of irregular size and shape, most of them are elongate and resemble rugulae, 4–10 μm wide, 3–4 μm tall, 1–2 μm apart; close to the laesurae they are smaller and circular, 1–3 μm wide, 1–2 μm tall, and 1 μm apart.

Dimensions. Equatorial diameter length 40–60 μm ; equatorial diameter width 40–60 μm ; P/dv length/width 1, nm = 2, no = 2.

Comparisons. *Verrucatotriteles etayoi* Dueñas 1980 differs in lacking verrucae with variable size and shape around laesura like the specimen described here and in verrucae being more closely spaced. *Verrucatotriteles bullatus* Van Hoeken-

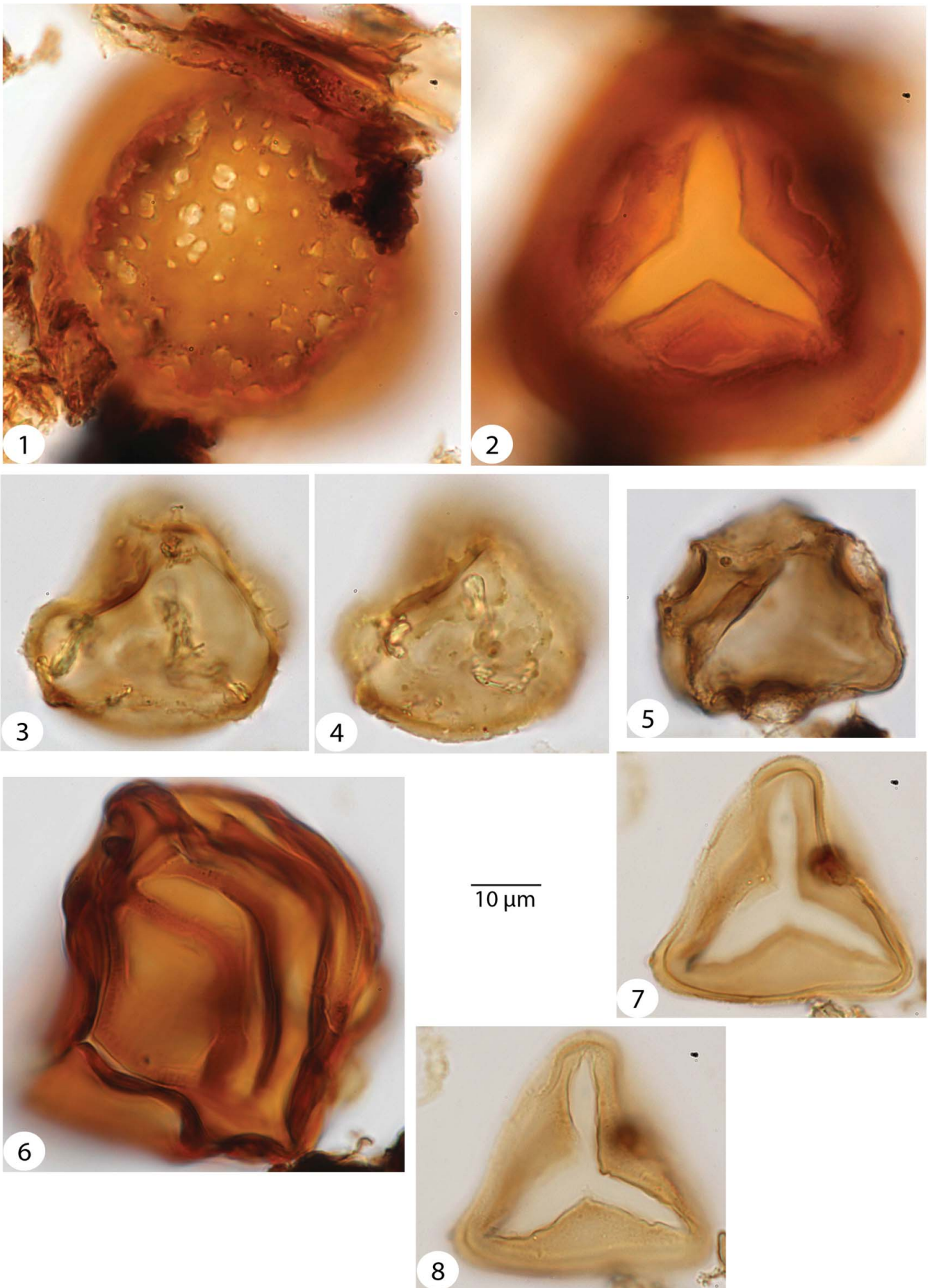


Plate 2. 1–2. *Cyatheacidites annulatus*; 3–4. *Echinatisporis parviechinatus* sp. nov.; 5. *Kuylisporites waterbolkii*; 6. *Magnastriatites grandiosus*; 7–8. *Matonisporites muelleri*.

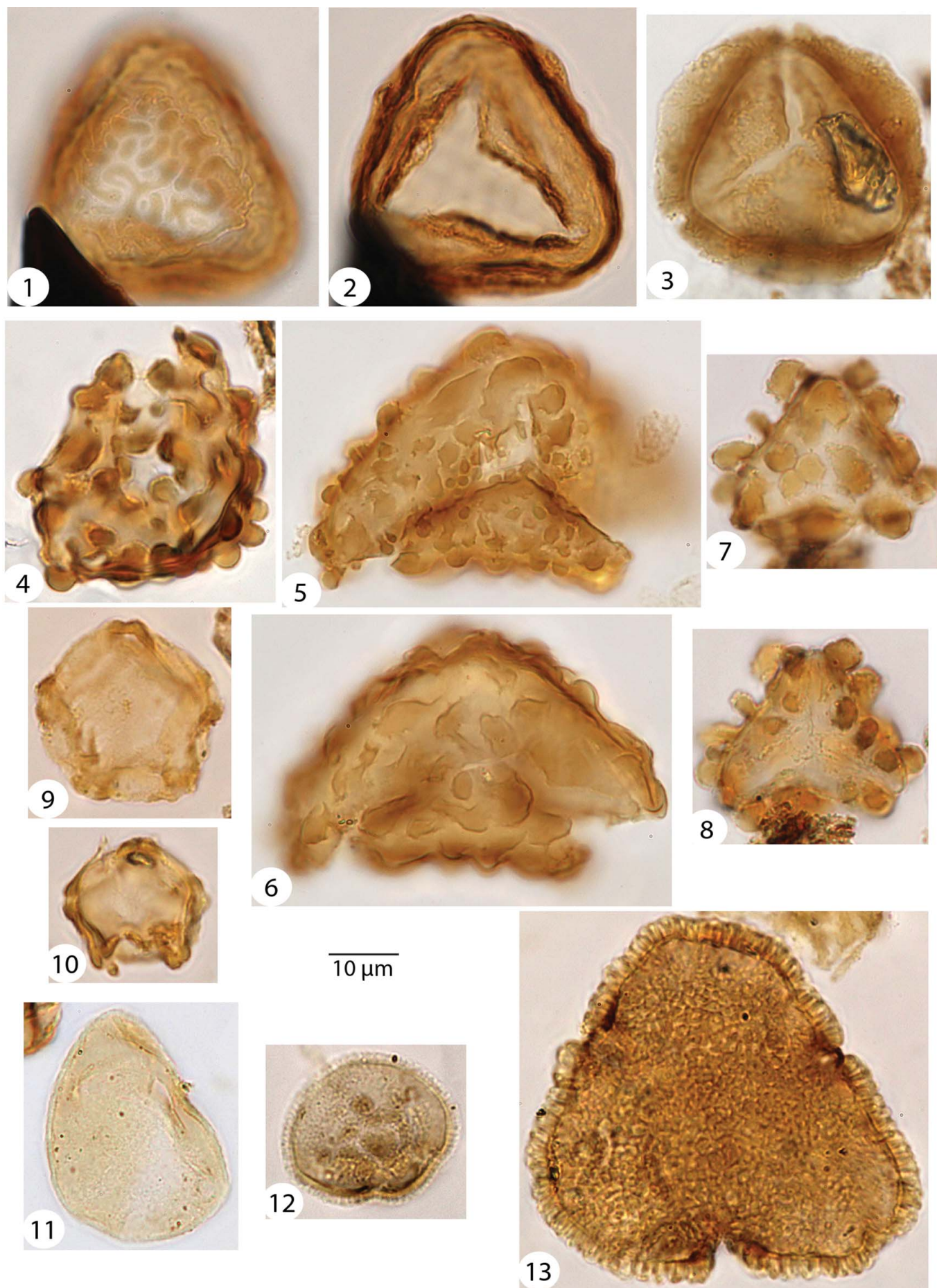


Plate 3. 1–2. *Polypodiaceoisporites amazonensis*; 3. *Psilatriletes lobatus*; 4. *Verrucatotrilletes etayoi*; 5–6. *Verrucatotrilletes laesuraverrucatus* sp. nov.; 7–8. *Verrucatotrilletes tortus* sp. nov.; 9–10. *Alnipollenites verus*; 11. *Arecipites regio*; 12. *Clavainaperturites microclavatus*; 13. *Bombacacidites ciriloensis*.

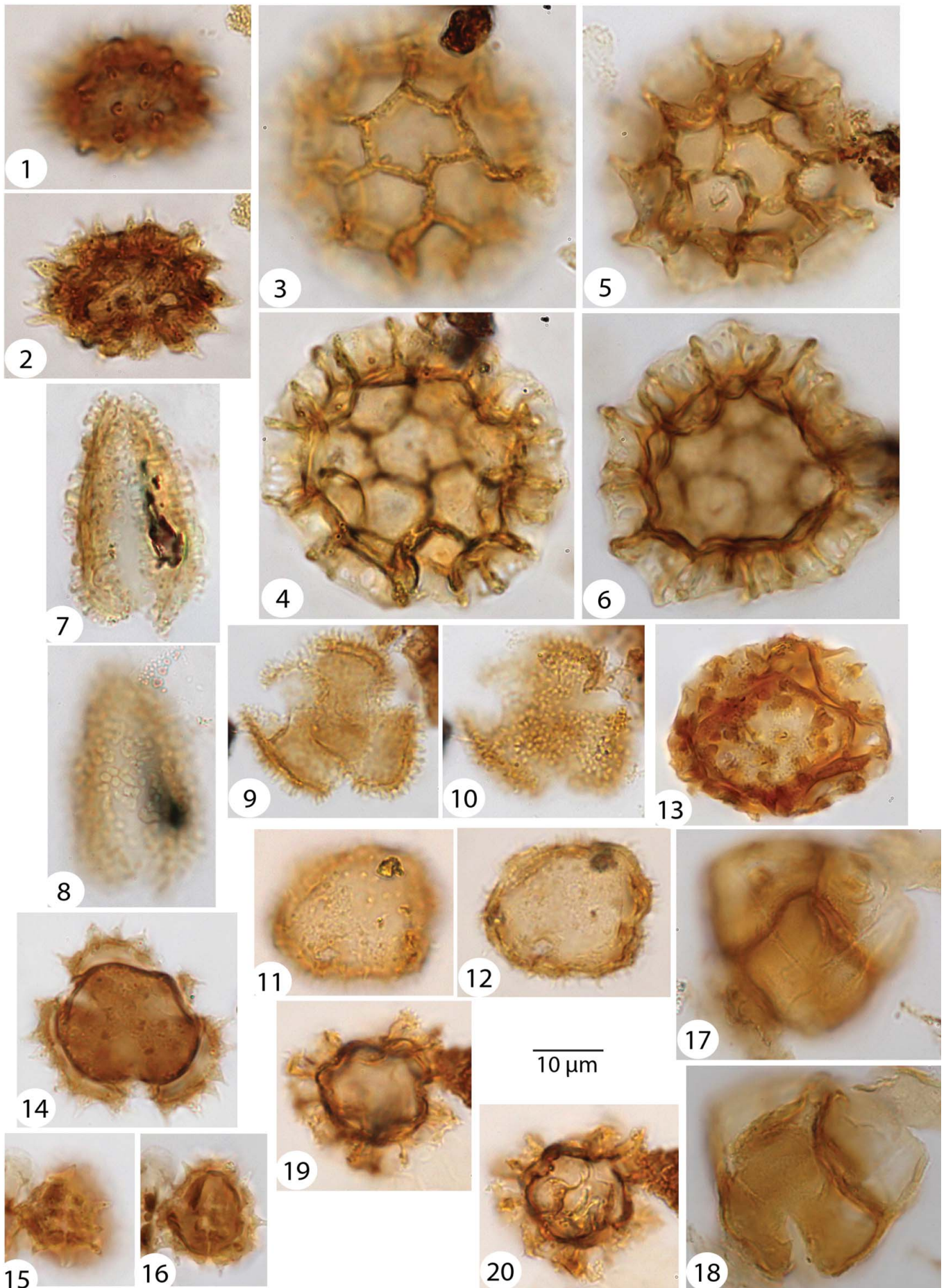


Plate 4. 1–2. *Cichoreacidites longispinosus*; 3–4. *Cichoreacidites? igapoensis* sp. nov. (holotype); 5–6. *C. igapoensis* sp. nov. (paratype); 7–8. *Clavamonocolpites lorentei*; 9–10. *Crototricolpites finitus*; 11–12. *Echiperiporites akanthos*; 13. *Echiperiporites lophatus*; 14–16. *Echitricolporites spinosus*; 17–18. *Ericipites* aff. *annulatus*; 19–20. *Fenestrites spinosus*.

Klinkenberg 1964 has much larger verrucae, more closely spaced and less variable in shape.

Derivation of name. After verrucae around laesura.

Verrucatotriletes tortus sp. nov.

Holotype. Plate 3, figures 7–8, sample sp68, EF L-37-1.

Description. Spores single, symmetry radial, triangular-obtuse-straight; trilete, curvatura absent, laesura distinct, straight, radii 13 μm long, almost reaching equator, TLI 0.86, margo absent, commissure distinct, straight, ends pointed; intexine 1 μm . Verrucate-baculate over the entire surface of the spore. Distally and around the equator most ornamentation elements are baculae 4–10 μm tall, 4–5 μm wide and 1–3 μm apart, with a constant width from base to top and twisted usually at 90 degrees. Proximally there are fewer elements, verrucae 4–5 μm wide, 4–5 μm tall, circular to slightly elongate, 1–2 μm apart. Surface around the laesurae is laevigate.

Dimensions. Equatorial diameter length 20 μm ; equatorial diameter width 30 μm ; P/dv length/width 0.66, nm = 1, no = 1.

Comparisons. *Verrucatotriletes bullatus* van Hoeken-Klinkenberg 1964 has large, rounded verrucae. *Verrucatotriletes etayoi* Dueñas has irregular dense verrucae. *Baculatisporites* species are circular, having small, dense baculae. *Verrucatotriletes tortum* is placed in *Verrucatotriletes* because both baculae and verrucae are present and because its overall shape is similar to that of most *Verrucatotriletes* species.

Derivation of name. After verrucae being bent (from Latin 'tortus', meaning twisted).

4.2. Pollen

Genus *Cichoreacidites* Sah 1967

Type species. *Cichoreacidites spinosus* Sah 1967

Cichoreacidites? igapoensis sp. nov.

Plate 4, figures 3–6

Synonymy. *Fenestrites* sp. 2 Silveira & Souza (2015)

Holotype. Plate 4, figures 3–4, sample ap47, EF K-50-1/2.

Paratype. Plate 4, figures 5–6, sample ap47, M-21-1/3.

Description. Monad, radial, isopolar, circular; apertures not visible; tectate, tectum imperforate, exine 8–10 μm thick, nexine 1 μm thick, columellae 6–7 μm thick, 1–2 μm wide, 1 μm apart, tectum 1–2 μm thick. Columellae tips often bifurcate irregularly, giving the wall stratification an alveolar texture. Fenestrate (lophate), fenestrae are polygonal, mostly hexagonal, 10 μm wide, sides 6–10 μm long each. Muri of fenestrae are psilate, simplicolumellate, columellae seen through tectum; lumina also psilate. At vertices of lumina (where sides from different lumina meet), wall is ~ 1 μm taller, giving the outline a slightly spiky/undulating appearance.

Dimensions. Equatorial length 42–45 μm ; equatorial width 42–45 μm ; equatorial diameter length/width 1, nm = 2, no = 2.

Comparisons. *Fenestrites spinosus* Van der Hammen 1956 and *C. longispinosus* Lorente 1986 (Silva-Caminha et al. 2010) are echinate. *Fenestrites gemmatus* Regali et al. 1974 is gemmate. *Cichoreacidites* Sah 1967 accommodates tricolporate grains with fenestrae and echinae, so we provisionally place our new species in this genus as it cannot be placed in any formal genus

and because *Fenestrites* van der Hammen 1956 is an invalid name.

Derivation of the name. After the black-water environments of Amazonia, called 'igapó'.

Botanical affinity. *Pacourina/Vernonia* (Asteraceae).

Genus *Ericipites* Wodehouse 1933

Type species. *Ericipites longisulcatus* Wodehouse 1933

Ericipites aff. *annulatus*

Specimen. Plate 4, figures 17–18, sample ap47, EF L-11-3/4.

Description. Tetrad tetrahedral. Monads are radial, isopolar, triangular-obtuse-straight; tricolporate, colpi simple, mid-sized, 20 μm long, ends pointed, slightly invaginated; pore characteristics not clear; tectate, exine 1.5 μm thick, nexine 0.5 μm thick, columellae 0.5 μm thick, tectum 0.5 μm . Psilate. Tetrad coaperturate.

Dimensions. Entire tetrad 38–39 μm wide, 35–38 μm long, equatorial diameter of a single grain 25–28 μm ; nm = 2, no = 4.

Comparisons. *E. annulatus* Gonzalez 1967 is larger and has pronounced pores, sometimes vestibulate.

Genus *Foveotricolporites* Pierce 1961

Type species. *Foveotricolporites rhombohedralis* Pierce 1961

Foveotricolporites ponticulus sp. nov.

Holotype. Plate 5, figures 1–3, sample sp68, EF M-33-1/3.

Description. Monad, radial, isopolar, prolate; tricolporate, colpi long, 25 μm long, CPI 0.83, costate, costae 1.5 μm thick, 2 μm wide, borders invaginated, ends pointed, pores simple, lalongate, very narrow, 5 \times 2 μm long; tectate, tectum perforate, exine 3–4 μm thick, nexine 1 μm thick, columellae 1.5 μm thick, tectum 1 μm thick; foveolate, homobrochate, lumina < 0.5 μm wide, 0.5 μm apart, circular, densely and evenly distributed over the entire grain.

Dimensions. Polar diameter 30 μm , equatorial diameter 20 μm , polar/equatorial 1.5, nm = 1, no = 1.

Comparisons. *Foveotricolporites lenticuloides* Silva-Caminha et al. 2010 has simple colpi and much shorter columellae; *F. flor-schutzii* (Van der Hammen) Van der Hammen & Wijmstra 1964 has indistinct columellae; *F. brevicolpatus* Jaramillo et al. 2007 is brevicolpate. *Paleosantalaceapites cingulatus* Jaramillo et al. 2010 is cingulate.

Derivation of name. After the locality being a bridge (from the Latin 'pontis').

Genus *Ladakhipollenites* Mathur & Jain 1980

Type species. *Ladakhipollenites pachyexinous* Couper ex. Mathur & Jain 1980

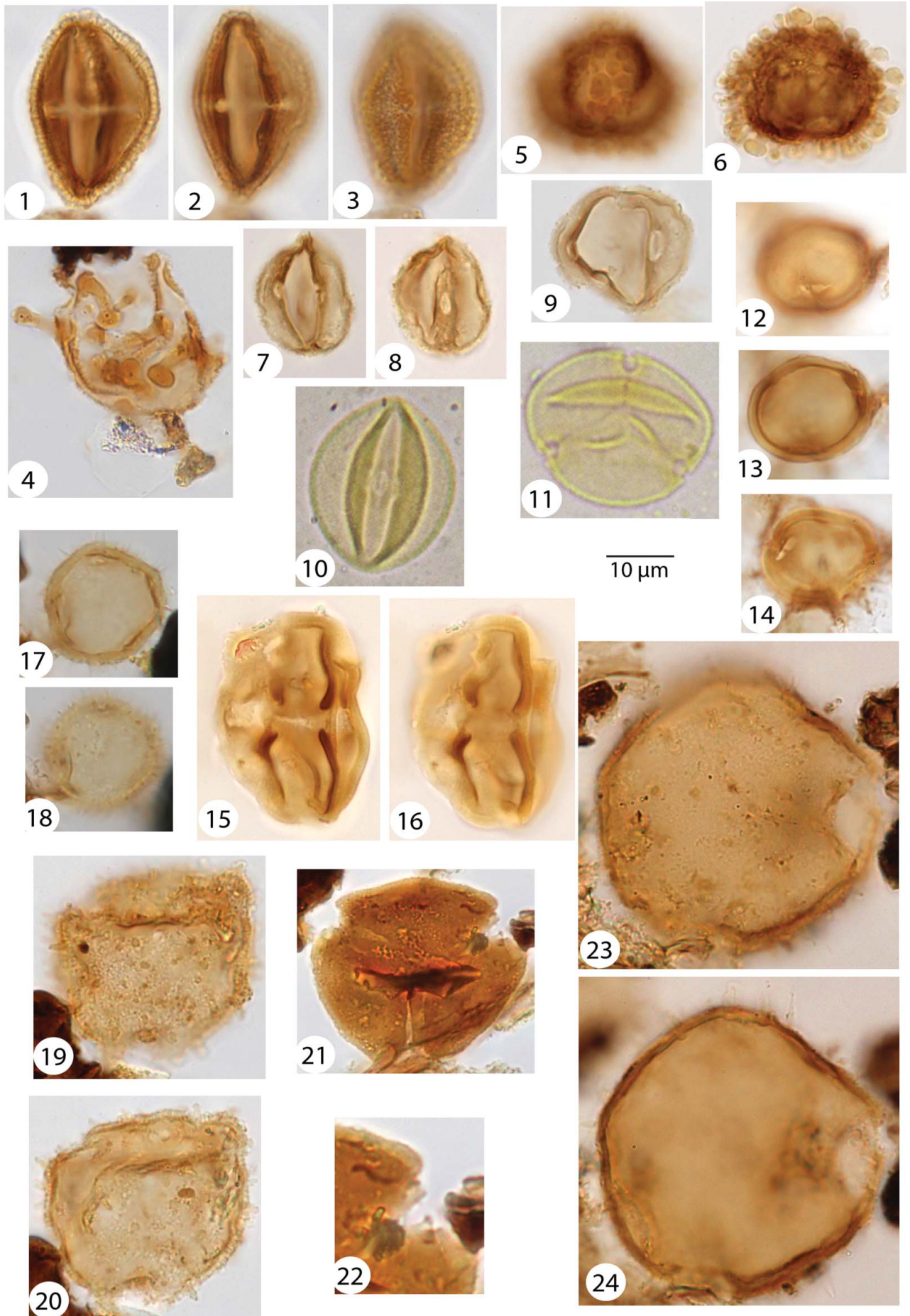
Ladakhipollenites? lolongatus sp. nov.

Plate 5, figures 7–9

Holotype. Plate 5, figures 7–8, sample sp68, EF V-16-1.

Paratype. Plate 5, figure 9, sample sp68, EF W-44.

Description. Monad, radial, isopolar, subspheroidal to prolate spheroidal; tricolporate, colpi simple, long, 17 μm long, CPI 0.89, borders invaginated, polar area rounded, very small; pores simple, lalongate, 4–5 μm \times 2–3 μm long; tectate, tectum imperforate, exine 1–1.5 μm thick, nexine 0.3 μm thick,



columellae 0.3 μm thick, indistinct, tectum 0.3 μm thick; psilate to micropitted.

Dimensions. Polar diameter 19 μm , equatorial diameter 22–15 μm , polar/equatorial 0.86–1.2, $\text{nm} = 2$, $\text{no} = 2$.

Comparisons. All tricolporate morphologies with lolongate pores are foveolate or reticulate. Psilate tricolporate morphologies with lolongate pores have not been recorded.

Derivation of name. After the lolongate pores.

Botanical affinity. *Symmeria paniculata* (Polygonaceae) (Plate 5, figures 10–11).

Ladakhpollenites? porolenticularis sp. nov.

Holotype. Plate 5, figures 12–14, sample ap47, EF E-16.

Description. Monad, radial, isopolar, subspheroidal; tricolporate, endocolpi long, 10 μm long, costate, costae 1 μm thick, slightly invaginated, ends pointed; ectopores lalongate, lens-shaped, 7 $\mu\text{m} \times 2 \mu\text{m}$ long, simple; atectate, exine 2 μm thick; psilate. Pores gradually thin and are pointed in their extremities, resulting in an arrowhead appearance.

Dimensions. Polar diameter 16 μm , equatorial diameter 20 μm , polar/equatorial 0.8, $\text{nm} = 1$, $\text{no} = 1$.

Comparisons. *Psilabrevitricolporites simpliformis* Van der Kaars 1983 and *P. sp. 2* Jaramillo & Dilcher 2001 are atectate psilate species, but both are brevicolpate.

Derivation of name. After lens-shaped pores.

Botanical affinity. Marcgraviaceae?

Ladakhpollenites? densicolumellatus sp. nov.

Holotype. Plate 5, figures 15–16, sample ap47, EF E-45-1.

Description. Monad, radial, isopolar, prolate; tricolporate, colpi long, 29 μm long, $\text{CPI} = 0.85$, borders straight, ends rounded, costae 2 μm wide, polar area is rounded; endopores are simple and coalesce forming an endocingulum, 4 μm wide; tectate, exine 2 μm thick, nexine 0.5 μm thick, columellae 1 μm thick, distinct, packed, tectum 0.5 μm thick. Psilate.

Dimensions. Polar diameter 34 μm , equatorial diameter 24 μm , polar/equatorial 1.4, $\text{nm} = 1$, $\text{no} = 1$.

Comparisons. *Psilatricolporites costatus* Dueñas has costate and much smaller pores; *P. normalis* Gonzalez 1967 has a much smaller pore and less rounded polar area; *P. osbcurus* Gonzalez 1967 is much thicker; *P. pachydermatus* Lorente 1986 has narrower pores; *P. atalayensis* Hoorn 1993 is tectate perforate (psilate-microreticulate) and the poles are less rounded; *P. crassoexinatus* Hoorn 1993 is spheroidal and has constricted pores; *P. magniporatus* Hoorn 1993 has a thick tectum and short, distinct columellae.

Derivation of name. After dense columellae layer.

Genus *Malvacipollis* Harris 1965

Type species. *Malvacipollis diversus* Harris 1965

Malvacipollis minutispinulosa sp. nov.

Holotype. Plate 5, figures 17–18, sample ap47, EF R-25-4.

Description. Monad, radial, isopolar, circular; stephanoporate, ectopores simple, endopores costate, costae 1 μm thick, 5–6 pores, pores 5 μm wide, 5 μm long, circular; tectate, exine 3 μm thick, nexine < 0.5 μm thick, columellae 0.5 μm thick, tectum 2 μm thick; echinate, spines 2 μm long, 1 μm wide, conical, 1 μm apart, interspine surface psilate.

Dimensions. Equatorial length 17 μm ; equatorial width 17 μm ; equatorial diameter length/width 1, $\text{nm} = 1$, $\text{no} = 1$.

Comparisons. *Malvacipollis spinulosa* is larger and thinner and has less dense spines.

Derivation of name. After being smaller than *M. spinulosa*.

Genus *Malvacipolloides* Anzótegui & Garalla 1986

Type species. *Malvacipolloides densiechinata* Anzótegui & Garalla 1986

Malvacipolloides aff. *M. maristellae*

Specimen. Plate 5, figures 19–20, sample sp68, EF K-10-2.

Description. Monad, radial, isopolar, circular; tricolporate, colpi short, 10 μm long, $\text{CEi} = 0.33$, simple, almost indistinct, pores circular (?), 5 \times 5 μm long, simple; tectate, exine 2.5 μm thick, nexine ca. 0.5 μm thick, columellae 1.5 μm thick, distinct, tectum 0.5 μm thick; echinate, spines 2–3 μm long, 1.5 μm wide, 2–3 μm apart, slightly conical, of constant height, interspine surface micropitted.

Dimensions. Equatorial length 30 μm ; equatorial width 35; equatorial diameter length/width 0.85, $\text{nm} = 1$, $\text{no} = 1$.

Comparisons. *Malvacipolloides maristellae* (Muller et al. 1987) Silva-Caminha et al. 2010 has more conical spines, exine increasing towards base of spines and spines longer near aperture, and exine is denser and darker at the base of the spines.

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

Type species. *Margocolporites tsukadai* Ramanujam 1966

Margocolporites aff. *M. fastigiatus* Silva-Caminha et al. 2010

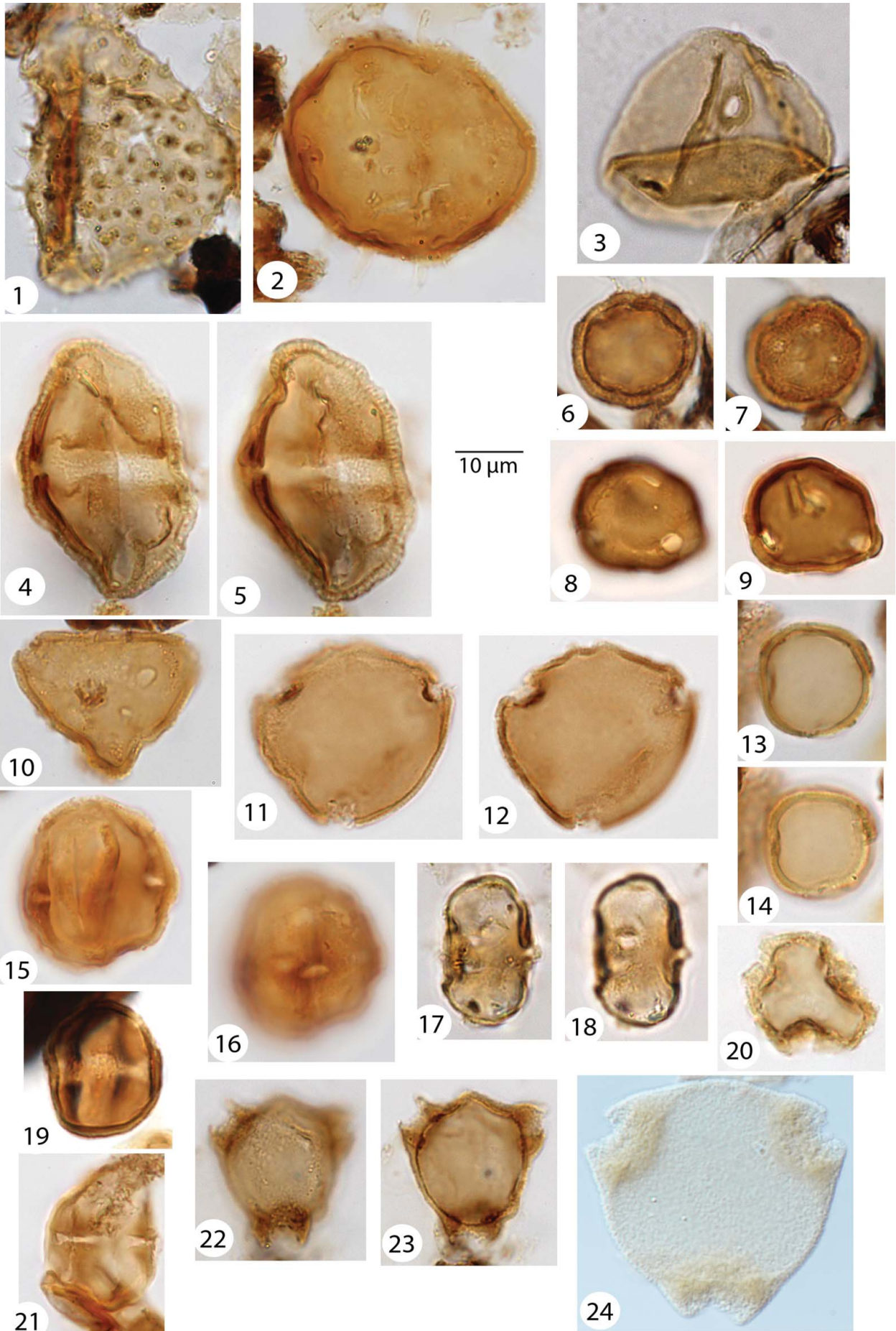
Specimen. Plate 5, figures 21–22, sample sp68, EF S-24-1/3.

Description. Monad, radial, isopolar, small polar area, 10 μm wide, triangular-obtuse-convex; tricolporate, colpi long, colpi 20 μm long, $\text{CEi} = 0.32$, ectocolpi marginate, margo distinct, 2 μm wide, margo produced by a thinning of the exine around the colpi, borders straight, ends pointed, endopores simple, 5 μm wide, lalongate; tectate, tectum imperforate, exine 2 μm thick, nexine 0.5 μm thick, columellae 0.5 μm thick, indistinct, tectum 1 μm thick. Psilate. Pores are apparently fastigate.

Dimensions. Equatorial length 31 μm , equatorial width 31 μm , equatorial diameter length/width 1, $\text{nm} = 1$, $\text{no} = 1$.

Comparisons. *Malvacipolloides fastigiatus* Silva-Caminha et al. 2010 is micropitted, heterobrochate and psilate around the margo.

Genus *Psilabrevitricolporites* Van der Kaars 1983



Type species. *Psilabrevitricolporites simpliformis* Van der Kaars 1983

Psilabrevitricolporites niger sp. nov.

Holotype. Plate 6, figures 11–12, sample ap47, EF V-11-1/3.

Description. Monad, radial, circular to triangular-obtuse-convex; tricolporate, colpi short, 12 colpi μm long, simple, CEi 0.2, borders straight, ends rounded, pores circular, $4 \times 4 \mu\text{m}$ long; tectate, exine $1.5 \mu\text{m}$ thick, sexine $0.5 \mu\text{m}$ thick, columellae $0.5 \mu\text{m}$ long, indistinct, tectum $0.5 \mu\text{m}$ thick; psilate to micropitted.

Dimensions. Equatorial length $30 \mu\text{m}$; equatorial width $28 \mu\text{m}$; equatorial diameter length/width 1.07, nm = 1, no = 1.

Comparisons. *Psilabrevitricolporites simpliformis* Van der Kaars 1983 is atectate and triangular; *P. sp. 1* Jaramillo & Dilcher 2001 is smaller ($19 \mu\text{m}$) and circular; *P. sp. 2* Jaramillo & Dilcher 2001 is atectate; *P. triangularis* (Van der Hammen & Wijmstra 1964) Jaramillo & Dilcher 2001 has thick costae and indistinct columellae; *P. devriesii* (Lorente 1986) Silva-Caminha et al. 2010 has much thicker exine and costae.

Derivation of name. After the black waters of the Negro River.

Genus *Psilastephanocolporites* Leidelmeyer 1966

Type species. *Psilastephanocolporites fissilis* Leidelmeyer 1966

Psilastephanocolporites brevissimus sp. nov.

Holotype. Plate 6, figures 13–14, sample ap47, EF J-23-3/4.

Description. Monad, radial, isopolar, circular to quadrangular, polar area large, $14 \mu\text{m}$ wide; stephanocolporate, 4-colporate, colpi simple, very short, $6 \mu\text{m}$ long, CEi 0.35, ends pointed, pores indistinct; tectate, exine $1.5 \mu\text{m}$ thick, nexine $0.5 \mu\text{m}$ thick, columellae $0.5 \mu\text{m}$ thick, indistinct, tectum $0.5 \mu\text{m}$ thick. Psilate.

Dimensions. Equatorial length $17 \mu\text{m}$; equatorial width $17 \mu\text{m}$; equatorial diameter length/width 1, nm = 1, no = 1.

Comparisons. *Psilastephanocolporites globulus* van Hoeken-Klinkenberg 1966 is intectate and exine is thicker; *P. marinamensis* Hoorn 1994 has large distinct pores; *P. matapiorum* Hoorn 1994 is longicolporate; *P. schneideri* Hoorn 1994 has much long colpi and large pores. Other species of *Psilastephanocolporite* have more than four colpi.

Derivation of name. After the rather short (brevi-) colpi.

Botanical affinity. *Myrsine?* (Myrsinaceae)

Genus *Psilastephanocolporites* Leidelmeyer 1966

Type species. *Psilastephanocolporites fissilis* Leidelmeyer 1966

Psilastephanocolporites aff. *P. marinamensis* Hoorn 1994

Specimen. Plate 6, figures 15–16, sample sp68, EF F-23-1/2.

Description. Monad, radial, isopolar, prolate spheroidal, stephanocolporate, 4-colporate, colpi simple, middle sized, $15 \mu\text{m}$ long, CEi 0.6, ends pointed, large polar area, $17 \mu\text{m}$ wide; pores lalongate, lenticular, $5 \mu\text{m}$ long, $3 \mu\text{m}$ wide, costate, costae

$1 \mu\text{m}$ thick, $1 \mu\text{m}$ wide; tectate, exine $2 \mu\text{m}$ thick, nexine $0.7 \mu\text{m}$ thick, columellae $0.7 \mu\text{m}$ tall, indistinct, tectum $0.7 \mu\text{m}$ thick. Psilate.

Dimensions. Equatorial length $25 \mu\text{m}$; polar length $26 \mu\text{m}$; equatorial diameter length/width 1.04, nm = 1, no = 1.

Comparisons. *Psilastephanocolporites marinamensis* Hoorn 1994 has indistinct colpi and simple pores with a different shape (oval).

Genus *Psilatirporites* Van der Hammen 1956 ex. Hoorn 1993

Type species. *Psilatirporites sarmientoi* Hoorn 1993

Psilatirporites aspidatus sp. nov.

Holotype. Plate 6, figures 22–23, sample ap47, EF S-27-4.

Description. Monad, radial, isopolar, triangular obtuse-convex; triporate, ectopores aspidate, apparently circular, $3 \mu\text{m} \times 3 \mu\text{m}$ long, also marginate, margo produced by an increasing of a thickening of the sexine towards the pores, $1 \mu\text{m}$ thick, endopores simple, of same dimensions as ectopore; tectate exine $1.2 \mu\text{m}$ thick, nexine $0.4 \mu\text{m}$ thick, columellae $0.4 \mu\text{m}$ thick indistinct, tectum $0.4 \mu\text{m}$ thick. Psilate.

Dimensions. Equatorial length $23 \mu\text{m}$; equatorial width $25 \mu\text{m}$; equatorial diameter length/width 0.92, nm = 1, no = 1.

Comparisons. *Corsinipollenites* and other *Psilatirporites* are not aspidate; *P. aspidatus* sp. nov. differs from triporate specimens assigned to *Faramea* by Graham (1991, Pliocene Gatun Fm, Panama) (Plate 6, figure 24) and Graham (1967, Miocene of Veracruz, Mexico) (Plate 6, figure 25) in being psilate rather than reticulate and also in the shape of apertures.

Derivation of name. After aspidate pores.

Botanical affinity. *Faramea* (Rubiaceae). Modern species (Plate 7, figures 1–4) vary in size and ornamentation, but all are aspidate triporate morphologies like *P. aspidatus* sp. nov.

Genus *Retimonocolpites* Pierce 1961

Type species. *Retimonocolpites dividius* Pierce 1961

Retimonocolpites ordinarius sp. nov.

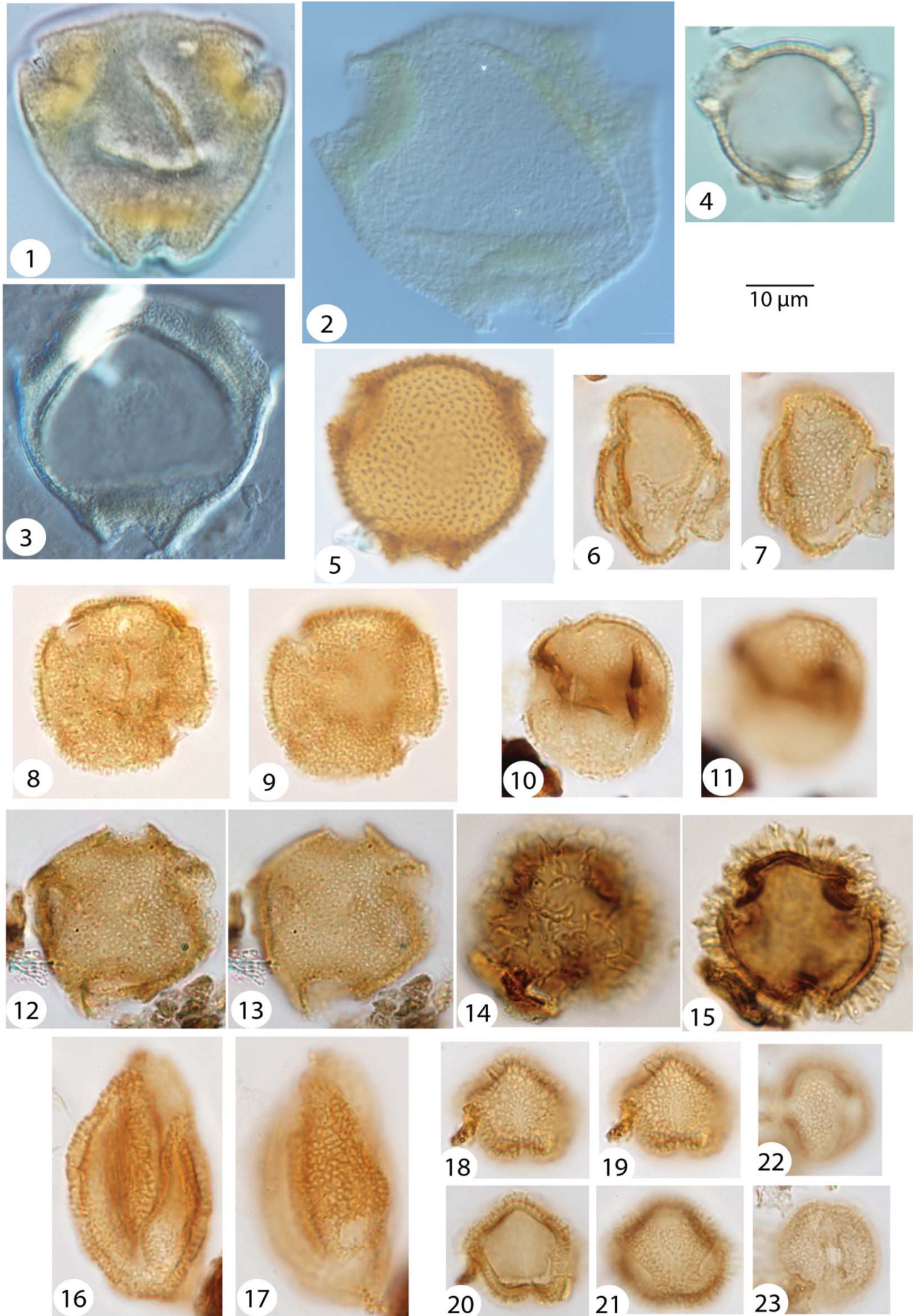
Holotype. Plate 7, figures 6–7, sample sp68, EF L-9-2.

Description. Monad, bilateral, isopolar, prolate; monocolpate, colpi long, straight, $24 \mu\text{m}$ long, CPi 0.85, marginate, margo $1.5 \mu\text{m}$ wide, rounded poles; tectate, exine $2 \mu\text{m}$ thick, nexine $0.4 \mu\text{m}$ thick, columellae $0.3 \mu\text{m}$ long, distinct, tectum $0.4 \mu\text{m}$ thick; reticulate, lumina ca. $0.5 \mu\text{m}$, circular to elongated, homobrochate, muri $< 0.5 \mu\text{m}$ thick.

Dimensions. Polar diameter $28 \mu\text{m}$, equatorial diameter $19 \mu\text{m}$, polar/equatorial 1.47, nm = 1, no = 1.

Comparisons. *Retimonocolpites bernardii* Gonzalez 1967 is larger and has broad polar area; *R. claris* Sarmiento 1992 has indistinct columellae and can be intectate; *R. longicolpatus* Lorente 1986 has colpus reaching poles and is micropitted; *R. nigeriensis* Van Hoeken-Klinkenberg 1966 has larger lumina and is heterobrochate; *R. retifossulatus* Lorente 1986 has much

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Plate 6. 1. *Mauritiidites franciscoi* var. *minutus*; 2. *Mauritiidites franciscoi* var. *pachyexinatus*; 3. *Monoporopollenites annulatus*; 4–5. *Paleosantaceae* *cingulatus*; 6–7. *Parsonsoidites? brenacii*; 8–9. *Perisyncolporites pokorny*; 10. *Proteacidites triangulatus*; 11–12. *Psilabrevitricolporites niger* sp. nov.; 13–14. *Psilastephanocolporites brevissimus* sp. nov.; 15–16. *Psilastephanocolporites* aff. *marinamensis*; 17–18. *Psilatirporites labiatus*; 19–20. *Ranunculacidites operculatus*; 21. *Psilatirporites silvaticus*; 22–23. *Psilatirporites aspidatus* sp. nov. (holotype); 24. fossil *Faramea* (Rubiaceae) from the Gatun Formation in Panama (slide SL103-253_9, EF H20, in Graham 1991, p. 211, fig. 45).



larger lumina and is reticulate to foveolate; *R. spendidus* Gonzalez 1967 is larger and thicker; *R. tertarius* Gonzalez is intectate; *R. absyae* Hoorn 1993 is heteropolar and has simple colpi; *R. maximus* Hoorn 1993 is larger.

Derivation of name. After its rather common (ordinary) morphology.

Genus *Retistephanocolpites* Leidelmeyer 1966

Type species. *Retistephanocolpites angeli* Leidelmeyer 1966

Retistephanocolpites quadraticus sp. nov.

Holotype. Plate 7, figures 8–9, sample ap47, EF M-34-1/3.

Description. Monad, radial, isopolar, circular to polygonal; stephanocolpate, four colpi, colpi simple, brevicolpate, colpi 6 μm long, CEI 0.22, borders straight, ends pointed, broad polar area, 15 μm wide; tectate, exine 2 μm thick, nexine 0.7 μm thick, columellae 0.7 μm long, distinct, tectum 0.7 μm thick; microreticulate, lumina ca. 0.5 μm wide, homobrochate, circular, muri ca. 0.5 μm wide.

Dimensions. Equatorial length 27 μm ; equatorial width 29 μm ; equatorial diameter length/width 0.93, nm = 1, no = 1.

Comparisons. *Retistephanocolpites angeli* Lindelmeyer 1966, *R. circularis* Silva-Caminha et al. 2010, *R. gracilis* Regali et al. 1974, *R. finalis* Gonzalez 1967, *R. williamsi* Germeraad et al. 1968 and *R. fossulatus* Jaramillo & Dilcher 2001 have more than four colpi. *Retistephanocolpites minutus* Gonzalez 1967 has long colpi and a small polar area; *R. sp. 2* Jaramillo & Dilcher 2001 has wider lumina and costate colpi; *R. tropicalis* Dueñas 1980 has longer colpi with rounded ends and a wider reticulum.

Derivation of name. After the quadrangular amb.

Genus *Retistephanocolporites* Van der Hammen & Wijmstra 1964

Type species. *Retistephanocolporites quadriporus* Van der Hammen & Wijmstra 1964

Retistephanocolporites centrimaculatus sp. nov.

Holotype. Plate 7, figures 10–11, sample ap47, EF G-11-3/4.

Description. Monad, radial, isopolar, prolate spheroidal; stephanocolporate, colpi short, 13 μm long, CPI 0.5, ectocolpi simple, ends pointed, endopores slightly lalongate, 4 \times 3 μm long, costate, costae 2 μm thick, costae of different colpi coalesce forming a darkened area in the mesocolpium; tectate, exine 2 μm thick, nexine 0.6 μm thick, columellae 0.8 μm long, distinct, tectum 0.6 μm thick; reticulate, lumina 0.5–1 μm , heterobrochate, circular to elongate, muri 0.5–1 μm wide, heterobrochate, lumina size decreasing towards mesocolpium, where surface becomes micropitted.

Dimensions. Polar diameter 26 μm , equatorial diameter 23 μm , polar/equatorial 1.13, nm = 1, no = 1.

Comparisons. *Retistephanocolporites festivus* Gonzalez 1967 has thick and protruding costae; *R. fossulatus* Jaramillo & Dilcher 2001 is reti-foveo-foveolate and has indistinct pores.

Derivation of name. After the mesocolpium being darkened.

Genus *Retistephanoporites* Gonzalez 1967

Type species. *Retistephanoporites angelicus* Gonzales 1967

Retistephanoporites amazonicus sp. nov.

Holotype. Plate 7, figures 12–13, sample ap47, EF L-47.

Description. Monad, radial, isopolar, circular; stephanoporate, four pores, pores large, 10 μm \times 10 μm long, circular, aspidate, pores slightly protruding, annulus 2 μm wide, 2 μm thick; tectate, exine 2 μm thick, nexine 0.5 μm thick, columellae 0.5 μm long, distinct, tectum 1 μm thick; foveolate-reticulate, lumina 0.5 μm , homobrochate, circular, muri 0.5–1 μm wide.

Dimensions. Equatorial length 28 μm ; equatorial width 28 μm ; equatorial diameter length/width 1, nm = 1, no = 1.

Comparisons. *Retistephanocolporites angelicus* Gonzalez 1967, *R. crassinexinatus* Jaramillo & Dilcher 2001 and *R. minutiporus* Jaramillo & Dilcher 2001 have more pores; *R. crassiannulatus* Lorente 1986 usually has more pores and a thicker annulus.

Derivation of name. After Amazonia.

Genus *Rhoipites* Wodehouse 1933

Type species. *Rhoipites bradleyi* Wodehouse 1933

Rhoipites? basicus sp. nov.

Holotype. Plate 7, figures 16–17, sample sp68, EF U-11-2.

Description. Monad, radial, isopolar, prolate; tricolpate, colpi 27 μm long, CPI 0.7, simple, borders straight, ends rounded, polar area rounded; tectate, exine 2 μm thick, nexine 0.6 μm thick, columellae 0.8 μm thick, distinct, tectum 0.6 thick; reticulate, lumina 0.5–1 μm wide, circular to elongate, homobrochate, densely and evenly distributed over entire grain, muri 0.5 μm wide.

Dimensions. Polar diameter 39 μm , equatorial diameter 22 μm , polar/equatorial 1.77, nm = 1, no = 1.

Comparisons. *Retitricolpites absolutus* (Gonzalez 1967) Jaramillo & Dilcher 2001 has very short colpi; *R. adultus* Gonzalez 1967 has shorter colpi and is micropitted; *R. bonus* Gonzalez is foveoreticulate and has marginate colpi; *R. brevicolpatus* Sarmiento 1992 is brevicolpate; *R. caquetanus* Hoorn 1994 has short colpi; *R. colpiconstrictus* Hoorn 1994 has constrictions on colpi at the mesocolpia; *R. incisus* Gonzalez 1967 has very short colpi; *R. josephinae* Sarmiento 1992 has larger lumina and is heterobrochate; *R. marginatus* Van Hoeken-Klinkenberg 1966 has larger lumina and marginate colpi; *R. microreticulatus* (Van der Hammen 1956) Van der Hammen & Wijmstra 1964 is strongly heterobrochate, with psilate margo; *R. obtusus* Van Hoeken-Klinkenberg 1966 has flattened apocolpia where exine is thicker; *R. wijningae* Hoorn 1994 has coarser reticulum.

Derivation of name. After its very basic morphology.

Rhoipites manausensis sp. nov.

Holotype. Plate 7, figures 18–21, sample ap47, EF M-23-2/4.

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Plate 7. 1. Fossil *Faramea* from Veracruz (Mexico) (slide 9_1 EF P33, in Graham 1967, p. 834, fig. 179); 2. *Faramea coarinnensis* Müll. Arg.; 3. *F. hyacinthina* Mart.; 4. *F. jefensis* Dwyer & M.V. Hayden; 5. *F. calophylla* Standl.; 6–7. *Retimonocolpites ordinarius* sp. nov.; 8–9. *Retistephanocolpites quadraticus* sp. nov.; 10–11. *Retistephanocolporites centrimaculatus* sp. nov.; 12–13. *Retistephanoporites amazonicus* sp. nov.; 14–15. *Retitrescolpites? irregularis*; 16–17. *Rhoipites? basicus* sp. nov.; 18–21. *Rhoipites manausensis* sp. nov. (holotype); 22–23. *Rhoipites minuticirculus* sp. nov.

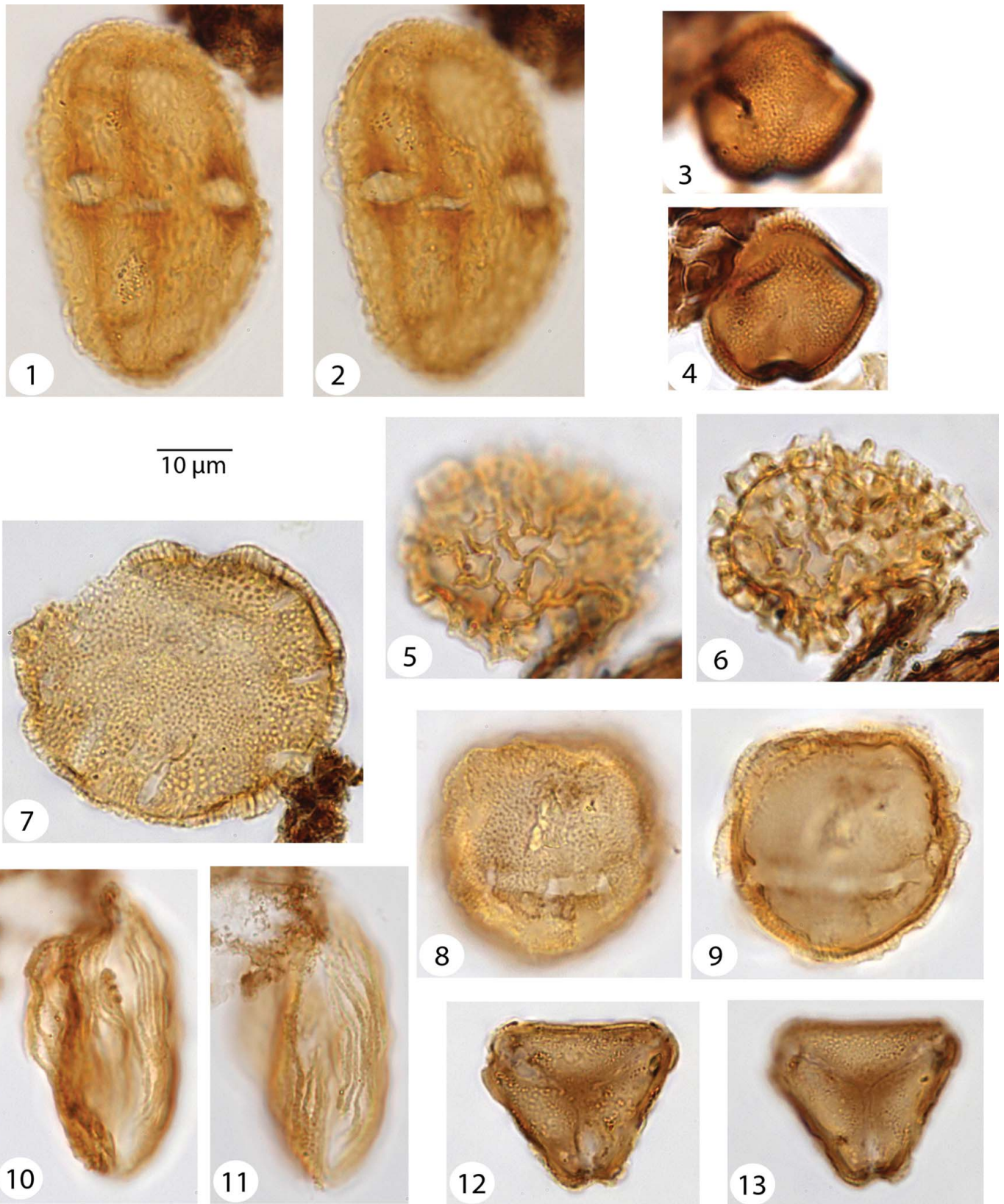


Plate 8. 1–2. *Rhoipites negroensis* sp. nov. (holotype); 3–4. *Siltaria* cf. *dilcheri*. 5–6. *Spirosyncolpites spiralis*; 7–9. *Stephanocolpites evansii*; 10–11. *Striatopollis catatumbus*; 12–13. *Syncolporites* aff. *anibalii*.

Description. Monad, radial, isopolar, pentagonal amb in oblique view; tricolporate, colpi 10 μm long, narrow, ends rounded, marginate, margo produced by a variation in lumina size, smaller lumina around colpi, margo ca. 1 μm wide, borders highly invaginated, endopores 1–2 μm \times 8 μm long, lalongate, very narrow and simple; tectate, exine 3 μm thick, nexine 1 μm thick, columellae 0.5 μm thick, distinct, tectum 1.5 thick; reticulate, lumina < 0.5–1 μm wide, variable, from circular and elongate to irregularly polygonal, heterobrochate, muri ca. 0.5 μm wide. Smaller lumina also seen surrounding larger lumina.

Dimensions. Polar diameter 18 μm , equatorial diameter 22 μm , polar/equatorial 0.8, nm = 1, no = 1.

Comparisons. *Ulmoideipites* is verrucate.

Derivation of name. After the city of Manaus.

Botanical affinity. *Schefflera* (Araliaceae).

Rhoipites minuticirculus sp. nov.

Holotype. Plate 7, figures 22–23, sample sp68, EF L-9-3

Description. Monad, radial, isopolar, spheroidal; tricolporate, ectocolpi 13 μm long, CPI 0.72, costate, costae 1 μm wide, ends rounded, endopores 4 \times 4 μm long, circular, simple; tectate, exine 2 μm thick, nexine 0.7 μm thick, columellae 0.7 μm thick, distinct, tectum 0.7 thick; reticulate, lumina 0.5 μm wide, circular to elongate, homobrochate, densely and evenly distributed over entire grain, muri < 0.5 μm wide.

Dimensions. Polar diameter 18 μm , equatorial diameter 18 μm , polar/equatorial 1, nm = 1, no = 1.

Comparisons. *Rhoipites crassicostatus* Van der Hammen & Wijmstra 1964 has thick costae; *R. oblatius* Hoorn 1994 has costae and lalongate pores; *R. milnei* Hoorn 1993 has narrow, lalongate pores; *R. solimoensis* Hoorn 1993 has very short colpi and costate pores.

Derivation of name. After its small size and circular shape.

Rhoipites negroensis sp. nov.

Holotype. Plate 8, figures 1–2, sample ap47, EF G-26-1/3.

Description. Monad, radial, isopolar, prolate; tricolporate, ectocolpi long, 45 μm long, CPI 0.88, very thin and simple, ends pointed, borders straight; endopores 10 μm \times 5 μm long, lalongate, lens-shaped, pores costate, costae 2 μm wide, restricted to the top and bottom of pores; tectate, exine 3 μm thick, nexine 1 μm thick, columellae 1 μm thick, distinct, well-spaced, ca. 2 μm apart, tectum 1 μm thick, simplicolumellate. Reticulate, lumina 3–4 μm wide, oval to elongate, aligned longitudinally giving a striate resemblance, homobrochate, muri 1 μm wide.

Dimensions. Polar diameter 51 μm , equatorial diameter 31 μm , polar/equatorial 1.64, nm = 1, no = 2.

Comparisons. *Rhoipites cienaguensis* (Dueñas 1980) Barreda 1997 and *R. guianensis* (Van der Hammen & Wijmstra 1964) Jaramillo & Dilcher 2001 have smaller lumina and margo produced by lumina decreasing towards the colpi; *R. hispidus* (Van der Hammen & Wijmstra 1964) Jaramillo & Dilcher 2001 has smaller lumina and narrower pores; *R. squarrosus* (Van der Hammen & Wijmstra 1964) Jaramillo & Dilcher 2001 has fine reticulation and indistinct pores and is subprolate; *R. planipolaris* Jaramillo et al. 2010 is heterobrochate, with reticulate apocolpia and foveolate-psilate mesocolpia; *R.? perprolatus* Rodriguez et al.

2012 is colpate; *R. gigantoporus* Silva-Caminha et al. 2010 has simple colpi and smaller lumina.

Derivation of name. After the Negro River.

Genus *Syncolporites* Van der Hammen 1954

Type species. *Syncolporites lisamae* Van der Hammen 1954

Syncolporites aff. *S. anibalii* Hoorn 1994

Specimen. Plate 8, figures 12–13, sample sp68, EF H-50-1/3.

Description. Monad, radial, isopolar, triangular amb; syncolporate, ectocolpi 14 μm long, apocolpial field absent, CEI 0.6, colpi costate, costae 1 μm thick, 1 μm wide, ends rounded, borders slightly invaginated; endopores not visible; tectate, exine 1.5 μm thick, nexine 0.5 μm thick, columellae 0.5 μm thick, distinct, tectum 0.5 thick. Psilate.

Dimensions. Equatorial diameter length 23 μm , equatorial diameter width 26 μm , Equatorial diameter length/width = 1.3, nm = 1, no = 1.

Comparisons. *Syncolporites anibalii* Hoorn 1994 is micropitted.

Botanical affinity. Sapindaceae?

5. Conclusions

Herein we provide the detailed palynology of a thin deposit from the Negro River in central Amazonia. This deposit, a relict of large-scale fluvial activity from the Piacenzian to the Gelasian (~3.6 to 1.9 Ma) (Soares et al. 2017), was traced for ~1.8 km across the river channel. Age was established by a rich and well-preserved pollen and spore assemblage, where we detected 95 species of which 25 were erected as new and compared to published records of northern South America. Five botanical affinities were established with extant genera and families (*Pacourina/Vernonia* (Asteraceae), *Myrsine?* (Myrsinaceae), *Symmeria* (Polygonaceae), *Faramea* (Rubiaceae), *Schefflera* (Araliaceae), and possibly a Marcgraviaceae). We highlight the potential of palynomorphs for correlating strata in central Amazonia and their relevance for biodiversity studies.

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