Acta Botanica Brasilica - 31(4): 720-735. October-December 2017.
doi: 10.1590/0102-33062017abb0160

Miocene fern spores and pollen grains from the Solimões Basin, Amazon Region, Brazil

Natália de Paula Sá[1*] and Marcelo de Araujo Carvalho[1]

Received: April 27, 2017
Accepted: July 11, 2017

ABSTRACT

This work documents fern spores and pollen grains (miospores) recovered from rocks of the Solimões Formation (Solimões Basin), their botanical affinities, ecology and distribution in the Miocene of the Amazon Region. The assemblage of miospores is well preserved and diverse. They are identified, illustrated and assigned to the ten families of ferns and 22 families of spermatophytes. All miospores were identified to the taxonomic level of species except for two taxa (*Perinomonoletes* and *Podocarpidites*). The families Pteridaceae and Arecaceae were most representative of ferns and spermatophytes, respectively. This work contributes to the knowledge of the paleoflora and will aid in paleoenvironmental, paleoecological and biostratigraphic interpretations of the Miocene of the Amazon Region.

Keywords: Miocene, miospores, Neogene, palynology, Solimões, vegetation

Introduction

The Amazon is the largest tropical rainforest ecosystem and its high diversity can be explained by ecological, environmental and paleontological models. Climate changes in the Pleistocene caused the expansion and retraction of the rainforest cycles. The changes were considered the triggers for the speciation and accumulation of species (Haffer 1969) and this theory has long been the basis for interpreting the current diversity patterns. However, numerous studies (e.g., Gentry 1982; Frailey 1986; Hooghiemstra & Hammen 1998; Monsch 1998**;** Jaramillo *et al*. 2006; Cozzuol 2006; Hoorn *et al*. 2010a) have shown that the diversification of biota is pre-Quaternary, reassembling to the last 60 Ma (million years).

The Neogene of Amazon region shows a very diversified flora. The records of this flora are based mainly on fossil woods and palynomorphs (e.g., spores, pollen grains) and a large part of this material allows establishing botanical affinities. For Miocene age, the palynology has been the most used technique to understand the past of the Amazon, especially miospores, which inform about the diversity and richness of the paleoflora. Several studies (e.g. Lorente 1986; Hoorn 1993; 1994a; b; c; Hoorn *et al*. 1995; Silva-Caminha *et al*. 2010; Hoorn *et al*. 2010b; Silveira & Souza 2015; 2016; Leite *et al*. 2016; D'Apolito 2016) show a paleoflora rich in pteridophytes (Anemiaceae, Cyatheaceae, Polypodiaceae, Pteridaceae) and gymnosperms (Araucariaceae and Podocarpaceae). Angiosperms are a separate case because it is currently the most important flora in the Amazon region. Since the Miocene, almost all the families (e.g. Annonaceae, Arecaceae, Asteraceae, Bombacaceae, Euphorbiaceae, Fabaceae, Malvaceae, Melastomataceae, Malpighiaceae, Sapotaceae) were already present in the region (Gentry 1982; Burnham & Graham 1999; Jaramillo *et al*. 2010; Hoorn *et al*. 2010c; 2017).

[1] Laboratório de Paleoecologia Vegetal, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro, 20940-040, Rio de Janeiro, RJ, Brazil

* Corresponding author: napaulasa@gmail.com

The recognition of the Miocene flora also allows paleoecological and paleoenvironmental inferences, as well as support the biostratigraphy framework the region (Lorente 1986; Hoorn 1993; 1994c; Silva-Caminha *et al*. 2010; Leandro 2012; Silveira & Souza 2015; 2016; Leite *et al*. 2016).

Therefore, this work seeks to inventory fern spores and pollen grains found in the Miocene rocks (Solimões Formation), their affinities and ecology in order to facilitate taxonomic identification and to support paleoenvironmental, paleoecological and biostratigraphic studies of the Miocene in the Amazon.

Materials and methods

Study area

The Solimões Basin is located in the western portion of the Amazon, bordered to the west by the Iquitos Arch and to the east by the Purus Arch. It is Paleozoic intracratonic depression, covering about 950,000 km^2 (Barata & Caputo 2007) is between 2°-8°S 62°-72°W (Fig. 1). Internally, there is a north-south regional control characterized to distribute the sediments in the basin, called the Carauari Arch. This subdivides the depression into the Juruá sub-basin to the east and the Jandiatuba sub-basin to the west (Wanderley-Filho *et al*. 2007, Fig. 1).

According to Eiras *et al*. (1994), the Solimões Basin covers six depositional sequences: ordovician, siluro-devonian, devonian-carboniferous, carboniferous-permian, cretaceous and cenozoic. In the last sequence are recognizing the Solimões and Içá formations.

The Solimões Formation extends for about 500,000 km^2, with sedimentary thickness ranging from 300 to 400 m, and can reach up to 1000 m near the Iquitos Arch. It covers Acre and west Amazonas, as well as the territories of Peru (Marañon and Putumayo basins) and Colombia (Caquetá and Putumayo basins) (Maia *et al*. 1977; Hoorn *et al*. 2010a). The Solimões Formation rocks comprise shales, siltstones and sandy shales, clayey silts and medium to fine-grained sands, lignites, carbonaceous clays and limestones (Maia *et al*. 1977).

In relation to the paleoenvironments during the Miocene, several studies indicate a heterogeneous and dynamic environment composed of rivers, lakes, flood plains, mangroves and coastal plains. It is also found elements of transitional and / or marine environments such

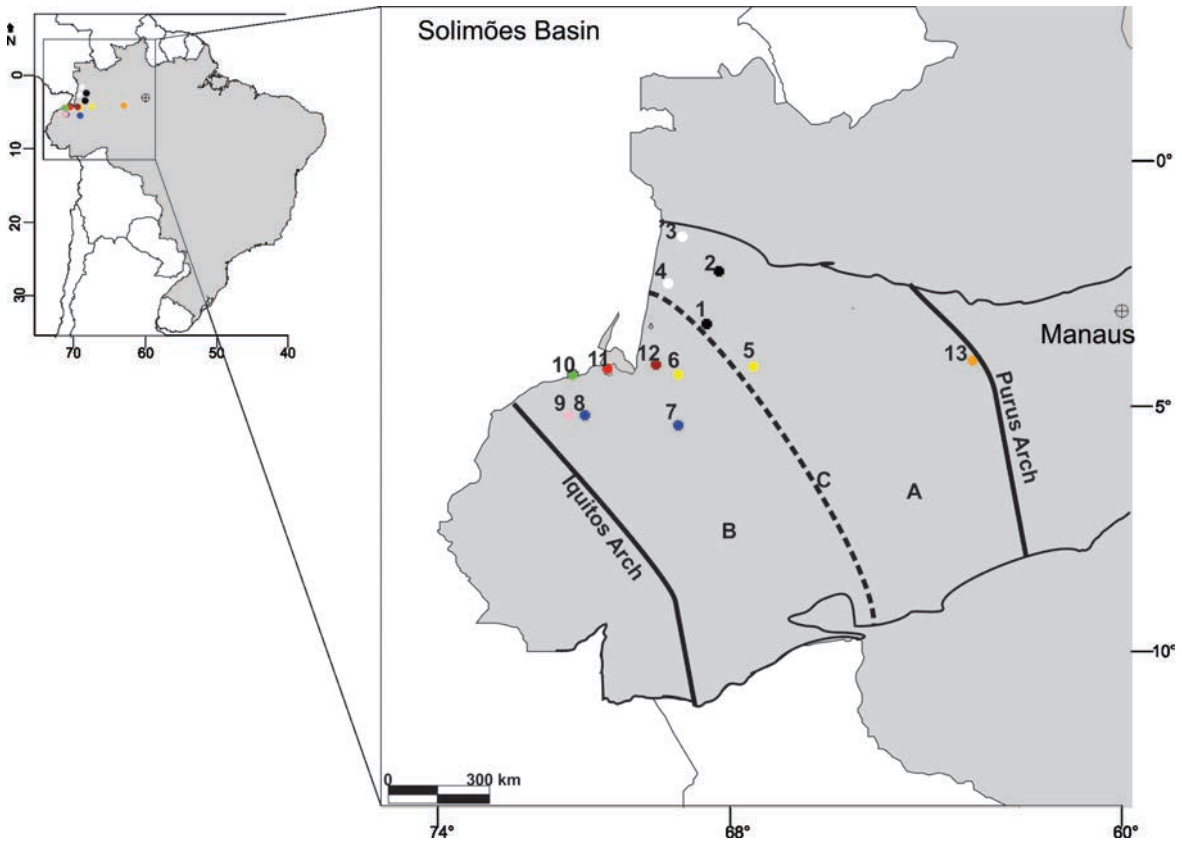

Figure 1. Solimões Basin location. **A**. Juruá sub-basin. **B**. Jandiatuba sub-basin. **C**. Carauari High. Legends: black dots 1-AS-37-AM (1) e 1-AS-46-AM (2); red dot: 1-AS-4a-AM (11); green dot: 1-AS-32-AM (10); yellow dots: 1-AS-19-AM (6) and 1-AS-27-AM (5); white dots: 1-AS-51-AM (4) and 1-AS-52-AM (3); blue dots: 1-AS-31-AM (7) and 1-AS-34-AM (8); pink dot: 1-AS-33-AM (9); brown dot: 1-AS-105-AM (12) and orange dot: Coari and Alto Solimões outcrops (13). Please see the PDF version for color reference.

as microforaminifera linings, molluscs and dinoflagellate cysts (e.g. Hoorn 1993; 1994a; Räsänen *et al*. 1995; Latrubesse *et al*. 1997; 2007; 2010; Lovejoy 1998; Vonhof *et al*. 1998; 2003; Wesselingh *et al*. 2002; 2006; Wesselingh 2006; Wesselingh & Salo 2006; Ramos 2006; Hoorn *et al*. 2010a; Gross *et al*. 2011; 2013; Linhares *et al*. 2011; Nogueira *et al*. 2013; Boonstra *et al*. 2015).

Metodology

In Solimões Basin investigations for energy resources were conducted by the federal government in the 1970s by the Geological Survey of Brazil (CPRM) and the National Department of Mineral Production (DNPM). The project entitled "Coal Alto Solimões" did a survey of areas with coal mining potential. A total of 84 wells was drilled in an area of 320,000 km^2 in northwest Brazil and this material was deposited at CPRM/DNPM - Manaus - AM (Maia *et al*. 1977). The wells 1-AS-37-AM and 1-AS-46-AM were chosen for palynological analysis considering its position in the Solimões Basin and the state of conservation.

The well 1-AS-37-AM is at an altimetric elevation of 60 m and coordinates 03°30'S 68°51'W near the Jandiatuba River. Its thickness is 242.60 m, and the initial 12 m corresponds to Holocene deposits in contact with the top of the Solimões Formation. The lithology is predominantly pelitic with higher occurrence of lignite layers (Maia *et al*. 1977).

The well 1-AS-46-AM is located in the northwestern portion of the Solimões Basin, coordinates 02°23'S 68°28'W, altimetry 101 m and thickness of 200.90 m. In this well, the Içá Formation represents the initial 6.0 m in erosive contact with the Solimões Formation. The lithology is pelitic and there are fewer layers of lignite (Maia *et al*. 1977).

For the study were selected 100 core samples from each well, from which 10g/sample was processed by standard technique in palynology to eliminate the inorganic material by means of acidic attacks (see Uesugui 1979; Erdtman 1969; Faegri & Iversen 1966).

The miospores recovered from the cores were identified by comparison with works of Germeraad *et al*. (1968); Regali *et al*. (1974a; b); Lorente (1986); Hoorn (1993; 1994c); Silva-Caminha *et al*. (2010); Jaramillo *et al*. (2011); D'Apolito (2016) and the website http://biogeodb.stri.si.edu/jaramillo/palynomorph/pollen, which hosts an atlas with images of several publications of palynomorphs from North of South America. The botanical affinities, ecology and distribution of spores and pollen grains were attributed according to the studies above and Tryon & Lugardon (1991); Jaramillo *et al*. (2010; 2011); Jaramillo & Rueda (2013) and Silveira & Souza (2015; 2016).

The photographs were obtained in Axioplan microscope and AxioCam MRc camera, with 1000x magnification by the program Axiovision and processed in the software Corel Draw 17.0. Each miospore was referenced using the "England Finder" coordinates associated with the number slides. The slides were deposited in the Laboratory of Plant Paleoecology of the Department of Geology and Paleontology of the National Museum of the Federal University of Rio de Janeiro.

Results

Sixty miospores were selected for this work, which include 19 fern spores and 41 pollen grains. The spores are distributed into 10 families, being the family Pteridaceae the most frequent. The pollen grains are distributed into 22 families (according to Cronquist 1988), with emphasis on the family Arecaceae. The miospores were systematized in two categories: spores and pollen grains, following the alphabetical order. Botanical affinity, ecology and distribution in the Solimões Formation (Tab. 1, Fig. 1) were attributed based on the literature.

Anteturma SPORITES Potonié 1893
Genus *Cingulatisporites* Thomson emend. Potonié 1956
Cingulatisporites laevigatus Silva-Caminha *et al*. 2010 (Fig. 2A)
Botanical affinity: unknown
Ecology: unknown

Genus *Crassoretitriletes* Germeraad *et al*, 1968
Crassoretitriletes vanraadshoovenii Germeraad *et al*. 1968 (Fig. 2B)
Ecology: pantropical, it occurs throughout South America (Tryon & Lugardon 1991), wetlands and swamps.

Genus *Deltoidospora* Miner 1935
Deltoidospora adriennis (Potonié & Gelletich 1933) Fredericksen 1983 (Fig. 2C)
Botanical affinity: family Pteridaceae, *Acrostichum aureum*
Ecology: pantropical, it occurs in coastal environments on all continents (Tryon & Lugardon 1991), mangrove (Jaramillo *et al*. 2010)

Genus *Distaverrusporites* Muller 1968
Distaverrusporites margaritatus Muller 1968 (Fig. 2D)
Botanical affinity: unknown
Ecology: unknown

Genus *Echinatisporis* Krutzsch 1959
Echinatisporis infantus D'Apolito 2016 (Fig. 2E)
Botanical affinity: families Thelypteraceae/Athyriaceae/Marathiaceae
Ecology: unknown

Echinatisporis muelleri Krutzsch 1967 (Fig. 2F)
Botanical affinity: families Thelypteraceae/Athyriaceae/Marathiaceae (D'Apolito 2016)
Ecology: unknown

Table 1. Miospores documented in this study and in the previous works for Solimões Formation. For the location of the wells, see Figure 1.

Miospores	Records in Solimões Formation*								
	1-AS-04-AM	1-AS-32-AM	1-AS-19-AM 1-AS-27-AM	1-AS-51-AM 1-AS-52-AM	1-AS-31-AM 1-AS-34-AM	1-AS-33-AM	1-AS-105-AM	Coari e Alto Solimões	No/EF
Cingulatisporites laevigatus			X						1-AS-46-AM 655/W10
Crassoretitriletes vanraadshoovenii	X	X	X	X	X	X	X	X	1-AS-37-AM 379/ W60
Deltoidospora adriennis	X	X	X	X			X	X	1-AS-46-AM 588/W51-2
Distaverrusporites margaritatus			X	X			X		1-AS-46-AM 588/ X64-4
Echinatisporis infantus							X		1-AS-46-AM 698/O56-4
Echinatisporis muelleri			X		X		X	X	1-AS-46-AM 579/ Z60-4
Kuylisporites waterbolkii			X				X	X	1-AS-46-AM 670/Y64-2
Laevigatosporites tibuiensis			X				X		1-AS-37-AM 577/Q68
Magnastriatites grandiosus	X	X	X	X		X	X	X	1-AS-37-AM 385-2/O57-4
Nijssenosporites fossulatus						X	X		1-AS-37-AM 373/W63-4
Perinomonoletes sp.								X	1-AS-46-AM 693/X53-4
Polypodiaceoisporites amazonensis			X						1-AS-37-AM 398/Y35-1
Polypodiaceoisporites potoniei	X			X				X	1-AS-46-AM 643/Y60-3
Polypodiisporites aff. *specious*			X				X		1-AS-46-AM 695/R66-1
Psilatriletes lobatus			X				X		1-AS-37-AM 573/Z29-03
Retitriletes sommeri									1-AS-46-AM 755/S57-1
Verrucatosporites usmensis		X		X				X	1-AS-37-AM 573/N53-2-4
Verrucatotriletes bullatus	X		X					X	1-AS-46-AM 696/K74
Verrucatotriletes etayoi			X	X					1-AS-46-AM 746/X69-4
Cyclusphaera scabrata							X		1-AS-37-AM 478/W62-4
Podocarpidites sp.	X	X	X	X		X		X	1-AS-46-AM 703/U52-3
Arecipites perfectus			X	X			X		1-AS-37-AM 535/R75-3
Bombacacidites baculatus	X		X	X	X	X	X	X	1-AS-37-AM 513/V59-1
Bombacacidites fossulatus		X	X	X	X				1-AS-37-AM 379/Z62-1
Bombacacidites lorenteae	X						X		1-AS-46-AM 588/S58-2
Bombacacidites nacimientoensis	X	X	X	X			X	X	1-AS-37-AM 535/Y-62

Table 1. Cont.

Miospores	Records in Solimões Formation*								
	1-AS-04-AM	1-AS-32-AM	1-AS-19-AM 1-AS-27-AM	1-AS-51-AM 1-AS-52-AM	1-AS-31-AM 1-AS-34-AM	1-AS-33-AM	1-AS-105-AM	Coari e Alto Solimões	No/EF
Cichoreacidites longispinosus			X		X	X	X	X	1-AS-37-AM 378/T50
Corsinipollenites oculusnoctis	X	X	X	X	X	X	X		1-AS-37-AM 379/Y71
Echiperiporites akanthos	X		X			X	X	X	1-AS-46-AM 589/Z33-4
Echiperiporites estelae	X	X	X	X		X	X	X	1-AS-37-AM 573/L56
Echiperiporites lophatus			X			X	X		1-AS-37-AM 557/W24-3-4
Echiperiporites scrabrannulatus									1-AS-37-AM 385/P60
Echitricolporites spinosus	X	X	X	X	X	X	X	X	1-AS-46-AM 535/R69-1
Echitriporites trianguliformis			X						1-AS-46-AM 695/R51-4
Fenestristes garciae				X					1-AS-37-AM 535/Q61-3
Fenestrites spinosus				X	X	X	X	X	1-AS-37-AM 513/N42-4
Grimsdalea magnaclavata	X	X	X	X	X	X	X	X	1-AS-46-AM 746/W62-4
Inaperturopollenites solimoensis			X			X			1-AS-37-AM 573/J57-1
Ladakhipollenites? caribbiensis			X	X	X	X	X	X	1-AS-46-AM 740/K52
Loranthacites digitatus			X						1-AS-37-AM 483/Y43-4
Malvacipollis spinulosa				X			X		1-AS-37-AM 561/M61-3-4
Malvacipolloides maristellae	X	X	X	X	X		X		1-AS-37-AM 573/U63-2
Margocolporites "hornii"									1-AS-37-AM 411/W61-2
Margocolporites vanwijhei	X		X		X	X	X		1-AS-37-AM 533/S63-3
Mauritiidites franciscoi var. franciscoi	X	X	X	X		X	X	X	1-AS-37-AM 411/S63-1
Perisyncolporites pokornyi	X	X	X	X		X	X	X	1-AS-46-AM 588/W54
Polyadopollenites marileae						X			1-AS-46-AM 602/Y24
Proteacidites triangulatus			X	X		X	X	X	1-AS-37-AM 528/Z55-2
Proxapertites tertiaria	X		X	X			X	X	1-AS-37-AM 577/L65-4
Psilamonocolpites amazonicus	X						X		1-AS-37-AM 579/Y55-4
Psilaperiporites multiporatus			X				X		1-AS-37-AM 378/U65-1
Psilastephanoporites herngreenii	X		X			X	X		1-AS-37-AM 557/Y27

Table 1. Cont.

Miospores	Records in Solimões Formation*								
	1-AS-04-AM	1-AS-32-AM	1-AS-19-AM 1-AS-27-AM	1-AS-51-AM 1-AS-52-AM	1-AS-31-AM 1-AS-34-AM	1-AS-33-AM	1-AS-105-AM	Coari e Alto Solimões	No/EF
Psilastephanoporites tesseroporus				X		X		X	1-AS-46-AM 740/H65-1
Psilatricolporites silvaticus	X						X		1-AS-46-AM 755/Y52-3
Retistephanoporites crassinanulatus	X		X			X	X		1-AS-37-AM 535/T61
Retitrescolpites irregularis	X		X	X		X	X	X	1-AS-46-AM 752/Y68-1
Retitrescolpites traversei			X				X		1-AS-37-AM 422/Y41-4
Retitriporites dubiosus	X			X				X	1-AS-37-AM 533/J61-1
Rhoipites guianensis	X		X	X		X	X	X	1-AS-46-AM 755/Y51-2
Rhoipites toigoi							X		1-AS-37-AM 573/M64-1

* Based on the studies of Hoorn 1993 (1-AS-04-AM); Silva 2004 (1-AS-32-AM); Silva-Caminha *et al*. 2010 (1-AS-19-AM 1-AS-27-AM); Leandro 2012 (1-AS-51-AM 1-AS-52-AM); Kachniasz & Silva-Caminha 2016 (1-AS-31-AM; 1-AS-34-AM); Leite et al. 2016 (1-AS-33-AM); D´Apolito 2016 (1-AS-105-AM) and Silveira & Souza 2015; 2016 (Coari e Alto Solimões outcrops).

Genus *Kuylisporites* Potonié 1956
Kuylisporites waterbolkii Potonié 1956 (Fig. 2G)
Botanical affinity: family Cyatheaceae, *Cyathea horrida*
Ecology: mountain areas (Jaramillo *et al*. 2010)
Genus *Laevigatoporites* Ibrahim
Laevigatosporites tibuiensis (Van der Hammen 1956a) Jaramillo & Dilcher 2001 (Fig. 2H)
Botanical affinity: unknown
Ecology: unknown

Genus *Magnastriatites* Germeraad *et al*. 1968, emend. Dettmann & Clifford 1992
Magnastriatites grandiosus (Kedves & Sole de Porta 1963) Dueñas 1980 (Fig. 2I)
Botanical affinity: Family Pteridaceae, genus *Ceratopteris*
Ecology: aquatic genus (Tryon & Lugardon 1991), rivers and shallow lakes (Jaramillo *et al*. 2010)

Genus *Nijssenosporites*
Nijssenosporites fossulatus Lorente 1986(Fig. 3A)
Botanical affinity: Family Adianthaceae, Genus *Pityrogramma*
Ecology: pantropical genus (Tryon & Lugardon 1991), plain.

Genus *Perinomonoletes* Krutzsch, 1967
Perinomonoletes sp. (Fig. 3B)
Botanical affinity: families Aspleniaceae/ Thelypteraceae (Jaramillo *et al*. 2010)
Ecology: unknown

Genus *Polypodiaceoisporites* Potonié 1951 ex Potonié 1956
Polypodiaceoisporites amazonensis Silva-Caminha *et al*. 2010 (Fig. 3C)
Botanical affinity: family Pteridaceae
Ecology: unknown

Polyapodiaceoisporites potoniei Kedves 1961 (Fig. 3D)
Botanical affinity: family Pteridaceae, *Pteris*
Ecology: open vegetation, riverine banks (Tryon & Lugardon 1991).

Genus *Polypodiisporites* Potonié 1956 emend Khan and Martin 1971
Polypodiisporites aff. *specious* Sah 1967 1961 (Fig. 3E)
Botanical affinity: family Polypodiaceae
Ecology: plain (D'Apolito 2016)

Genus *Psilatriletes* van der Hammen 1954 ex Potonié 1956
Psilatriletes lobatus Hoorn 1994 (Fig. 3F)
Botanical affinity: unknown
Ecology: unknown

Genus *Retitriletes* Pierce 1961
Retitriletes sommeri Regali *et al*. 1974 (Fig. 3G)
Botanical affinity: family Lycopodiaceae?
Ecology: unknown

Genus *Verrucatosporites* Thomson & Pflug 1953
Verrucatosporites usmensis (Van der Hammen 1956)

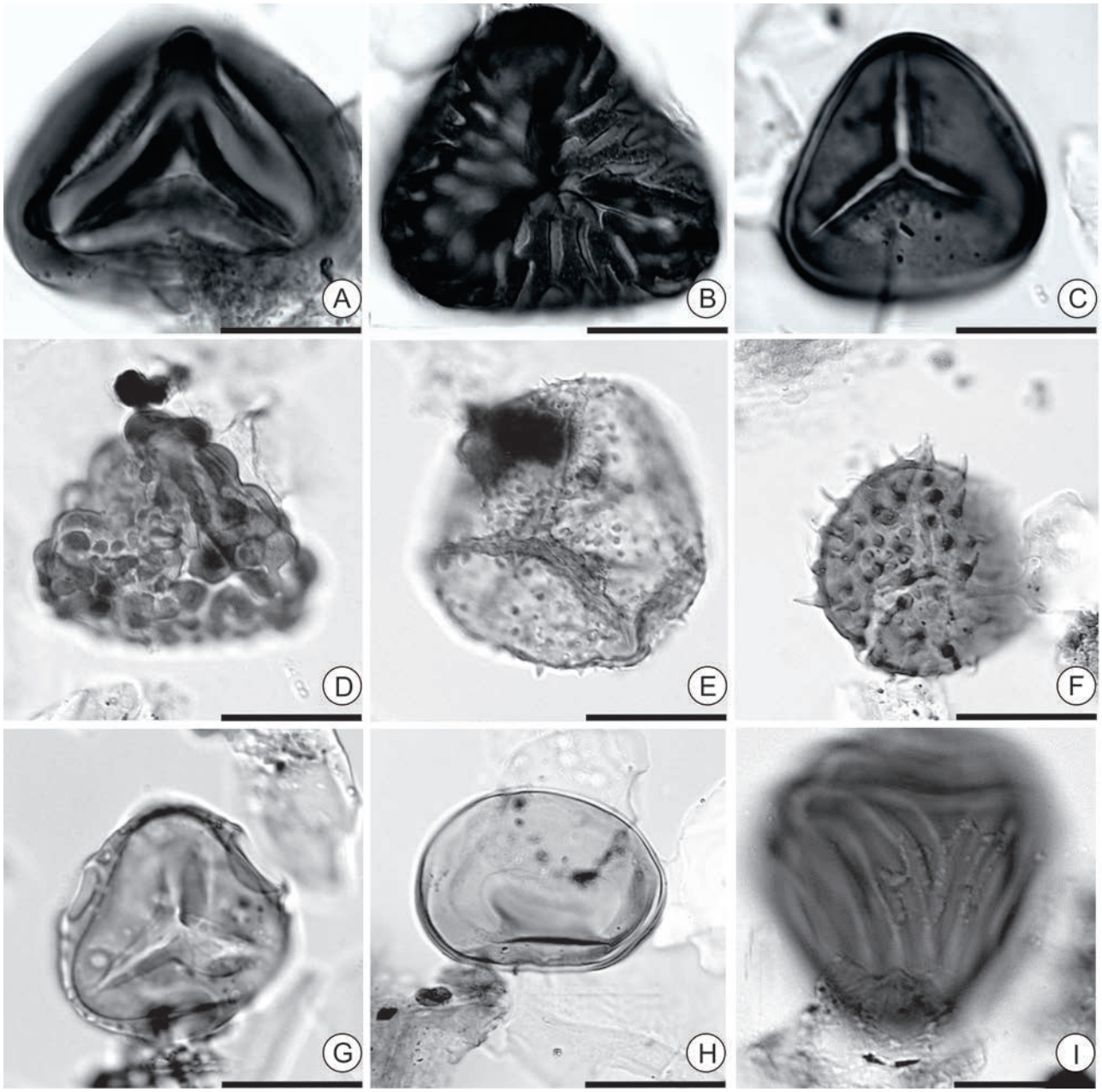

Figure 2. Fern spores recorded in the studied sections. **A**. *Cingulatisporites laevigatus*. **B**. *Crassoretitriletes vanraadshoovenii*. **C**. *Deltoidospora adriennis*. **D**. *Distaverrusporites margaritatus*. **E**. *Echinatisporis infantus*. **F**. *Echinatisporis muelleri*. **G**. *Kuylisporites waterbolkii*. **H**. *Laevigatosporites tibuiensis*. I. *Magnastriatites grandiosus*. Scale bar= 20 µm.

Germeraad *et al*. 1968 (Fig. 3H)
Botanical affinity: family Polypodiaceae, *Stenochlaena palustris*
Ecology: highland forest and e plain (Jaramillo *et al*. 2010)
Genus *Verrucatotriletes* Van Hoeken-Klinkenberg 1964
Verrucatotriletes bullatus Van Hoeken-Klinkenberg 1964 (Fig. 3I)
Botanical affinity: family Cyatheaceae, *Alsophyla*
Ecology: pantropical genus (Tryon & Lugardon1991), highland (Jaramillo *et al* 2010).
Verrucatotriletes etayoi Dueñas, 1980 (Fig. 3J)
Botanical affinity: unknown
Ecology: unknown
Anteturma POLLENITES Potonié 1893
Gimnosperms pollen grains
Genus *Cyclusphaera* Elsik 1966
Cyclusphaera scabrata Jaramillo & Dilcher, 2001 (Fig. 4A)
Botanical affinity: Family Araucariaceae
Ecology: mountain area

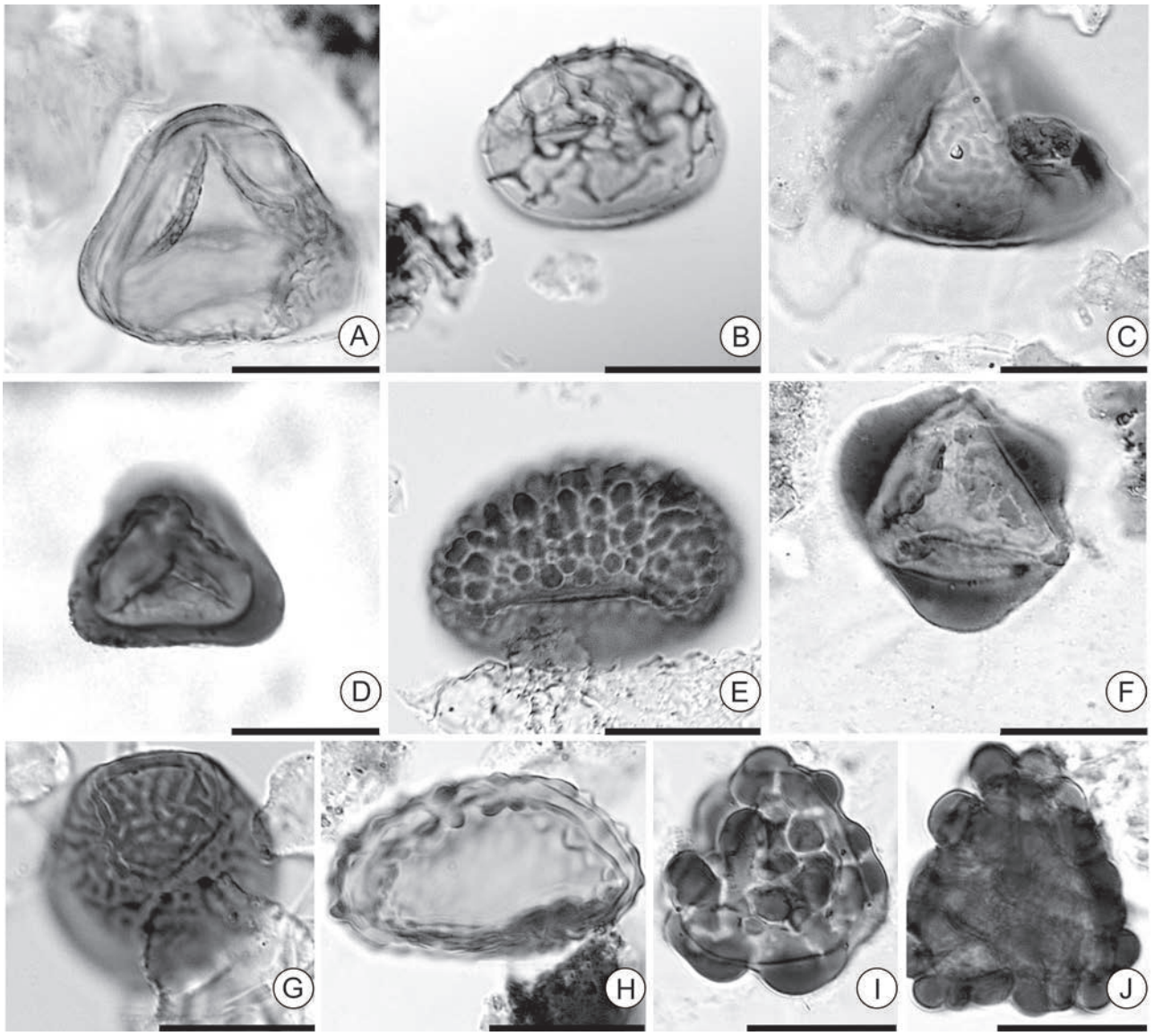

Figure 3. Fern spores recorded in the studied sections. **A**. *Nijssenosporites fossulatus*. **B**. *Perinomonoletes*. **C**. *Polypodiaceoisporites amazonensis*. **D**. *Polypodiaceoisporites potoniei*. **E**. *Polypodiisporites* aff. *specious*. **F**. *Psilatriletes lobatus*. **G**. *Retitriletes sommeri*. **H**. *Verrucatoporites usmensis*. **I**. *Verrucatotriletes bullatus*. **J**. *Verrucatotriletes etayoi*. Scale bar= 20μm.

Genus *Podocarpidites* Cookson 1947
Podocarpidites sp. Cookson 1947 ex Couper 1953 (Fig. 4B)
Botanical affinity: family Podocarpaceae, *Podocarpus*
Ecology: mountain and lownland forest (Jaramillo *et al.* 2010)

Angiosperms pollen grains
Genus *Arecipites* Wodehouse 1933, emend. Nichols *et al.* 1973
Arecipites perfectus Silva-Caminha *et al* 2010 (Fig. 4C)
Botanical affinity: family Arecaceae
Ecology: unknown

Genus Bombacacidites Couper 1960

Bombacacidites baculatus Muller *et al*. 1987 (Fig. 4D)
Botanical affinity: family Bombacaceae, *Pachira aquatica*
Ecology: tropical forest, swamps and along rivers

Bombacacidites fossulatus Silva-Caminha *et al*. 2010 (Fig. 4E)
Botanical affinity: family Bombacaeae
Ecology: unknown

Bombacacidites lorenteae (Hoorn 1993) D'Apolito 2016 (Fig. 4F)
Botanical affinity: family Bombacaeae, *Bombax*
Ecology: along creeks and rivers

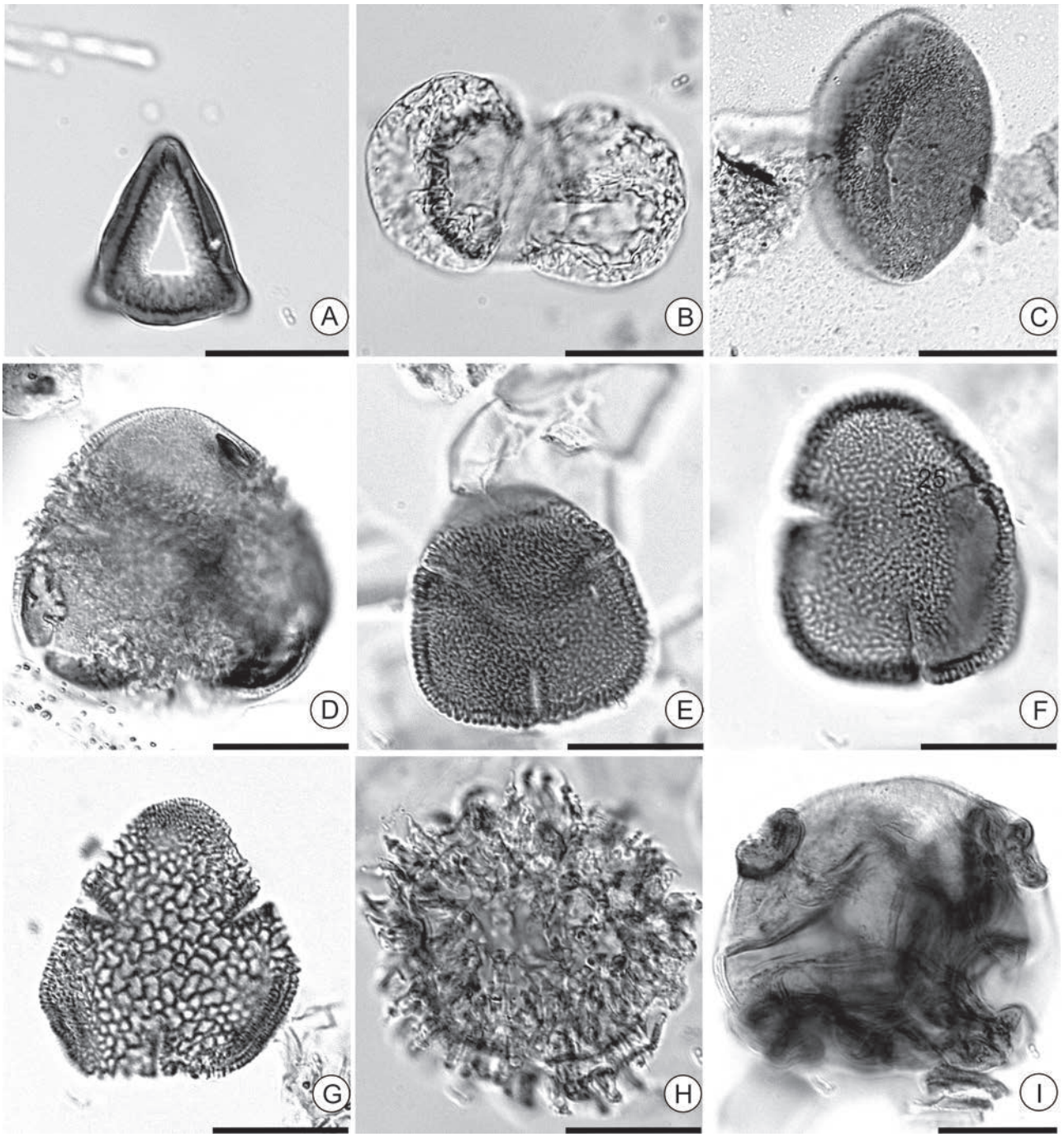

Figure 4. Pollen grains recorded in the studied sections. **A**. *Cyclusphaera scabrata*. **B**. *Podocarpidites*. **C**. *Arecipites perfectus*. **D**. *Bombacacidites baculatus*. **E**. *Bombacacidites fossulatus*. **F**. *Bombacacidites lorenteae*. **G**. *Bombacacidites nacimientoensis*. **H**. *Cichoreacidites longispinosus*. **I**. *Corsinipollenites oculusnoctis* (tetrad). Scale bar= 20μm.

Bombacacidites nacimientoensis (Anderson1960) Elsik 1968 (Fig. 4G)
Botanical affinity: Family Bombacaeae, genus *Bombax*
Ecology: plains, along watercourses (Jaramillo *et al*. 2010)
Genus *Cichoreacidites* Sah 1967
Cichoreacidites longispinosus (Lorente 1986) Silva-Caminha 2010 (Fig. 4H)
Botanical affinity: family Asteraceae
Ecology: swamps, open vegetation and savannahs

Genus *Corsinipollenites* Nakoman 1965
Corsinipollenites oculusnoctis (tétrade) (Thiergart 1940); Nakoman (Fig. 4I)
Botanical affinity: family Onagraceae, *Ludwigia*
Ecology: marshes (Jaramillo *et al*. 2010)

Genus *Echiperiporites* Van der Hammem & Wymstra 1964
Echiperiporites akanthos Van der Hammem & Wymstra 1964 (Fig. 5A)
Botanical affinity: family Alismataceae, *Sagittaria*/*Echinodorus*
Ecology: swamps and lakes (D'Apolito 2016)

Echiperiporites estelae Germeraad *et al*. 1968 (Fig. 5B)
Botanical affinity: families Malvaceae/Convolvulaceae
Ecology: coastal vegetation

Echiperiporites lophatus Silva-Caminha *et al*. 2010 (Fig. 5C)
Botanical affinity: family Convolvulaceae?
Ecology: herbaceous liana? (D'Apolito 2016)

Echiperiporites scabrannulatus Jaramillo *et al*. 2010 (Fig. 5D-E)
Botanical affinity: unknown
Ecology: unknown

Genus *Echitricolporites* Van der Hammen 1956 ex Germeraad *et al*. 1968
Echitricolporites spinosus Van der Hammen 1956 ex Germeraad *et al*. 1968 (Fig. 5F)
Botanical affinity: family Asteraceae
Ecology: open vegetation

Genus *Echitriporites* Van der Hammen 1956
Echitriporites trianguliformis Van Hoeken Klinkenberg 1964 (Fig. 5G)
Botanical affinity: family Proteaceae (Jaramillo & Rueda 2013)
Ecology: unknown

Genus *Fenestrites* Van der Hammen, 1956
Fenestrites garciae Leite 2006 (Fig. 5H)
Botanical affinity: family Amaranthaceae, *Gomphrena*
Ecology: unknown

Fenestrites spinosus Van der Hammen, 1956 (Fig. 5I)
Botanical affinity: family Asteraceae (Germeraad *et al*. 1968)
Ecology: unknown

Genus *Grimsdalea* Germeraad *et al*. 1968
Grimsdalea magnaclavata Germeraad *et al*. 1968 (Fig. 5J)
Botanical affinity: family Arecaceae?
Ecology: unknown
Genus *Inaperturopollenites* Nilsson 1958
Inaperturopollenites solimoensis Leite 2006 (Fig. 5K)
Botanical affinity: family Rubiaceae, *Psychotria*?
Ecology: unknown

Genus *Ladakhipollenites* Mathur & Jain 1980
Ladakhipollenites? caribbiensis (Muller *et al*. 1987) Silva-Caminha *et al*. 2010 (Fig. 5L)
Botanical affinity: family Euphorbiaceae, *Sapium*
Ecology: terra firme forest and varzea forest

Genus *Loranthacites* Mtchedlishvili in Samoilovitch & Mtchedlishvili 1961
Loranthacites digitatus Silva-Caminha *et al*. 2010 (Fig. 6A)
Botanical affinity: family Loranthaceae (Jaramillo & Rueda 2013)
Ecology: unknown

Genus *Malvacipollis* Harris 1965
Malvacipollis spinulosa Frederiksen, 1983 (Fig. 6B-C)
Botanical affinity: family Euphorbiaceae (Leite 2006)
Ecology: unknown

Genus *Malvacipolloides* Anzótegui & Garalla 1986
Malvacipolloides maristellae (Muller *et al*. 1987) Silva-Caminha *et al* 2010 (Fig. 6D)
Botanical affinity: family Bombacaceae
Ecology: terra firme forest

Genus *Margocolporites* Ramanujam 1966 ex Srivastava 1969, emend. Pocknall & Mildenhall 1984
Margocolporites "hornii" (Fig. 6E)
Botanical affinity: family Apocynaceae?
Ecology: unknown

Margocolporites vanwijhei Germeraad *et al*. 1968 (Fig. 6F)
Botanical affinity: family Caesalpiniaceae, *Caesalpinea*
Ecology: coastal vegetation

Genus *Mauritiidites* van Hoeken-Klinkenberg 1964
Mauritiidites franciscoi var. franciscoi Van der Hammen, 1956) Van Hoeken Klinkenberg 1964 (Fig. 6G)
Botanical affinity: family Arecaceae, *Mauritia*
Ecology: plain and swamps

Genus *Perisyncolporites* Germeraad *et al*. 1968
Perisyncolporites pokornyi Germeraad *et al*. 1968 (Fig. 6H)
Botanical affinity: family Malpighiaceae
Ecology: plain and terra firme forest

Genus *Polyadopollenites* Pflug and Thomson 1953
Polyadopollenites marileae Leite 2006 (Fig. 6I)
Botanical affinity: family Mimosaceae
Ecology: unknown
Genus *Proteacidites* Cookson emend. Couper 1953
Proteacidites triangulatus Lorente 1986 (Fig. 6J)

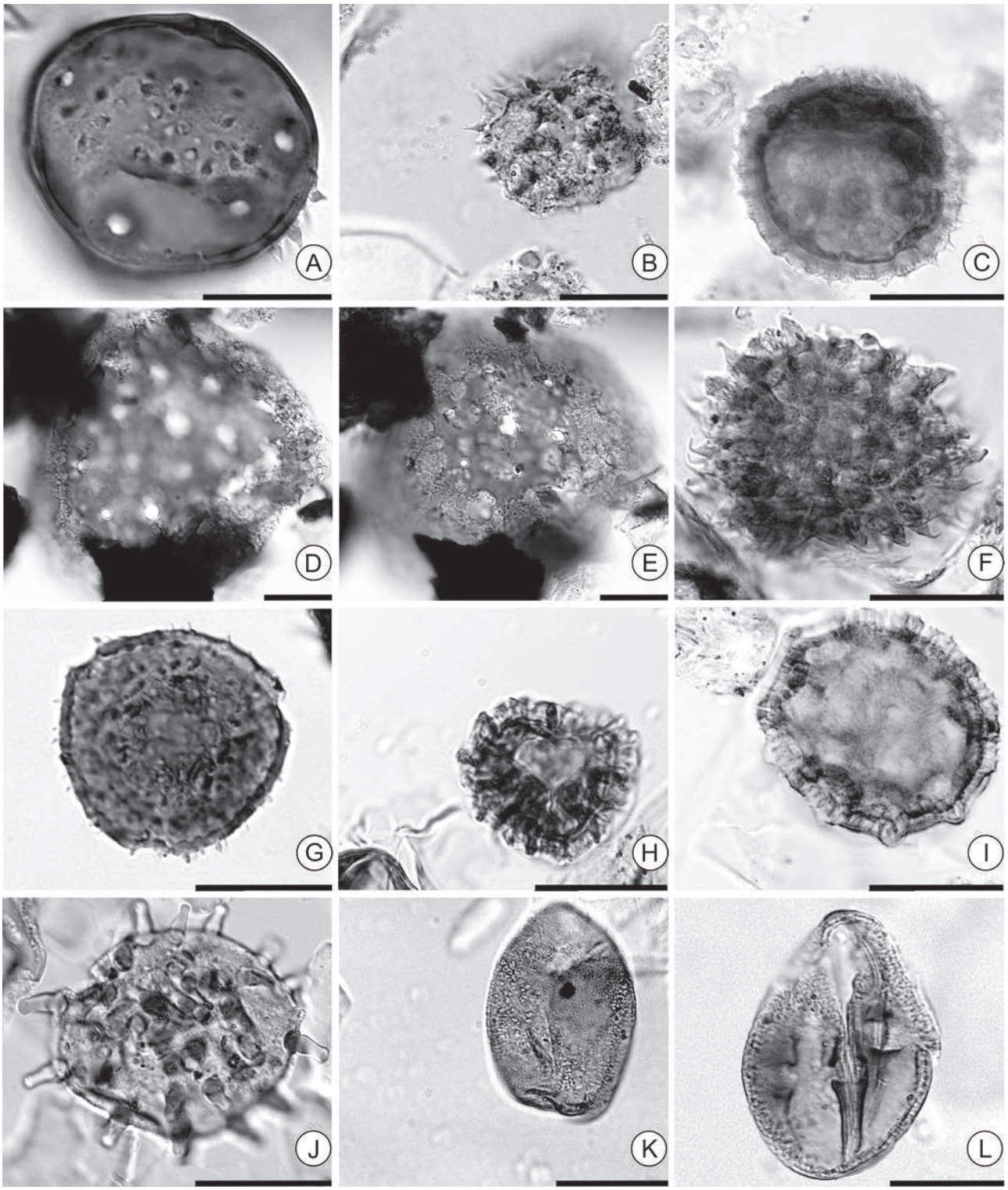

Figure 5. Pollen grains recorded in the studied sections. **A**. *Echiperiporites akanthos*. **B**. *Echiperiporites estelae*. **C**. *Echiperiporites lophatus*. **D-E**. *Echiperiporites scrabrannulatus*. **F**. *Echitricolporites spinosus*. **G**. *Echitriporites trianguliformis*. **H**. *Fenestristes garciae*. **I**. *Fenestrites spinosus*. **J**. *Grimsdalea magnaclavata*. **K**. *Inaperturopollenites solimoensis*. **L**. *Ladakhipollenites? caribbiensis*. Scale bar= 20μm.

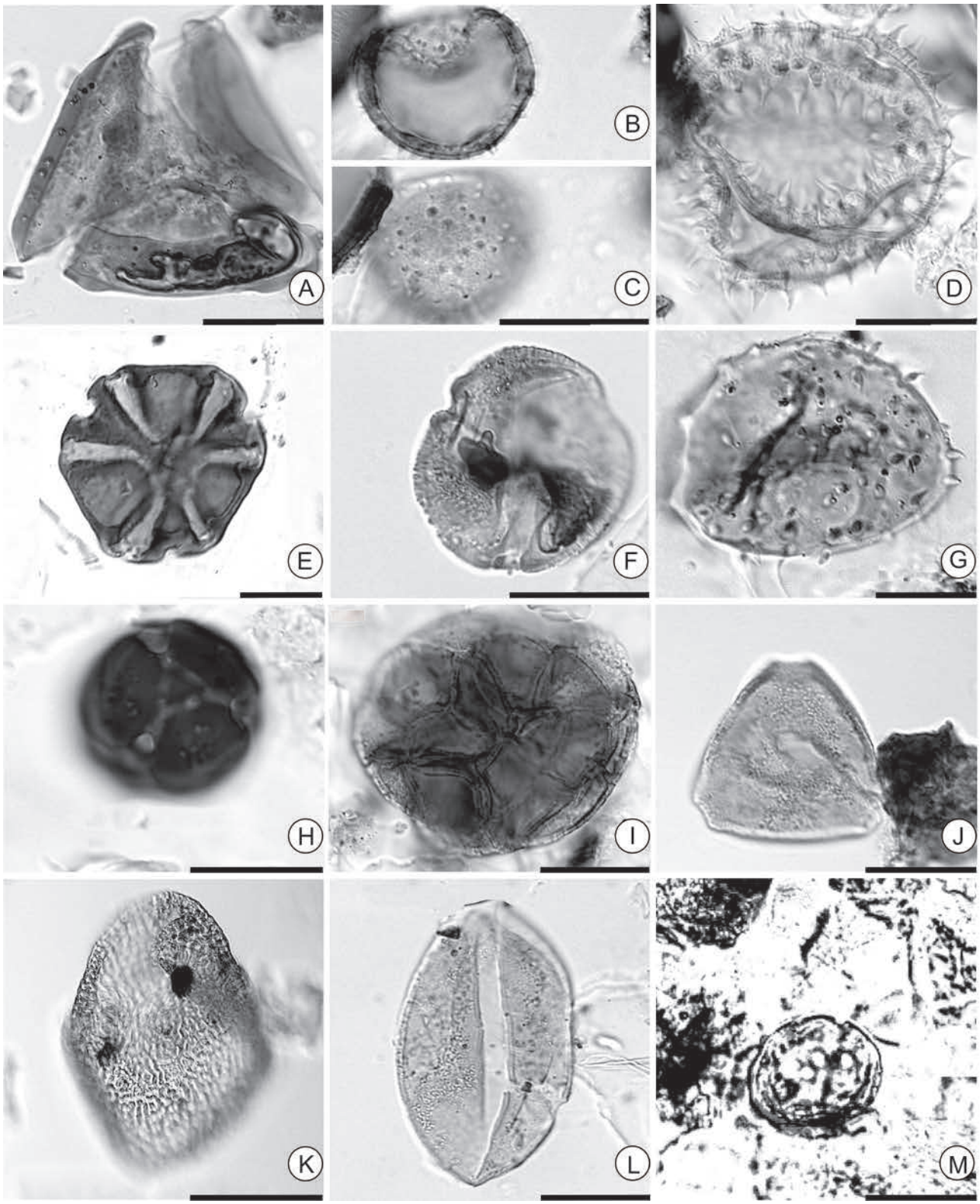

Figure 6. Pollen grains recorded in the studied sections. **A**. *Loranthacites digitatus*. **B-C**. *Malvacipollis spinulosa*. **D**. *Malvacipolloides maristellae*. **E**. *Margocolporites "hornii"*. **F**. *Margocolporites vanwijhei*. **G**. *Mauritiidites franciscoi var. franciscoi*. **H**. *Perisyncolporites pokornyi*. **I**. *Polyadopollenites marileae*. **J**. *Proteacidites triangulatus*. **K**. *Proxapertites tertiaria*. **L**. *Psilamonocolpites amazonicus*. **M**. *Psilaperiporites multiporatus*. Scale bar= 20μm.

Botanical affinity: families Sapindaceae/Proteaeceae
Ecology: tropical forest and montane forest

Genus *Proxapertites* Van der Hammen 1956
Proxapertites tertiaria Van der Hammen & García de Mutis 1966 (Fig. 6K)
Botanical affinity: family Annonaceae, *Crematosperma*
Ecology: lowland forest (Jaramillo *et al*. 2010).

Genus *Psilamonocolpites* Van der Hammen & C. Garcia de Mutis 1966
Psilamonocolpites amazonicus Hoorn 1993 (Fig. 6L)
Botanical affinity: family Arecaceae, *Euterpe*
Ecology: varzea forest, plain and swamps

Genus *Psilaperiporites* Regali *et al*. 1974
Psilaperiporites multiporatus Hoorn 1994 (Fig. 6M)
Botanical affinity: unknown
Ecology: unknown

Genus *Psilastephanoporites* Van der Hammen 1956
Psilastephanoporites herngreenii Hoorn 1993 (Fig. 7A)
Botanical affinity: family Apocynaceae
Ecology: lowland forest

Psilastephanoporites tesseroporus Regali *et al*. 1974 (Fig. 7B)
Botanical affinity: family Apocynaceae, *Prestonia*? (Leite 2006)
Ecology: unknown

Genus *Psilatricolporites* Pierce 1961
Psilatricolporites silvaticus Hoorn 1993 (Fig. 7C)
Botanical affinity: family Burseraceae/Sapotaceae
Ecology: lowland forest

Genus *Retistephanoporites* González-Guzmán 1967
Retistephanoporites crassinanulatus Lorente 1986 (Fig. 7D)
Botanical affinity: family Malvaceae, *Quararibea*
Ecology: lowland forest

Genus *Retitrescolpites* Sah 1967
Retitrescolpites irregulares (Van der Hammen & Wymstra 1964) Jaramillo & Dilcher 2001 (Fig. 7E)
Botanical affinity: family Euphorbiaceae, *Amanoa*
Ecology: lowland forest, along watercourses (Jaramillo & Rueda 2013)

Retitrescolpites traversei Silva-Caminha *et al* 2010 (Fig. 7F)
Botanical affinity: family Acanthaceae, *Teliostachya*
Ecology: lowland forest
Genus *Retitriporites* (Van der Hammen, 1956) Gonzalez-Guzmán, 1967

Retitriporites dubiosus Gonzalez-Guzmán, 1967 (Fig. 7G)
Botanical affinity: family Rubiaceae, *Psychotria/ Alibertia* (Leite 2006)
Ecology: unknown

Genus *Rhoipites* Wodehouse 1933
Rhoipites guianensis (Van der Hammen & Wymstra 1964) Jaramillo & Dilcher 2001(Fig. 7H-I)
Botanical affinity: family Malvaceae, *Firmiana/ Hildegardia/Glossostemon/ Trichospermum* (Germeraad *et al* 1968)
Ecology: unknown

Rhoipites toigoi D'Apolito 2016 (Fig. 7J)
Botanical affinity: family Rubiaceae?
Ecology: unknown

Discussion

This catalogue lists 60 taxa miospores present in the Miocene of the Brazilian Amazon, with photomicrographs and brief description of botanical affinity, ecology and distribution. This serves to support for paleoenvironmental and biostratigraphic studies for the region.

The assemblage of miospores is well preserved and well diversified. The spores are arranged in 16 genera and 19 species, included in ten families, with Pteridaceae the most representative family followed by Polypodiaceae and Cyatheaceae.

In Solimões Formation, the fern spores *Crassoretitriletes vanhadshoovenii Magnastriatites grandiosus* and *Deltoidospora adriennis* were recorded in almost all those previous studies. These species have habitats related to the aquatic environment as mangroves, swamps, rivers and lakes.

The spermatophytes group (pollen grains) encompasses two families of gymnosperms: Aracauariaceae (*Cyclusphaera scabrata*) and Podocarpaceaeae (*Podocarpidites*). It is the second record of the family Araucariaceae of the Solimões Formation. And the angiosperms are represented by 20 families, containing 31 genera and 41 species. The genus *Bombacacidites* and *Echiperiporites* exhibit the largest number of species.

The angiosperms species with numerous records in Solimões Formation were *Bombacacidites baculatus, Corsinipollenites oculusnoctis, Echiperiporites estelae, Echitricolporites spinosus, Grimsdalea magnaclavata, Mauritiidites franciscoi* and *Perisyncolporites pokornyi*, which indicate water-related environments such as plains, mangroves, marshes and coast vegetation, except *E. spinosus*, typical of open vegetation.

Two new miospores were recorded for Solimões Formation: the fern spore *Retitriletes sommeri* and the pollen grain *Echiperiporites scabrannulatus*.

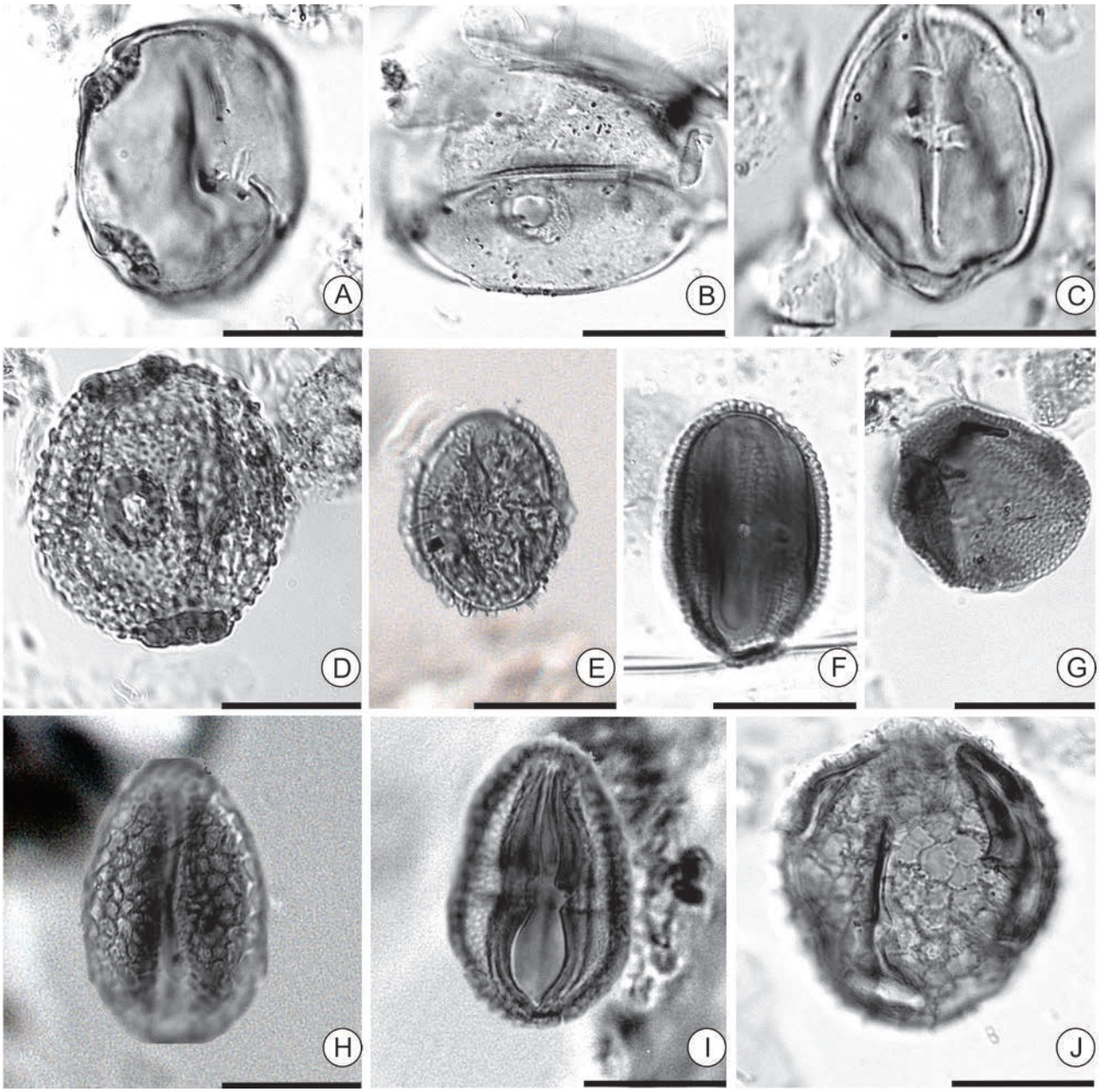

Figure 7. Pollen grains recorded in the studied sections. **A**. *Psilastephanoporites herngreenii*. **B**. *Psilastephanoporites tesseroporus*. **C**. *Psilatricolporites silvaticus*. **D**. *Retistephanoporites crassinanulatus*. **E**. *Retitrescolpites irregularis*. **F**. *Retitrescolpites traversei*. **G**. *Retitriporites dubiosus*. **H-I**. *Rhoipites guianensis*. **J**. *Rhoipites toigoi*. Scale bar= 20 µm.

Acknowledgements

We express our thanks to the Geological Survey of Brazil (CPRM) for giving N.P. Sá the opportunity to study the material and the Brazilian National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq) for the scholarship and the financial support to N.P. Sá (Grant no. 140408/2013-4). We thank three anonymous reviewers for helpful suggestions.

References

Barata CF, Caputo MV. 2007. Geologia do petróleo da Bacia do Solimões - O Estado da Arte. Campinas, PDPETRO.

Boonstra M, Ramos MIF, Lammertsma EI, Antonie PO, Hoorn C. 2015. Marine connections of Amazonia: Evidence from foraminífera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). Palaeogeography, Palaeoclimatology, Palaeoecology 417: 176-194.

Burnham RJ, Graham A. 1999. The history of Neotropical vegetation: new developments and status. Annais Missouri Botanical Garden 86: 546-589.

Cozzuol M. 2006. The Acre vertebrate fauna: diversity, geography and time. Journal of South American Earth Sciences 21: 185-203.
Cronquist A. 1988. The evolution and classification of flowering plants. 2nd. edn. New York, New York Botanical Garden.
D'Apolito C. 2016. Landscape evolution in Western Amazonia: palynostratigraphy, palaeoenvironments and diversity of the Miocene Solimões formation, Brazil. PhD Thesis, University of Birmingham, Birmingham.
Eiras JF, Becker CR, Souza EM, Gonzaga FG, Silva JGF, Daniel LMF. 1994. Bacia do Solimões. Boletim de Geociências da Petrobrás 8: 17-45.
Erdtman G. 1969. Handbook of palynology. Copenhagen, Scandinavian University Books.
Faegri K, Iversen J. 1966. Textbook of pollen analysis. Copenhagen, Scandinavian University Books.
Frailey CD. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Rio Acre region, Western Amazonia. Contribution in Science, Natural History Museum of Los Angeles County 374: 1-46.
Gentry AH. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the andean orogeny? Annals of the Missouri Botanical Garden 69: 557-593.
Germeraad JH, Hopping CA, Muller J. 1968. Palynology of Tertiary sediments from tropical areas. Review of Paleobotany and Palynology 6: 189-348.
Gross M, Piller WE, Ramos MI, Paz JDS. 2011. Late Miocene sedimentary environments in south-western Amazonia (Solimões Formation; Brasil). Journal of South American Earth Sciences 32: 169-181.
Gross M, Ramos MI, Caporaletti M, Pilner WE. 2013. Ostracods (Crustacea) and their palaeoenviromental implication for the Solimões Formation (Late Miocene; Western Amazonia/Brazil). Journal of South American Earth Sciences 42: 216-241.
Haffer J. 1969. Speciation in amazonian forest birds. Science 165: 131-137.
Hooghiemstra H, Hammen T. 1998. Neogene and Quaternary development of the Neotropical rain forest: the forest refugia hypothesis, and a literature overview. Earth — Science Review 44: 147-183.
Hoorn C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazônia: results of Palynostratigraphic study. Palaegeography, Palaeoclimatology, Palaeocology 105: 267-309.
Hoorn C. 1994a. Fluvial palaeoenvironments in intracratonic Amazonas Basin (Early Miocene-Early Middle Miocene, Colombia). Palaegeography, Palaeoclimatology, Palaeocology 109: 1-54.
Hoorn C. 1994b. An environmental reconstruction of the palaeo-Amazon River sytem (Middle to Late Miocene, NW Amazonia). Palaeogeography, Palaeoclimatology, Paleoecology 112: 187-238.
Hoorn C. 1994c. Miocene palynostratigraphy and paleoenvironments of Northwestern Amazonia. PhD Thesis, University of Amsterdan, Amsterdan.
Hoorn C, Bernardes-de-Oliveira MEC, Dino R, *et al*. 2010c. Neogene climate evolution in Amazonia and the Brazilian Northeast. In: Carvalho IS, Garcia MJ, Lana CC, Strohschoen Jr O. (eds.) Paleontologia: Cenários de Vida—Paleoclimas. Rio de Janeiro, Interciência. p. 277-310.
Hoorn C, Bogotá-A GR, Romero-Baez M, *et al*. 2017. The Amazon at sea: Onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin. Global and Planetary Change 153: 51-65.
Hoorn C, Guerreiro J, Sarmiento G. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene Northern South America. Geology 23: 237-240.
Hoorn C, Wesselingh FP, Hovikoski J, Guerrero J. 2010b. The Amazonian mega-wetland (Miocene; Brazil, Colombia, Peru, Bolivia). In: Hoorn C, Wesselingh FP. (eds.) Amazonia, Landscape and Species Evolution: Look into the Past. Oxford, Wiley-Blackwell. p. 123-143.
Hoorn C, Wesselingh FP, Steege H, *et al*. 2010a. Amazonia Through Time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330: 927-931.
Jaramillo C, Hoorn C, Silva SAF, *et al*. 2010. The origin of the modern Amazon rainforest: implications of the palynological and paleobotanical record. In: Hoorn C, Wesselingh FP. (eds.) Amazonia: landscape and species evolution – a look into the past. Oxford, Blackwell Publishing. p. 317-334
Jaramillo C, Rueda MJ. 2013. A morphological electronic database of Cretaceous Tertiary and extant pollen and spores from Northern South America. v. 2012/2013. http://biogeodb.stri.si.edu/jaramillo/palynomorph/. 25 Apr. 2017.
Jaramillo C, Rueda M, Mora G. 2006. Cenozoic plant diversity in the Neotropics. Science 311: 1893-1896.
Jaramillo C, Rueda M, Torres V. 2011. A palynological zonation for the Cenozoic of the Llanos and Llanos Foothills of Colombia. Palynology 35: 46-84.
Kachniasz KE, Silva-Caminha SAF. 2016. Palinoestratigrafia da Formação Solimões: comparação entre bioestratigrafia tradicional e o método de associações unitárias. Revista Brasileira de Paleontologia 19: 481-490.
Latrubesse E, Bocquentin J, Santos JCR, Ramonell CG. 1997. Paleoenvironmental model for the late Cenozoic southwestern Amazonia paleontology and geology. Acta Amazonica 27: 103-118.
Latrubesse E, Caminha-Silva S, Cozzuol M, Absy M. 2007. Late Miocene continental sedimentation in the southwestern Amazonia and its regional significance: Biotic and geological evidence. Journal of South American Earth Science 23: 61-80.
Latrubesse E, Cozzuol M, Rigsby C, Silva S, Absy ML, Jaramillo C. 2010. The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. Earth-Science Reviews 99: 99-124.
Leandro LM. 2012. Análises palinoestratigráficas da Formação Solimões na porção noroeste do Alto Solimões, Amazonas, Brasil. MSc Thesis, Universidade do Vale do Rio dos Sinos, São Leopoldo.
Leite FPR. 2006. Palinologia da Formação Solimões, Neógeno da Bacia do Solimões, estado do Amazonas: Implicação paleoambientais e bioestratigráficas. PhD Thesis, Universidade de Brasília, Brasília.
Leite FPR, Paz J, Carmo DA, Silva-Caminha S. 2016. The effects of the inception of Amazonian transcontinental drainage during the Neogene on the landscape and vegetation of the Solimões Basin, Brazil. Palynology 40: 1-11.
Linhares AP, Ramos MIF, Gross M, Piller WE. 2011. Evidence for marine influx during the Miocene in southwestern Amazonia, Brazil. Geología Colombiana 36: 91-104.
Lorente M. 1986. Palynology and palynofacies of the Upper Tertiary in Venezuela. Cramer, Berlin/Stuttgart Band, Dissertationes Botanicae.
Lovejoy N. 1998. Marine incursion into South America. Nature 396: 421-422.
Maia RGN, Godoy HK, Yamaguti HS, *et al*. 1977. Projeto de carvão no Alto Solimões. Relatório Final. Manaus, CPRM-DNPM.
Monsch KA. 1998. Miocene fish faunas from the northwestern Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions. Palaeogeography, Palaeoclimatology, Palaeoecology 143: 31-50.
Nogueira ACR, Silveira R, Guimarães JTF. 2013. Neogenee-Quaternary sedimentary and paleovegetation history of the eastern Solimões Basin, central Amazon region. Journal of South American Earth Sciences 46: 89-99.
Ramos MI. 2006. Ostracods from the Neogene Solimões Formation (Amazonas, Brazil). Journal of South American Earth Sciences 21: 87-95.
Räsänen ME, Linna AM, Santos JCR, Negri FR. 1995. Late Miocene tidal deposits in the Amazonian foreland basin. Science 269: 386-389.
Regali MSP, Uesugui N, Santos AS. 1974a. Palinologia dos sedimentos meso-cenozóicos do Brasil – I. Boletim Técnico da Petrobrás 17: 177-191.
Regali MSP, Uesugui N, Santos AS. 1974b. Palinologia dos sedimentos meso-cenozóicos do Brasil – II. Boletim Técnico da Petrobrás 17: 263-301.
Silva, SAF. 2004. Palinologia do Neógeno da Amazônia Sul Ocidental, Brasil. MSc Thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus.
Silva-Caminha SAF, Jaramillo CA, Absy ML. 2010. Neogene palynology of the Solimões Basin, Brazilian Amazonia. Palaeontographica 283: 1-67.
Silveira RR, Souza PA. 2015. Palinologia (grãos de pólen de angiospermas) das formações Solimões e Içá (bacia do Solimões), nas regiões de Coari e Alto Solimões, Amazonas. Revista Brasileira de Paleontologia, 18: 455-474.
Silveira RR, Souza PA. 2016. Palinologia (esporos de fungo e pteridófitas, grãos de pólen de gimnospermas, cistos de algas e escolecodonte) das

formações Solimões e Içá (Neógeno e Pleistoceno, Bacia do Solimões), Amazonas, Brasil. Pesquisas em Geociências 43:17-39.

Tryon AF, Lugardon B. 1991. Spores of the Pteridophyta. Surface, wall structure and diversity based on electron microscope studies. New York, Springer.

Uesugui N. 1979. Palinologia; técnicas de tratamento de amostras. Boletim Técnico da Petrobrás 22: 229-240.

Vonhof HB, Wesselingh FP, Ganssen GM. 1998. Reconstruction of the Miocene western Amazonian aquatic system using molluscan isotopic signatures. Palaeogeography, Palaeoclimatology, Paleoecology 141: 85-93.

Vonhof HB, Wesselingh FP, Kaandorp RJG. 2003. Paleogeography of Miocene western Amazonia: isotopic composition of molluscan shells constrains the influence of marine incursions. Geology Society of America Bulletin 115: 983-993.

Wanderley-Filho JR, Eiras JF, Vaz PT, *et al* 2007. Bacia do Solimões. Boletim de Geociências da Petrobrás 15: 217-225.

Wesselingh FP. 2006. Molluscs from the Miocene Pebas Formation of Peruvian and Colombian Amazonia. Scripta Geologica 133: 19-290.

Wesselingh FP, Ranzi A, Räsänen ME. 2006. Miocene freshwater Mollusca from western Brazilian Amazonia. Scripta Geologica 133: 419-437.

Wesselingh FP, Räsänen ME, Irion G, *et al*. 2002. Lake Pebas: a palaeoecological reconstruction of a Miocene, a long-lived lake complex in western Amazonia. Cainozoic Research 1: 35-81.

Wesselingh FP, Salo JA. 2006. A Miocene perspective on the evolution of the Amazonian biota. Scripta Geologica 133: 439-458.