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Fluvial palaeoenvironments in the intracratonic Amazonas Basin (Early Miocene–early Middle Miocene, Colombia)

Carina Hoorn

Hugo de Vries-Laboratory¹ *, Department of Palynology and Paleo/Actuo-ecology, University of Amsterdam, Kruislaan
318, 1098 SM Amsterdam, The Netherlands

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Abstract

Based on a detailed study of Early Miocene to early Middle Miocene sediments in the Caquetá River area (Amazonas Basin, Colombia), a reconstruction of the palaeoenvironmental and palaeogeographical history is made. Sediment composition, sedimentary sequences and transport directions indicate that the succession was deposited by a low sinuosity fluvial system with an anastomosing character that originated from the Guyana Shield. Basin subsidence, Precambrian and Palaeozoic palaeorelief, and a changing base level controlled deposition in this fluvial system. Sedimentary environments such as channels, abandoned channels, crevasse splays, backswamps and palaeosoils characterized this system where fluvial flooding was common. The Early Miocene to early Middle Miocene sequences have been truncated by a more recent fluvial system, probably of Pliocene to Pleistocene age, representing the precursor of the present Caquetá River.

Palynological analysis suggest that the sediments are part of the *Retitricolporites* and the *Psiladiopites*–*Crototricolpites* pollen zones. Fifteen new species are described which belong to the genera: *Psilatricolpites*, *Retitricolpites*, *Retitricolporites*, *Bombacacidites*, *Syncolporites* and *Psilastephanocolporites*. The palynological assemblages indicate that the area was characterized by palm swamps, riparian vegetation and a rather diverse tropical forest. Intervals rich in marine palynomorphs accompanied by high concentrations of mangrove pollen grains (*Zonocostites*) suggest periods of marine influences and mangrove development. It is thought that the marine intervals are related to the Late Burdigalian transgression.

1. Introduction

The origin of the Amazonian rain forest and its richness in number of species has been the subject of some debate. It has been proposed that the history of the rain forest goes back as far as the Early Tertiary (Wolfe, 1985; Colinvaux, 1987, citing Haffer 1969, 1974 and Prance, 1982). Several authors have shown that Amazonia was, and still

is, a highly dynamic environment. During the Miocene, marine incursions reached the area of the Solimões and the Amazonas Basins (Hoorn, 1993) and river systems changed drastically as west directed transport switches to east directed transport due to the influence of Andean tectonics (Katzer, 1903; Damuth and Kumar, 1975; Hoorn, 1993). Quaternary history has been particularly dynamic in the Andean foreland basins where relatively rapid subsidence has caused strong perturbations in the fluvial systems (Salo et al., 1986; Räsänen et al., 1987).

In the Early Miocene to early Middle Miocene,

¹Also in cooperation with the Department of Soil Sciences and Geology (Agricultural University, Wageningen) and Tropenbos–Colombia.

deposition in Northwestern Amazonia was dominated by a fluvial system that originated on the Guyana Shield. Between Early to Middle Miocene the sediment source changed and sediment supply of Andean origin started to dominate the area (Hoorn, 1993). This paper focuses on the Early Miocene to early Middle Miocene fluvial deposits of the Caquetá River area (Colombian Amazonia) with the aim of presenting a reconstruction of the palaeogeography and the palaeoenvironment of the area during this time.

The data presented result from a sedimentological and palynological study of outcrops between the villages of Araracuara and Santa Isabel (Fig. 1). This study started in 1988 as part of the geological project of Tropenbos–Colombia which aims to reconstruct the Neogene depositional history of Colombian Amazonia.

A first geological study was carried out by Van der Hammen (1954b), followed by a large general exploratory study of Colombian Amazonia by Proradam (1979). It included a thorough study of radar photos and a large field survey. Tropenbos–Colombia has continued research in the Amazonia with an extensive, interdisciplinary programme which is being carried out in the Caquetá River area. This programme is designed to study and stimulate research on vegetation, soils, geology etc. of Amazonia. The integrated approach should lead to a better understanding of the development of the Amazonian ecosystem through time and space. These data will form a basis on which an adequate plan for future, sustainable use of the area can be established.

2. Geography

The Caquetá River area is a “humid, tropical forest” according to the classification of Holdridge (1971). The annual precipitation is around 3000 mm with an almost unimodal distribution over the year. Precipitation is relatively low during the “dry season” (December–February) and relatively high during the “rainy season” (May–June). The average temperature is 26°C.

The Caquetá River is an Andean river and a major tributary of the Amazon River. In Brazil it

receives the name of Japurá. Baker (1978) describes the Japurá as a mixed source river with a wide, shallow channel, an extremely low bedload (2.3%) and a very high suspended load. The ratio of suspended load/bedload relates to the character of the Andean source rocks and chemical weathering. In general the Andean rivers are known as “white” rivers because of their high suspended load. This in contrast to the “clear” and “black” rivers of Amazonian origin which have a high bedload and varying amounts of dissolved organic matter. The Caquetá River shows different channel types along its course, from a braided pattern at the Andean foothills into a meandering pattern further eastwards. Once the river enters the domains of the intracratonic Amazonas Basin, the channel pattern becomes straight and moderately anastomosing. At Araracuara net erosion occurs, and the Caquetá River is confined to a particularly narrow channel incised into a Palaeozoic plateau (Fig. 2). Downstream of Araracuara the riverbed is controlled by rapids and bed-rock. The sinuosity index is low (1.3), and stable islands are abundant (Duivenvoorden and Lips, 1993). The most remarkable topographical features of the Araracuara area are determined by a Palaeozoic plateau and sporadic outcrops of Precambrian basement. The majority of the area is covered by Neogene sediments which result in a gentle relief that forms the so called *terra firme* or not inundated area. This is in contrast to the *varzea* or alluvial plain where large areas are temporarily or permanently inundated. The entire area is incised, and (?) Plio-Pleistocene river terraces are the result of this (Eden et al., 1982; Van der Hammen et al., 1992a,b). The present alluvial plain of the Caquetá River is incised into a low terrace of Middle Pleniglacial age (> 50,000–< 30,000 yr B.P.) while sedimentation initiated in the Late Glacial continuing in the Holocene (Van der Hammen et al., 1992a,b). The incision is relatively shallow (several metres), probably due to the presence of the Precambrian basement (Lips and Duivenvoorden, 1993). The altitude of the Araracuara area ranges from about 150 m above mean sea level (alluvial plain at low river level) to about 300 m a.m.s.l. (top of the Palaeozoic plateau).

During the “dry season” the river level is 6–10

Fig. 1. Geological map of Amazonia (modified after Ingeominas, 1988).

m below average and large sand bars are exposed. These sand bars can turn into permanent islands stabilized by vegetation. The “dry season” is the optimal time of the year for studying the rather small Tertiary outcrops along the riverside. In “rainy season” time the river reaches, occasionally, unusually high levels (1.7 m higher than average). This phenomenon is known as “la conejera”.

3. Geological setting

The study area forms part of the Colombian Amazonas Basin (Fig. 3). The Amazonas Basin is

an intracratonic basin with a Palaeozoic/Tertiary infill. The basin is limited to the east by the Guyana Shield and to the west by the high of Florencia which separates it from the Putumayo Basin. In the north the Vaupés Arch constitutes the division between the Amazonas Basin and the large Llanos (Andean foreland) Basin (Bueno, 1988). Towards the south the basin probably deepens and forms the shallower extension of the Solimões Basin in Brazil (M.V. Caputo, pers. commun., 1991). However, this has not been proven.

Fig. 1 shows the general geology of southern Colombia, including Colombian Amazonia. The N–S oriented ridge formed by the Palaeozoic

Fig. 2. The Araracuara Cañon. The Precambrian basement crops out in the Caquetá river and is overlain by the Palaeozoic Araracuara Formation.

Araracuara Formation is striking (Bogotá, 1983; Théry et al., 1985). This formation unconformably overlies the Precambrian basement. Both, basement and Palaeozoic, are part of the Florencia Arch which continues towards the south as the Iquitos Arch. Initially, shallow-marine, clastic deposits of the Araracuara Formation must have covered a major part of Amazonia. Post-Ordovician block faulting altered the palaeotopography and at a later stage, possibly during a phase of subsidence accompanied by a change in base level, new accommodation space was created and Miocene sediments were deposited. Miocene sedimentation stopped when the area was gradually uplifted and dissected by the ancestor of the present Caquetá River leaving relict terraces at different altitudes (Eden et al., 1982). The conglomerates that constitute the terrace sediments, composed of chert, lithic fragments among others, are of Andean origin. The uppermost terrace is situated at an altitude of 300 m a.m.s.l., whereas the present alluvial plain of the Caquetá River is at 150 m a.m.s.l. For this reason the uplift since

(?)Pliocene to present is estimated to be around 150 m. The alluvial fan that constitutes the piedmont of the Palaeozoic plateau at Araracuara possibly originated during the same time interval. A NW–SE section shows the different units that characterize the landscape of the Caquetá River area nearby Araracuara (Fig. 4).

According to Dumont et al. (1988) the Iquitos Arch was affected by post-Miocene extensional tectonics originating river terrace formation (40,000 and 13,000 yr B.P.) in Peruvian Amazonia. It is likely that the uplift of the Palaeozoic plateau at Araracuara was related to this extensional tectonic event.

4. Stratigraphy

Galvis et al. (1979) divided the Tertiary sediments of Colombian Amazonia into a brackish–lacustrine clay unit (Terciario Inferior Amazónico) and a fluvial, sandy unit (Terciario Superior Amazónico). The Terciario Inferior

Fig. 3. Sedimentary basins of northwestern South America (modified after Cavalcante and De Paula, 1991). The following abbreviations are used: Basins: A = Amazonas; S = Solimões; P = Putumayo; N = Napo; M = Marañón; A' = Acre; U = Ucayali and MD = Madre de Dios; Arches, V = Vaupes; F/I = Florencia/Iquitos; F = Fitzcarrald and J = Jutai.

Fig. 4. NW-SE profile illustrating the Caquetá River area nearby Araracuara.

Amazónico has subsequently been included in the Pebas formation in order to avoid excessive names for the same sedimentary unit (Khobzi et al., 1980; Hoorn, 1990). The Pebas formation was informally described in Peruvian Amazonia (Gabb, 1869; Katzer, 1903; Steinmann, 1930; De Gréve, 1938; Ruegg and Rosenzweig, 1949; Pardo and

Zúñiga, 1976). In Brazil the Amazonian Tertiary sediments are known as Solimões Formation (Moraes Rego, 1930) which is equivalent to the Terciario Amazónico (Inferior and Superior) of Colombia.

The Terciario Superior Amazónico is the subject of this study and will here be referred to, informally, as Mariñame sand unit because the chronostratigraphic name used by Galvis et al. (1979) generates confusion. No formal formation name can be proposed since some essential information about the basal contact and the thickness is missing. A description of the Mariñame sand unit follows together with details on sedimentary environments, lithofacies and facies associations. A more detailed map shows the precise location of the studied outcrops (Fig. 5).

5. The Mariñame sand unit

The type section of the lithostratigraphic Mariñame sand unit is located on the concave side of a meander of the Caquetá River between the islands of Mariñame and Maria Cristina (Fig. 6). The outcrop has a height of approximately 60 m and is illustrated in Fig. 7 (III). The lithology is mainly quartz sand with mica as a minor component. The sands alternate with sandy clays, clays and lignite. The age is established on the basis of palynological analysis as Early Miocene to early Middle Miocene, i.e. *Retitricolporites* and *Psiladiporites-Crototricolporites* zones (Hoorn, 1993). The sediments were deposited in a low sinuosity fluvial system with an anastomosing character. Additional laterally equivalent sections are described at Mariñame, Tres Islas and Santa Isabel (Figs. 1, 7 and 8). A precise correlation of Mariñame, Tres Islas and Santa Isabel is not possible because of the large distance between the sections. Another outcrop where sediments of the Mariñame sand unit are represented is located along the Agua Negra, a side river of the Yari river (Fig. 1).

No basal contact was observed although the Precambrian basement that crops out in the surroundings is thought to, directly, underlie the Mariñame sand unit. Galvis et al. (1979) suggests

Fig. 5. Maps with the precise locations of the sections (based on radar image nr. 523, 532, 511 and 512).

Fig. 6. Mariñame section III.

that the basal part of the Terciario Superior Amazónico is a ferruginous oolitic crust observed at Mitú. A similar phenomenon was previously observed by Van der Hammen (1954b) in the Apaporis area where a ferruginous conglomerate is accompanied by manganese. The top of the

Mariñame sand unit is cut off by a (?) Plio-Pleistocene high terrace.

6. Lithofacies and sedimentary environments of the Mariñame sand unit (Figs. 7 and 8)

Channel, transitional bank/flood basin and flood basin deposits are distinguished. Chemical precipitations are presented as a separate unit.

6.1. Channel deposits

Sand bars

The channel facies is well represented in the Mariñame sections (e.g. Mariñame III, 21–40 m, Fig. 7) and characterized by unsorted, subangular quartz sands with mica as minor component. Grain size ranges from medium to very coarse sand and fine gravel although fine sand is also observed. No fining upward- or coarsening upward sequences were recognized. The sand is yellow and reddish in colour and locally cemented or coated with iron oxide. Intraclasts are present in the coarse fraction. The most common sedimentary structure is tabular cross-bedding (5 cm to 1 m high sets), whereas trough cross-bedding is less common. Very coarse sand and gravel pockets are concentrated on the foresets of the tabular cross-bedding (Fig. 9). A similar phenomenon was observed in the present Orinoco river and termed flow-toes (McKee, 1989). These tabular, large scale, cross bedded, sands are interpreted as sand bars. The cross-bedded sands are stacked and separated by erosion

Fig. 7. Sections of the Mariñame area.

surfaces. They were formed during fluvial floodings when vertical aggradation took place in the channel environment. Palaeocurrent directions indicated by cross-bedding structures suggest a relatively uniform northwestward transport of the sediments (Fig. 10).

The heavy mineral fraction is characterized by stable minerals such as zircon, tourmaline and

opaque minerals (Table 1). This, and the ubiquitous presence of quartz indicates a very mature sediment composition. The mature composition, angularity, grain size and palaeocurrent direction reveals the Guyana Shield as provenance area.

Studies on sediment composition of the present Amazon River (Franzinelli and Potter, 1983; Potter and Franzinelli, 1985) and the Orinoco

Fig. 8. Sections of the Tres Islas and Santa Isabel areas (legend in Fig. 7).

River (Johnsson et al., 1988) have shown that the basement granites which constitute most of the Guyana and Brazilian Shields yield first cycle quartz sands. Intense tropical weathering in combination with a low relief and tectonic quiescence preserves monocrystalline quartz and eliminates less stable minerals such as feldspars, and lithic fragments. The rivers draining the Shield transport these first cycle quartz sands and clays into the major rivers. It is here suggested that the Early Miocene to early Middle Miocene Mariñame sand unit was formed partly by processes similar to those observed in the present Amazonian rivers (e.g. Apaporis, Yari).

6.2. Transition bank/flood basin deposits

Crevasse splays deposits

In the Caquetá River area crevasse splays are a common feature. At Mariñame I (6–10 m, Fig. 7), III (7–12 m, Fig. 7) and Tres Islas II (0–10 m, Fig. 8), the crevasse splays deposits are developed as medium to very coarse quartz sand beds mixed

with quartz granules and clay intraclasts (10–15 cm) that alternate with sandy clay or clay beds. The sands do not reveal stratification and the changes from coarse to very fine grain size are very abrupt. At Tres Islas II, pieces of translucent, light yellow amber are found in the sandy clay. This amber is allocthonous.

The alternation of bedload and suspended load deposition together with the erosional, concave-up base characterizes this sequence. These sediments are thought to have accumulated in alternating episodes of high and low discharge. During the episodes of high discharge crevasses burst through the levees and gravel sheets (splays) spread out over the flood basin. This dynamic stage is followed by a stage of slack water and deposition of finer grain sizes.

6.3. Flood basin deposits

Abandoned channel deposits

In the Mariñame III section (40–50 m, Fig. 7) the abandoned channel facies is well preserved. A

Fig. 9. Tabular cross bedding with coarse sand/granule pockets.

10 m thick sequence of black, organic rich clay with millimetre thick lenses of fine sand fills a cut into the underlying channel sands. The clay is very rich in organic debris and contains a large number of pyrite nodules. Six and a half metre above the base, a layer of very sandy clay occurs containing organic inner linings of “microforaminifera” and mangrove pollen grains in the organic matter. This is followed by a grey clay layer grading into brown clay with sand lenses and abundant plant macrofossils and coaly fragments. At the transition of grey to brown clay the sediment has been disturbed by bioturbation. An iron pan cuts off the mudplug or abandoned channel infill and a new sand sequence follows. Laterally the black clay sequence changes into a succession of lignite and black to light coloured clay (see backswamp deposits). The

width of the abandoned channel is estimated at ± 500 m.

The infill of an abandoned channel is determined by fluvial flooding episodes. Growth of vegetation in the flood basin provides a high input of organic debris. According to Behrensmeyer et al. (1992, citing Gagliano and Howard, 1984) the infill of an abandoned channel is a relatively rapid process taking approximately 10^3 – 10^4 years. The presence of marine organisms and mangrove pollen grains indicates that the last phase of channel infill was affected by a flooding of marine character.

Backswamp deposits

In the Caquetá River area lignites are scarce and the organic matter is usually mixed with clastic input during fluvial flooding events resulting in an organic-rich, black, brown or dark grey coloured clay. However, lenticular lignite beds up to 50 cm thick were observed. The lignite forms the basal part of a black to light coloured, mottled clay sequence (e.g. Mariñame II, 37.7–39.5 m; Tres Islas III, 8.5–12.5 m and Santa Isabel, 6.5–9 m, Figs. 7 and 8). The lignite beds are rich in plant macrofossils and likely to be autochthonous in origin. The lignite–clay sequence was deposited in a swampy environment with changing clastic supply. When clastic input was low, organic matter accumulated forming peat. During fluvial flooding episodes, when the clastic input was high, the peat was then buried by a mixture of clay and organic matter after which eventually soil formation could take place.

According to McCabe (1984) no coal formation will occur in an active clastic environment. He describes the essential conditions for coal formation as: (1) no detrital influx, (2) watertable at or near ground level and (3) subsidence while vertical growth of peat keeps pace.

Mudflow deposits

The Tres Islas sections (Fig. 8) are dominated by suspended load deposits. Thick beds (4–7 m) of sandy clay characterize these sedimentary sequences (Fig. 11). The white, light grey or pink clays contain a matrix-supported fraction of medium to very coarse quartz sand and granules including purple clay pebbles and pyrite spicules

Fig. 10. Rose diagram of palaeocurrent directions.

Table 1

Heavy mineral composition of the Mariñame sections (percentage of transparent heavy minerals based on counting an average of 300 grains per slide, excluding the opaques)

Age	Section	m	Opaque	Transparent heavy mineral composition (%)							
				Tourmaline	Zircon	Rutile	Anatase	Staurolite	Andalusite	Sillimanite	Epidote
Plio.-Pleist.	III	56	100	—	—	—	—	—	—	—	—
Miocene	II	39	71	0	90	3	1	1	1	1	3
Miocene	II	38.5	46	15	77	2	4	1	0	0	1
Miocene	III	51	47	4	90	2	4	1	0	0	0
Miocene	III	49	61	12	71	4	8	2	0	0	3
Miocene	III	48.5	66	12	78	2	6	2	0	0	0
Miocene	IV	40	—	—	—	—	—	—	—	—	—
Miocene	IV	24.5	56	6	89	2	0	1	0	0	1

(e.g. Tres Islas I, 13–18 m; III, 13.5–20.7 m and Mariñame II, 39.5–43.5, Figs. 7 and 8). Also mottling and root structures were often observed. These sediments are similar to the sandy clay intervals of the previously described crevasse splay deposits.

The unsorted, nonstratified, heterogeneous, character of the sediments suggests that they resulted from a dense, water/sediment mixture that

originated under circumstances of abundant water supply (high discharge?) and high mud availability. It is thought that these sediments represent mud-flow deposits in the overbank environment. These were formed after a fluvial flooding when sediment load was no longer confined to the main channel or to the crevasses and spread out as large sheets over the riverbanks into the flood basin. These sediments are thought to constitute the lateral

Fig. 11. Tres Islas section II.

extension of the crevasse splay deposits. After deposition the sediments were exposed above the water table and soil formation could continue.

Palaeosoils

Palaeosoils are recognized by mottling and bioturbation structures in the sediments. These features are a result of geochemical changes, plant rooting and burrowing fauna which are related to the process of pedogenesis. These characteristics are commonly found in sediments which have been exposed for longer periods. Palaeosoils were often recognized in the end member of a drowned swamp sequence (Mariñame II and Tres Islas III; Figs. 7 and 8), in mudflow deposits that occasionally overlay a swamp sequence and in the clayey member of the crevasse splays (Tres Islas II, Fig. 8).

6.4. Chemical precipitations (pyrite and iron)

Pyrite nodules are common in the organic-rich clays of the Mariñame sand unit (Mariñame II and III, Fig. 7). In the light-coloured, mottled sandy clays also disseminated pyrite spiculae are

found. For a review on pyrite formation is referred to the work of Casagrande (1986). A small synopsis relevant to the discussion follows:

Syngenetic pyrite is formed by microorganisms that reduce sulphate ions to hydrogen sulphide (H_2S). This reacts with ferrous iron to produce pyrite and with organic matter to form organic sulphur. The sulphate reducing bacteria require specific pH and anaerobic conditions. Ferrous iron may be available through the deposition of clay particles from fluvial sources. The prevailing pH controls the redox potential of iron available (Fe^{2+} or Fe^{3+}). Marine-influenced areas have a much higher sulphur content than areas that are under freshwater-influence and are likely to be pyrite generating environments. Epigenetic pyrite can also form in freshwater peat swamps inundated by sea water after deposition. The presence of marine palynomorphs and mangrove pollen in the organic matter of the Mariñame sand unit are an evidence for marine influence. For this reason the pyrite is thought to be of marine origin.

Iron pans are thin (1–3 cm), iron-rich brown layers which were observed in all facies but are particularly noticeable at the base of lignite beds.

According to Pettijohn (1975) leaching of profiles takes place when soluble ions are dissolved and removed leaving only immobile ions. These immobile ions, like iron and aluminium, together with clays are mobilized as organic complexes and redeposited at lower levels in the profile.

7. Palynology

The following palynological study is presented in order to gain an insight into the palaeovegetation that characterized the Early Miocene and early Middle Miocene wetland environments in the Caquetá River area. These environments, including swamps, pools and abandoned channels, are particularly suitable for the accumulation and preservation of organic matter of local and regional origin.

8. Materials and methods

Four sections have been sampled in detail for palynological analysis. Mariñame section III provided the longest continuous record with 10 m of black, organic rich clay. In Mariñame II, two lignite/organic-rich clay sequences of 1.5 m were sampled which represent the lateral equivalent of section III. Two organic rich clay layers of 0.5 m and 1 m thickness in section I complete the sample set of the Mariñame area. Neither Tres Islas nor the Santa Isabel section present a continuous sequence of organic-rich lithologies and the palynological information is therefore scattered.

In total 80 samples were processed following the standard procedure of the Hugo de Vries-Laboratory. From each sample 1 cm³ of material is sieved through a 250 µm mesh. The organic-rich clays were treated with sodium pyrophosphate (Na₄P₂O₇·10H₂O) in a 10% solution with H₂O and lignites were oxidized with Schulze mixture (2HNO₃, 60%: KClO₃, 7%). Finally bromoform with density 2.0 g/cm³ was used to separate the inorganic fraction and the resulting organic residue was mounted in glycerine and sealed with paraffin.

Sporomorphs were counted taking a pollen sum ranging in general between 100 and 400 specimens.

The sum of each sample is represented in a curve next to the pollen percentage diagram. The data were stored and processed in a spreadsheet programme and classified with TWINSPAN (Two-way indicator species analysis; Hill, 1979). The pollen percentage diagram is constructed with "Pollen diagram" which was created by J.J. Duivenvoorden at the Hugo de Vries-Laboratory.

9. Age

A biostratigraphical framework of the Solimões Basin (Brazil) has been constructed previously, based on a the study of well samples (Hoorn, 1993). Five pollen zones were distinguished which in part coincide with the earlier defined Miocene zones in the Venezuelan basins (Lorente, 1986). These zones are related to the Caribbean foraminifera zonations (Germeraad et al., 1968).

Based on the abundance of *Retitricolporites guianensis* and the presence of the *Psiladiporites/Crototricolpites* assemblage, an age of Early Miocene and early Middle Miocene is suggested for the sediments that crop out at Mariñame, Tres Islas and Santa Isabel (Fig. 12). In contrast to the zonation presented in Hoorn (1993), *Retitricolporites* and the *Psiladiporites/Crototricolpites* assemblage are here considered as a single zone. An earliest Early Miocene age is not possible due to the absence of *Verrutricolporites rotundiporus*. A younger age than early Middle Miocene is excluded because of the absence of *Crassoretitritiles vanraadshoovenii*, *Grimsdalea magnaclavata*, *Echitricolporites spinosus* and *Fenestrites spinosus*.

10. Interpretation of the palynological diagrams

The pollen percentage diagrams (Figs. 13 and 14) could be divided into ecological zones based on the presence of ecological indicators and assemblages of ecologically similar species. Full names, taxonomic affinities and ecological significance of the species are presented in the systematic part. All taxa are numbered in order to make compari-

Fig. 12. Pollen zonation of the Solimões Basin and correlation with the Caquetá River area (Amazonas Basin).

son between the different diagrams easier. Cumulative diagrams representing the relation between *Verrucatosporites usmensis*, *Psilamonoletes tibui*, indeterminate Pteridophyta, the taxa included in the pollen sum and the indetermined angiosperms are included in Figs. 13 and 14. This is done in order to show the taxa of the pollen sum in relation to the total of sporomorphs counted in a sample.

The classification program TWINSpan was used in order to group ecologically similar species together. TWINSpan classifies species as well as samples in a tabular matrix. This program is widely used in vegetation studies and can also be applied with good results to a palynological data set (Sarmiento, 1993). The main difference with the vegetation studies is that a sample in a palynological study represents a spectrum and for this reason it is not comparable to a vegetation relevee (a predefined area of which the vegetation composition is described). TWINSpan classifies the vegetation relevees into vegetation "types". This has the disadvantage that spectra are grouped similarly

and the sample depth or position in the section is not taken into consideration. As a result the spectra are mixed up and have to be put back into order afterwards.

Before applying TWINSpan, eight cut levels (0.25, 0.50, 1, 2.5, 5, 10, 20 and 30%) were introduced. In the resulting matrix samples were grouped on similarity of composition and on lithology. This matrix was used to arrange the individual curves in the diagrams and as a base for an ecological zonation. The arrangement was made as follows: left, species dominating in the upper part of the section (40–50 m); middle, species common in the entire diagram although with predominance in certain zones; right, species dominating in the lower part of the diagram (3–16 m). This arrangement gives an indication about the taxa that characterize a palaeovegetation in a particular environment during a certain period of time.

TWINSpan has been applied exclusively to the Mariñame I and III data set since this composite section represents a relatively long continuous sequence across different subenvironments. The suggested arrangement was chosen as representative and applied to the other diagrams.

10.1. Mariñame (Fig. 13)

Ecological assemblage A (3–16 m)

The ecological assemblage is characterized by very high abundances of *Retitricolporites guianensis*, *Psilatricolporites operculatus*, *Echitricolporites maristellae*, *Magnastriatites grandiosus* and *Azolla* sp. Also abundant are *Psilatricolporites* cf. *varius*, *Retitricolporites crassicosatus*, *R. crassopolaris*, *Perisyncolporites pokorny*, *Crototricolporites annemariae*, *Crassietoapertites columbianus*, *Echiperiporites akanthos*, *Psilatricolporites acerbus*, *Psilatriporites desilvae* and *Psilamonocolporites* spp.

This assemblage is thought to represent an aquatic environment due to the abundances of *Azolla* sp. and *Magnastriatites grandiosus* (*Ceratopteris*). Species such as *Psilatricolporites operculatus* (*Alchornea*), *Retitricolporites guianensis* (*Sterculiaceae*–*Tiliaceae*), *R. crassicosatus* (*Rubiaceae*), *Crototricolporites annemariae* (*Croton*) and *Perisyncolporites pokorny* (*Malpigiaceae*) are

thought to be representatives of riparian vegetation. *Alchornea* grows at present in the Caquetá River area and is known to be tolerant to inundations (Urrego, 1991). The environmental significance of *Echitricolporites maristellae* (Bombacaceae–Malvaceae) is not clear but is probably also related to the riverbank forest. Additionally, the sedimentological data suggest that this zone was deposited in a regularly flooded pool in the overbank environment.

16–40 m: no palynological data

Ecological assemblage B (40–46 m)

In this ecological assemblage *Echitricolporites maristellae* and *Magnastriatites grandiosus* are virtually absent and *Retitricolporites guianensis* and *Psilatricolporites operculatus* have low percentages compared with assemblage A. High abundances of *Mauritiidites franciscoi*, *Heterocolpites incomptus* and *Retitricolporites irregularis* are counted accompanied by *Psilatricolporites garzonii*, *P. cf. operculatus*, *Psilatricolpites minutus*, *Syncolporites poricostatus*, *Retitricolpites caquetanus*, *Laevigatosporites catanejensis* and *Deltoidospora adriennis*. The aquatic algae *Botryococcus* sp. is present as a minor component. The pollen sum is relatively low in this interval (100–200 grains) due to the presence of very high amounts of organic debris.

The assemblage represents the palaeovegetation that surrounded an abandoned channel. This local palaeovegetation provided the main organic input into the abandoned channel environment. The sporomorphs are characterized by an association of *Mauritiidites franciscoi* (*Mauritia*), *Heterocolpites incomptus* (*Miconia?*, Melastomataceae) and *Retitricolporites irregularis* (*Amanoa*). *Mauritia* is nowadays known to grow on poorly drained soils in depressions on the floodplain. According to Urrego (1991) and Van Andel (1992), Melastomataceae are at present intermixed with the *Mauritia* vegetation on the alluvial plains of the Caquetá River.

Ecological assemblage C (46–49 m)

The most characteristic feature of this ecological assemblage is the abundance of marine palyno-

morphs (“microforaminifera” and dinoflagellate cysts). The assemblage is further characterized by a decrease of *Mauritiidites franciscoi*, *Heterocolpites incomptus* in comparison to assemblages A and B. *Retitricolporites irregularis*, *Psilatricolporites cf. varius* and *Perisyncolporites pokorny* are also abundant. Moderate abundances were observed of *Zonocostites ramonae*, *Retitricolporites caputoi*, *Psilamonocolpites nanus*, *Retitricolpites caquetanus*, *Psilamonocolpites amazonicus* and *Botryococcus* sp. In section II this interval is recognized by the presence of marine palynomorphs and *Zonocostites ramonae*. However, in section II also large quantities of *Botryococcus* sp. were counted.

This interval is characterized by a coarse clastic input into the abandoned channel environment. The presence of marine palynomorphs and the mangrove *Zonocostites ramonae* (*Rhizophora*) indicate that this clastic input was related to an influx of marine waters. The gradual decrease of *Mauritiidites franciscoi* (*Mauritia*) could be explained by the accumulation of the coarse clastic sediments in the environment (Kalliola et al., 1991). Besides, the influence of salt water possibly also had a negative effect on the *Mauritia* swamp.

The abandoned channel sequence of section III correlates with a drowned swamp sequence of section II. These drowned swamps are the lateral continuation of the abandoned channel forming shallow, channel sides where peat formation took place.

Ecological assemblage D (49–49.6 m)

In this ecological assemblage marine palynomorphs are absent. The following species dominate: *Psilatricolporites operculatus*, *Retitricolporites guianensis*, *R. crassicostatus*, *R. crassopolaris*, *Psilatricolporites cf. varius*, *Perisyncolporites pokorny*, *Echistephanoporites akanthos*. Low percentages of *Mauritiidites franciscoi*, *Heterocolpites incomptus* and *Retitricolporites irregularis* were counted. *Psilatricolpites minutus* is virtually absent as are the aquatic elements.

A pollen assemblage characterized by *Psilatricolporites operculatus* (*Alchornea*) and *Retitricolporites guianensis* (Sterculiaceae–Tiliaceae) is probably related to a palaeo vegeta-

Fig. 13. Pollen percentage diagram of Mariñame I, II and III (legend in Fig. 5). The vertical scale of Mariñame II exaggerated.

unity — Ecological boundary v Barren

I is slightly

Key

- V. usmensis*
- P. tibui*
- Indet. Pteridophyta
- Elements of the pollen sum
- Indet. Angiospermae

Fig. 14. Pollen percentage diagram of Tres Islas III and Santa Isabel (legend in Fig. 5).

onomic affinity — Ecological boundary v Barren

lative diagram

50 100

Key

- *V. usmensis*
- *P. tibui*
- Indet. Pteridophyta
- Elements of the pollen sum
- Indet. Angiospermae

tion of the riparian environment although not comparable to assemblage A since the aquatic elements and *Echitricolporites maristellae* are lacking. This interval constitutes the last phase of the abandoned channel infill with coarse clastic input. Taxa of a regional origin dominate the pollen content. *Mauritia* percentages are still very low because of the continuing clastic input into the environment.

10.2. Tres Islas III and Santa Isabel (Fig. 14)

In the Tres Islas III section, ecological assemblages D and C were distinguished. Assemblage D, as in Mariñame III, is characterized by the abundance of *Retitricolporites guianensis*, *R. crassicostatus*, *R. crassipolaris*, *Psilatricolporites operculatus*, *P. cf. varius*, *P. cf. operculatus*, *Perisyncolporites pokorny*, *Echiperiporites akantos*, *Psilatricolpites acerbus* and *P. minutus*. Assemblage C is distinguished based on the presence of *Zonocostites ramonae*, *Deltoidospora adriennis* and the marine palynomorphs.

The analysed intervals are interpreted as three consecutive drowned swamp sequences with the top one influenced by a marine influx.

The Santa Isabel section is classified as ecological assemblage C based on the presence of *Zonocostites ramonae* which is particularly abundant at the base of the section. However, no marine palynomorphs were observed. Other characteristic elements in this section are *Mauritidites franciscoi*, *Heterocolpites incomptus* and *Retitricolporites irregularis*, whereas at the top *Retitricolporites guianensis*, *Psilatricolporites operculatus* and *P. crassoexinatus* predominate. In the cumulative diagram relatively large abundances of *Psilamonoletes tibui* (5–30%) are indicated.

The environment is interpreted as a sequence of drowned swamps with marine influences similar to Tres Islas III. The Santa Isabel section is thought to represent the transition to the Middle to Late Miocene Pebas formation based on the presence of several turquoise, bluish clay intervals known to characterize this formation. Outcrops belonging to the Pebas formation have been observed at Puerto Remanso and Puerto Caiman (Fig. 1). This formation crops out more extensively at Los

Chorros, Pevas and Iquitos, along the Amazon River (Fig. 1).

11. Remarks on biodiversity

Today the highest species richness in Amazonia is found on the *terra firme*, whereas lower species richness is observed in the *varzea* (Richards, 1969; Junk, 1989; Duivenvoorden and Lips, 1993). The Early Miocene to early Middle Miocene environments that have been sampled during this study are all part of the wetlands of the flood basin, and for this reason are comparable to the *varzea*. In the samples of the Caquetá River area a total of 214 taxa have been recognized although in the pollen percentage diagrams only 124 selected taxa are represented. This indicates that a rather diverse tropical vegetation existed in this area during the Early Miocene and early Middle Miocene. Striking is the fact that in the Holocene pollen spectra and at present around 140 taxa were recognized in the flood plain environment (Th. van der Hammen, pers. commun., 1993), this would point to a higher Early Miocene to early Middle Miocene biodiversity than in Holocene and present times. However, comparing the taxonomic diversity of the Early Miocene to early Middle Miocene palaeovegetation to recent rain forest vegetation would require a detailed isotaphonomic approach.

Although palynological studies enable an approximation of the palaeovegetation to be made, it is difficult to give an estimate of the actual diversity. This is in the first place due to the fact that the palynological spectrum is not a true representation of the palaeovegetation. Pollen production of different species is unknown; some species have a large pollen production, whereas others produce very little. It is therefore plausible that certain species are overrepresented in the pollen spectrum. Furthermore, the pollen content of a sample represents pollen grains of local as well as regional origin (Muller, 1959). In a fluvial system an influx of river transported pollen grains can be expected in addition to those of local origin. The pollen concentration in samples from different lithologies also varies largely depending on the sedimentation rates. Additionally, the amount of

organic debris available differs for each environment. For instance, in the black clays and lignites of the abandoned channel and swamp environment (Figs. 13 and 14) pollen sums remain low. This is because the large amounts of organic debris provided by the local vegetation obscure the pollen content. The brown to grey clays and the sandy clays of the drowned swamp environment are less rich in organic debris, therefore, rather high pollen sums were obtained (Figs. 13 and 14).

The samples of Mariñame I and III were used for testing to what extent pollen sum and taxonomic diversity are related. It is shown that a strong correlation between pollen sum and total number of species exists (Fig. 15). For this reason it is concluded that only a general statement can be made on taxonomic diversity from the available data. In order to give a relatively accurate estimation of the diversity of a palaeovegetation by means of palynology, a constant, relatively high pollen sum (e.g. 500 pollen grains) is advisable.

12. Discussion and conclusions

The outcrops along the Caquetá River of Mariñame sand unit reflect an important part of

Fig. 15. Correlation between the number of taxa and the recovered pollen sum.

the Early Miocene to early Middle Miocene Amazonian sedimentary history. Sedimentological data indicate that these sediments represent a NW directed, low sinuosity, moderately anastomosing fluvial system. The palynological data give an indication of the age of these sediments and suggest that at the time a rather diverse wetland palaeovegetation composed of tropical taxa characterized the palaeoenvironment. The fluvial sequences are incised by (?)Pliocene–Pleistocene terraces originated by the palaeo-Caquetá River.

The interplay of basin subsidence, Precambrian and Palaeozoic palaeotopography and a changing base level determined deposition in the Early Miocene to early Middle Miocene fluvial system. The sediment source of this fluvial system were the crystalline rocks of the Guyana Shield. These parent rocks and the tropical weathering that affected them not only determined the composition (quartz, clay and an association of stable, heavy minerals) but also the bimodal grain size distribution that ranges from medium to very coarse grain sizes and clay fraction. Conglomeratic lag deposits are absent except for those formed by clay pebbles and quartz granules. Fine and very fine sands are also rare.

The main characteristics of the Early Miocene to early Middle Miocene fluvial system are: unimodal, NW directed palaeocurrent directions; bimodal grain size distribution; vertically aggraded channel deposits; crevasse splays deposits and diverse, often organic rich, flood basin deposits such as those resulting from the abandoned channel, pond and backswamp environments. These characteristics together with the absence of classical fining upward sequences (meandering system) and large granulometric differentiations (braided system) classifies this system as a low sinuosity fluvial system with an anastomosing character. Some examples of modern, anastomosing river deposits in a temperate climate are presented by Smith and Putnam (1980), Smith (1983, 1986) and Rust et al. (1984). The Miocene Amazonian fluvial system differs from a true anastomosing river because no multiple channels were observed and the channel facies are relatively well developed in relation to the flood basin deposits. The best analog for this system could be the present Caquetá

River. However, the Caquetá River has an eastward transport direction, it feeds the Amazon River and the sediments are of Andean origin. The Early Miocene to early Middle Miocene system to the contrary, had a NW palaeotransport direction and its origin in the Guyana Shield. This fluvial system was abandoned at some stage in the history of northwestern Amazonia and a major change in draining pattern took place which resulted in the activation of a new fluvial system of Andean origin. A study of a well drilled in the Solimões Basin (Brazil) indicates that this change occurred between the Early and Middle Miocene (Hoorn, 1993).

In the Late Burdigalian a global sea-level rise of 140 m is thought to have occurred (Haq et al., 1987). If we bear in mind that the Caquetá River area had an altitude of no more than 60 m a.m.s.l. during the Miocene, the Late Burdigalian sea-level rise could have affected Amazonia. The presence of marine palynomorphs and the high percentages of mangrove pollen grains (*Zonocostites*, 60% at Tres Islas III) in the organic matter confirm this view. It is thought that the marine incursion that affected NW Amazonia came from the north (via the area of the present lake Maracaibo, Venezuela) although an entrance from the West also seems feasible (via the area of Guayaquil, Ecuador) since no major topographical barriers existed at the time. However, no indications for a true shallow-marine environment were found and it seems that mere marine influence of an episodic character existed. This was probably the farthest southern extension of the Late Burdigalian transgression in N. South America.

The Early Miocene to early Middle Miocene vegetation of the Caqueta River area was rather diverse and, in general, characterized by tropical lowland taxa such as *Mauritia* and Bombacaceae, accompanied by other taxa common to forests and riparian environments. The absence of savanna elements, such as *Byrsonima* and *Curatella*, together with the lack of noticeable amounts of Gramineae, rule out more open vegetation types. Four ecological assemblages were distinguished with the classification programme TWINSPAN. These assemblages give an indication of the palaeovegetation that was associated to the different fluvial

subenvironments and the effect of a rising sea level on these.

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Appendix—species list

All species and genera applied in the pollen diagram are listed, accompanied by references and their number in the pollen diagram. Additionally, taxonomic affinity and ecology are presented. Suprageneric categories are after Iversen and Troels-Smith (1950), Potonié (1956) and Germeraad et al. (1968). The list includes 15 new species; these are formally described in the section Systematics. Plates I–IV illustrate holotypes of new species among others.

Pollenites

Inaperturatae

(112) *Ephedripites renzonii* Dueñas 1986 (Plate I, 4)

PLATE I

Monocolpatae

(124) *Echimonocolpites* spp. Van der Hammen et García de Mutis 1965

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

(1) *Mauritiidites franciscoi* (Van der Hammen 1956) Van Hoeken-Klinkenberg 1964

Taxonomic affinity: Palmae, *Mauritia*. Ecology: grows on poorly drained soils in permanently inundated, swampy areas.

(40) *Proxapertites tertiaria* Van der Hammen et García de Mutis 1965

Taxonomic affinity: Annonaceae, *Crematosperma*.

(108) *Psilamonocolpites* spp. Van der Hammen et García de Mutis 1965

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

Taxonomic affinity: Palmae.

(74) *Psilamonocolpites amazonicus* Hoorn 1993

Taxonomic affinity: Palmae, *Euterpe*.

(10) *Psilamonocolpites nanus* Hoorn 1993

Taxonomic affinity: Palmae.

(87) *Psilamonocolpites rinconii* Dueñas 1986 (Plate I, 1)

Taxonomic affinity: Palmae.

(39) *Retimonocolpites absyae* Hoorn 1993

Taxonomic affinity: Myristicaceae, *Virola*. Ecology: very common in marsh forests but also known from the rainforests.

(29) *Retimonocolpites maximus* Hoorn 1993

Taxonomic affinity: Palmae.

(120) *Trichotomosulcites* sp. Couper 1953 (Plate I, 2)

Remark: pollen grains of this form-genus with a taxonomic affinity to *Bactris* (Palmae) are here included.

Monoporatae

(68) *Monoporites annulatus* Van der Hammen 1954a

Taxonomic affinity: Gramineae. Ecology: forms part of open vegetations in a range of environments from humid to dry. Some members of this family act as pioneer vegetation in open water habitats (floating meadows) and on mud and sand flats.

Diporatae

(123) *Psiladiporites minimus* Van der Hammen et Wijmstra 1964

Taxonomic affinity: Moraceae, *Ficus*–*Artocarpus*–*Soroceae*.

(35) *Psiladiporites redundantis* González Guzmán 1967

Taxonomic affinity: Moraceae.

Remark: although the form-genus was originally named *Psilodiporites* (Varma et Rawat, 1963), at a later stage it was referred to as *Psiladiporites* (Van der Hammen et Wijmstra 1964; González Guzmán 1967). Since also a pollen zone was designated as *Psiladiporites* (Germeraad et al., 1968; Muller et al., 1987; Lorente, 1986) preference was given here to the latter in order to avoid confusions.

PLATE I

1000 ×

- 1.. *Psilamonocolpites rinconii*
2. *Trichotomosulcites* sp.
3. *Corsinipollenites oculusnoctis*
4. *Ephedripites renzonii*
5. *Retitriporites* sp. 1 (*Duroia* type)
- 6–7. *Retitriporites dubiosus*
8. *Retistephanoporites angelicus*
9. *Echiperiporites akanthos*
10. *Retistephanoporites crassianulatus*
11. *Perfotricolpites digitatus*
- 12–14. *Retitricolpites simplex*

Tricolpatae

(103) *Bacutricolpites* spp. Van der Hammen 1956
Remark: pollen grains of this form-subgenus were not identified at species level. This subgenus is at present not validated and is used here in an informal way since no well preserved pollen grains were available for validation.

(83) *Crototricolpites annemariae* Leide Meyer 1966
Taxonomic affinity: Euphorbiaceae, *Croton*.

(100) *Perforitricolpites digitatus* González Guzmán 1967 (Plate I, 11)

Taxonomic affinity: Convolvulaceae, *Merremia*.

(77) *Psilatritricolpites acerbus* González Guzmán 1967

(117) *Psilatritricolpites anconis* nov. sp. (Plate IV, 4)

(5) *Psilatritricolpites minutus* González Guzmán 1967 (Plate II, 8)

(104) *Psilatritricolpites* cf. *papilioniformis* Regali et al. 1974 (Plate IV, 3)

(17) *Psilatritricolpites pulcher* Wijmstra 1971

(88) *Psilatritricolpites simplex* González Guzmán 1967

(76) *Retitritricolpites antonii* González Guzmán 1967

(8) *Retitritricolpites caquetanus* nov. sp. (Plate II, 2)

Taxonomic affinity: Bombacaceae–Tiliaceae?

(66) *Retitritricolpites colpiconstrictus* nov. sp. (Plate IV, 2)

(42) *Retitritricolpites depressus* Wijmstra 1971

(15) *Retitritricolpites* cf. *maledictus* González Guzmán 1967

(52) *Retitritricolpites* cf. *maturus* González Guzmán 1967 (Plate II, 10)

(20) *Retitritricolpites simplex* González Guzmán 1967 (Plate I, 12–14)

Taxonomic affinity: Anacardiaceae?

Remarks: this species was originally described as tricolpate. Lorente 1986, observed that this species also can appear as tricolporate.

(16) *Retitritricolpites tuberosus* nov. sp. (Plate II, 3)

Taxonomic affinity: Bombacaceae–Tiliaceae?

(93) *Retitritricolpites wijningae* nov. sp. (Plate II, 6)

(33) *Retibrevitritricolpites catatumbus* González Guzmán 1967

(12) *Retibrevitritricolpites yavarensis* Hoorn 1993

(61) *Striatritricolpites catatumbus* González Guzmán 1967 (Plate III, 14–16)

Taxonomic affinity: Leguminosae, Caesalpinioideae, *Crudia*–*Macrolobium*–*Isobertlinia*. Ecology: grows along the riverbanks.

Remarks: in species are included some specimens which present oval shaped pori. Dueñas 1980 distinguished these porate pollen grains as *Striatritricolporites melenae*. However, following the example of Lorente 1986 and Germeraad et al. (1968), here these specimens are included in *Striatritricolpites catatumbus*.

Triporatae

(46) *Cricotriporites guianensis* Leide Meyer 1966

(70) *Corsinipollenites oculinoctis* (Thiergart 1940)

Nakoman 1965 (Plate I, 3)

Taxonomic affinity: Onagraceae, *Ludwigia*.

(122) *Proteacidites* spp. Cookson 1950 ex Couper 1953

PLATE II

1000 ×

1. *Bombacacidites baculatus*
2. *Retitritricolpites caquetanus* (holotype)
3. *Retitritricolpites tuberosus* (holotype)
4. *Bombacacidites baumfalkii*
5. *Echitritricolporites maristellae*
6. *Retitritricolpites wijningae* (holotype)
7. *Jandufouria saemrogiformis*
8. *Psilatritricolpites minutus*
9. *Retitritricolporites pygmaeus* (holotype)
10. *Retitritricolpites* cf. *maturus*
11. *Bombacacidites araracuarensis* (holotype)
12. *Psilastephanocolporites fissilis*
13. *Psilastephanocolporites matapiorum* (holotype)

PLATE II

PLATE III

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

(32) *Proteacidites* cf. *triangulatus* Lorente 1986 (Plate IV, 5)

Taxonomic affinity: Sapindaceae–Proteaceae.

(109) *Psilatiriporites* spp. Van der Hammen 1956 ex Hoorn 1993

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

(94) *Psilatiriporites corstanjei* Hoorn 1993

Taxonomic affinity: Onagraceae.

(97) *Psilatiriporites desilvae* Hoorn 1993

Taxonomic affinity: Leguminosae, Caesalpinoideae.

(38) *Psilatiriporites sarmientoi* Hoorn 1993

(43) *Retitriporites* sp. 1 (Van der Hammen 1956) Ramanujam 1966 (Plate I, 5)

Remark: pollen grains with a taxonomic affinity to *Duroia* (Rubiaceae) are here included.

(37) *Retitriporites dubiosus* González Guzmán 1967 (Plate I, 6–7)

Remarks: this pollen type variates from having 3 to 4 pores.

(36) *Scabratiriporites redundans* González Guzmán 1967

Tricolporatae

(118) *Bombacacidites* spp. Couper 1960

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

Taxonomic affinity: Bombacaceae.

(114) *Bombacacidites araracuarensis* nov. sp. (Plate II, 11)

Taxonomic affinity: Bombacaceae, *Ceiba*. Ecology: rain and marsh forests, especially along rivers and creeks.

(110) *Bombacacidites baculatus* Muller et al. 1987 (Plate II, 1)

Taxonomic affinity: Bombacaceae, *Pachira aquatica*. Ecology: common along rivers, in the rain forest and in mixed swamps.

(85) *Bombacacidites baumfalkii* Lorente 1986 (Plate II, 4)

Taxonomic affinity: Bombacaceae

Remark: an orthographical change has been introduced. Originally the name was published as *B. baumfalki*.

(67) *Bombacacidites bellus* Frederiksen 1983

Taxonomic affinity: Bombacaceae, *Bombax*.

(84) *Crassietoapertites columbianus* Dueñas 1980 (Plate III, 1–3)

Taxonomic affinity: Leguminosae, Papilionoideae, *Carnivalia eurocarpa*–*Dioclea virgata*.

Remarks: this pollen grain presents sometimes 4 apertures instead of 3.

(101) *Echitricolporites maristellae* Muller et al. 1987 (Plate II, 5)

Taxonomic affinity: Bombacaceae–Malvaceae.

(119) *Margocolporites vanwijhei* Germeraad et al. 1968

Taxonomic affinity: Leguminosae, Caesalpinoideae, *Caesalpineia bonduc*–*C. coriaria*. Ecology: coastal habitats, strands (*C. bonduc*); coastal, dry thorn forests (*C. coriaria*).

PLATE III

1000 ×

- 1–3. *Crassietoapertites columbianus*
4. *Retitricolporites crassopolaris*
5. *Retitricolporites crassopolaris* (holotype)
6. *Psilastephanocolporites marinamensis* (holotype)
- 7–8. *Retitricolporites santaisabelensis* (holotype)
- 9–10. *Retitricolporites crassicostatus*
11. *Retitricolporites oblatum* (holotype)
12. *Retitricolporites oblatum*
13. *Retitricolporites wijmstrae* (holotype)
- 14–16. *Striatricolporites catatumbus*
17. *Retitricolporites poriconspectus* (holotype)

PLATE IV

(86) *Psilatricolporites* spp. Van der Hammen 1956 ex Van der Hammen et Wijmstra 1964

Remark: pollen grains of this form-genus with a taxonomic affinity to Sapotaceae are here included.

(99) *Psilatricolporites costatus* Dueñas 1980

(55) *Psilatricolporites crassoexinatus* Hoorn 1993

(111) *Psilatricolporites crassus* Van der Hammen et Wijmstra 1964

Taxonomic affinity: Theaceae, *Pelliciera rhizophorae*. Ecology: forms part of the mangrove vegetation growing behind *Rhizophora* on more sandy soils.

(13) *Psilatricolporites cyamus* Van der Hammen et Wijmstra 1964

(14) *Psilatricolporites devriesii* Lorente 1986.

Taxonomic affinity: Humiriaceae, *Humiria*. Remark: an orthographic change has been introduced. The name was originally published as *P. devriesi*.

(47) *Psilatricolporites divisus* Regali et al. 1974

Taxonomic affinity: Sapotaceae.

(25) *Psilatricolporites exiguus* Hoorn 1993

(9) *Psilatricolporites garzonii* Hoorn 1993

(31) *Psilatricolporites labiatus* Hoorn 1993

Taxonomic affinity: Sapotaceae, *Pouteria*. Ecology: rain forest and along creeks and rivers.

(80) *Psilatricolporites magniporatus* Hoorn 1993

Taxonomic affinity: Leguminosae?

(71) *Psilatricolporites obesus* Hoorn 1993

Taxonomic affinity: Sapotaceae.

(56) *Psilatricolporites operculatus* Van der Hammen et Wijmstra 1964

Taxonomic affinity: Euphorbiaceae, *Alchornea*. Ecology: rain forests, premontane and montane forests. In the Caquetá River area this genus is

known to be tolerant to inundation and to grow on the river banks.

(4) *Psilatricolporites* cf. *operculatus* Van der Hammen et Wijmstra 1964

(24) *Psilatricolporites silvaticus* Hoorn 1993

Taxonomic affinity: Burseraceae–Sapotaceae.

(62) *Psilatricolporites transversalis* Dueñas 1980

Taxonomic affinity: Sapotaceae.

(6) *Psilatricolporites triangularis* Van der Hammen et Wijmstra 1964

(59) *Psilatricolporites* cf. *varius* Dueñas 1983

(41) *Psilatricolporites venezuelanus* Lorente 1986

(34) *Retitricolporites* sp. 1 Van der Hammen 1956 ex Van der Hammen 1964

Remark: pollen grains of this form-genus with a taxonomic affinity to *Avicennia* (Verbenaceae) are here included. Ecology: this species is tolerant to brackish water and common along the coast in the mangrove forest.

(64) *Retitricolporites* sp. 2 Van der Hammen 1956 ex Van der Hammen 1964

Remark: pollen grains of this form-genus with a taxonomic affinity to Rubiaceae are here included.

(23) *Retitricolporites caputoi* Hoorn 1993

(60) *Retitricolporites crassicostatus* Van der Hammen et Wijmstra 1964 (Plate III, 9–10)

Taxonomic affinity: Rubiaceae.

(69) *Retitricolporites crassopolaris* nov. sp. (Plate III, 4 and 5)

(44) *Retitricolporites ellipticus* Van Hoeken-Klinkenberg 1966

(57) *Retitricolporites guianensis* Van der Hammen et Wijmstra 1964

Taxonomic affinity: Sterculiaceae–Tiliaceae.

PLATE IV

1000 ×

1. *Spirosyncolpites spiralis*
2. *Retitricolpites colpiconstrictus* (holotype)
3. *Psilatricolpites* cf. *papilioniformis*
4. *Psilatricolpites anconis* (holotype)
5. *Proteacidites* cf. *triangulatus*
6. *Clavatriletes* spp.
7. *Syncolporites* cf. *incomptus*
8. *Syncolporites anibalii* (holotype)
9. *Laevigatosporites catanejensis*
10. Microforaminifera (500 ×)

(58) *Retitricolporites hispidus* Van der Hammen et Wijmstra 1964

(3) *Retitricolporites irregularis* Van der Hammen et Wijmstra 1964

Taxonomic affinity: Euphorbiaceae, *Amanoa*. Ecology: common along creeks and rivers on peaty mud.

(115) *Retitricolporites kaarsii* Hoorn 1993

Taxonomic affinity: Euphorbiaceae, *Dalechampia*.

(98) *Retitricolporites milnei* Hoorn 1993

(105) *Retitricolporites oblatum* nov. sp. (Plate III, 11 and 12)

(82) *Retitricolporites poriconspectus* nov. sp.

Taxonomic affinity: Leguminosae.

(78) *Retitricolporites pygmaeus* nov. sp. (Plate II, 9)

(89) *Retitricolporites santaisabelensis* nov. sp. (Plate III, 7 and 8)

(30) *Retitricolporites solimoensis* Hoorn 1993

(53) *Retitricolporites ticuneorum* Hoorn 1993

(28) *Retitricolporites wijmstrae* nov. sp. (Plate III, 13)

(96) *Rugutricolporites* spp. González Guzmán 1967

(51) *Rugutricolporites arcus* Hoorn 1993

Taxonomic affinity: Chrysobalanaceae, *Licania*.

(72) *Spirosyncolpites spiralis* González Guzmán 1967 (Plate IV, 1)

(106) *Syncolporites anibalii* nov. sp. (Plate IV, 8)

Taxonomic affinity: Sapindaceae.

(54) *Syncolporites* cf. *incomptus* Van Hoeken-Klinkenberg 1964 (Plate IV, 7)

Taxonomic affinity: Loranthaceae?

(7) *Syncolporites poricostatus* Van Hoeken-Klinkenberg 1966

Taxonomic affinity: Myrtaceae.

(22) *Zonocostites ramonae* Germeraad et al. 1968

Taxonomic affinity: Rhizophoraceae, *Rhizophora*. Ecology: grows on muddy soils forming part of the coastal tropical vegetation because of its tolerance to marine and brackish water.

(22b) *Zonocostites duquei* Dueñas 1980

Taxonomic affinity: Rhizophoraceae. Remark: an orthographical change has been introduced by Dueñas (1981). Originally the name was published as *Z. duquensis*.

Stephanocolpatae

(75) *Psilastephanocolpites marginatus* Wijmstra 1971

Stephanoporatae

(19) *Retistephanoporites angelicus* González Guzmán 1967 (Plate I, 8)

(90) *Retistephanoporites crassiannulatus* Lorente 1986 (Plate I, 10)

Taxonomic affinity: Bombacaceae, *Quararibaea*. Ecology: rain and marsh forests, along rivers and creeks.

(48) *Psilastephanoporites herngreenii* Hoorn 1993

Taxonomic affinity: Apocynaceae.

Stephanocolporatae

(65) *Jandufouria saemrogiformis* Germeraad et al. 1968 (Plate II, 7)

Taxonomic affinity: Bombacaceae, *Catostemma*. Ecology: rain forest.

(91) *Psilastephanocolporites fissilis* Leidelmeyer 1966 (Plate II, 12)

Taxonomic affinity: Polygalaceae.

(116) *Psilastephanocolporites marinamensis* nov. sp. (Plate III, 6)

Taxonomic affinity: Sapotaceae.

(102) *Psilastephanocolporites matapiorum* nov. sp. (Plate II, 13)

(26) *Psilastephanocolporites schneideri* Hoorn 1993

Taxonomic affinity: Rhizophoraceae?

Periporatae

(121) *Echiperiporites* spp. Van der Hammen et Wijmstra 1964

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

(79) *Echiperiporites akanthos* Van der Hammen et Wijmstra 1964 (Plate I, 9)

(107) *Magnaperiporites spinosus* González Guzmán 1967

(49) *Psilaperiporites minimus* Regali et al. 1974

Taxonomic affinity: Amarantaceae–Chenopodiaceae.

Pericolporatae

(73) *Perisyncolporites pokorny* Germeraad et al. 1968

Taxonomic affinity: Malpighiaceae.

Heterocolpatae

(2) *Heterocolpites incomptus* Van der Hammen 1956 ex Hoorn 1993

Taxonomic affinity: Melastomataceae, *Miconia*?. Ecology: grows in a large range of environments. In Amazonas *Miconia* is an important element of the understory in the *Mauritia* swamps.

(92) *Heterocolpites rotundus* Hoorn 1993

Taxonomic affinity: Combretaceae–Melastomataceae.

(27) *Heterocolpites verrucosus* Hoorn 1993

Taxonomic affinity: Melastomataceae.

Polyadeae

(81) *Polyadipollenites mariae* Dueñas 1980

Taxonomic affinity: Leguminosae, Mimosoideae, *Acacia*.

Vesiculatae

(45) *Podocarpidites* sp. Cookson 1947 ex Couper 1953

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

Taxonomic affinity: Podocarpaceae, *Podocarpus*. Ecology: common of the montane forest.

Sporites**Triletes**

(21) *Deltoidospora adriennis* (Potonié et Gelletich 1933) Frederiksen 1983

Taxonomic affinity: Polypodiaceae, *Acrostichum aureum*. Ecology: halophytic fern associated with the mangrove vegetation.

(63) *Echitriteles* cf. *muelleri* Regali et al. 1974

Taxonomic affinity: Sellaginellaceae?

(95) *Magnastriatites grandiosus* (Kedves et Solé de Porta 1963) Dueñas 1980

Taxonomic affinity: Parkeriaceae, *Ceratopteris*. Ecology: this small aquatic fern grows in shallow water in lakes and river banks on the alluvial plain and coastal swamps.

(50) *Polypodiaceoisporites* sp. Potonié 1951 ex Potonié 1956

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

Taxonomic affinity: Pteridaceae?

Genus *Clavatriletes* sp. Regali et al. 1974 (Plate IV, 6)

Remark: pollen grains of this form-genus that were not identified at species level form part of this group.

Taxonomic affinity: Sellaginellaceae?

Monoletes

(11) *Laevigatosporites catanejensis* Germeraad et al. 1968 (Plate IV, 9)

Taxonomic affinity: Blechnaceae, *Blechnum*. Ecology: freshwater fern common in marshes and swamps.

Psilamonoletes tibui Van der Hammen 1956

Verrucatosporites usmensis (Van der Hammen 1956) Germeraad et al. 1968

Taxonomic affinity: Polypodiaceae, *Stenochlaena palustris*.

Other palynomorphs

Marine palynomorphs: dinoflagellate cysts and organic inner linings of “microforaminifera” (Plate/IV,/10) aquatic elements: Chlorophyta, *Botryococcus* sp.; Pteridophyta (Salvinaceae), *Azolla* sp. (ecology: fern floating in stagnant, eutrophic or oligohaline water)

Systematics

A number of the new species recognized in the studied samples is placed within the form-genera *Psilatricolpites*, *Retitricolpites*, *Retitricolporites*, *Bombacacidites*, *Syncolporites* and *Psilastephancolporites*. The names of these taxa were originally proposed according to the concept for palynological nomenclature developed by Van der Hammen (1954a, 1956). Contrary to the provisions of the International Code of Botanical Nomenclature (ICBN), this concept allowed for a typification of taxa of fossil pollen and spores by selecting recent types. According to Jansonius and Hills (1976) such a procedure would create illegitimate names that are later synonyms of recent taxa and ought to be discarded in the classification of fossil pollen grains and spores. However, following the interpretation of the Index Nominum Genericorum

Plantarum (Farr et al., 1979) such names are invalid. Since invalid names have no status under the ICBN they can be subsequently validated. Pending a review (Van der Hammen, in prep.) of the present status of all the names proposed by Van der Hammen (1954a, 1956), it can be confidently claimed that *Psilatricolpites*, *Retitricolpites*, *Retitricolporites*, *Bombacacidites*, *Syncolporites* and *Psilastephanocolporites* have already been correctly validated by designating fossil types.

The new species were described according to their structure, sculpture, shape, size, variability of size (measured on 5 different pollen grains). The accompanying plates illustrate all holotypes and others characteristic pollen grains. The holotypes are stored at the Hugo de Vries-Laboratory of the University of Amsterdam. The following information is given for each holotype: sample location (Tres Islas etc.) followed by the sample number or depth in metres; the residue number at the Hugo de Vries-Laboratory and the location of the pollen grains on the slides. Coordinates were measured with a Leitz microscope PO 6 in the Hugo de Vries-Laboratory.

The following abbreviations have been used in the descriptions: Lg, + longitud; Lt, + transverse longitud; ex-M, + thickness of the exine. When possible, taxonomic affinities are suggested based on Germeraad et al. (1968), Lorente (1986), Dueñas (1980) and Hoorn (1993). The ecological significance of some of the present related species was indicated based on the previously mentioned authors and, in addition, Lindeman (1953), Van der Hammen (1963), Van Roosmalen (1985), Graham (1988) and Van Andel (1992) were consulted. Also a number is accompanying the taxa indicating their position in the diagram and to facilitate the comparison between the different diagrams.

Form-genus *Psilatricolporites* Van der Hammen 1956 ex Van der Hammen et Wijmstra 1964

(117) *Psilatricolpites anconis* nov. sp.

Holotype: 3 Islas 142-HdV15863; Location in slide: 98.3/46.9 (Plate IV, 4).

Derivatio nominis: named after the characteristic elbow shaped thickenings of the costae colpi.

Diagnosis: Tricolpate, psilate pollen grain. Small sized with subspheroidal shape. Radially symmetrical. Isopolar; polar area small. Columellae indistinct. Costae colpi particularly thick in equatorial area.

Dimensions: Lg, + = 20 µm; Lt, + = 17.5; ex-M, + = 1 µm.

Variability in size: Lg, + = 20–23 µm; Lt, + = 14.5–22 µm.

Taxonomic affinities: unknown.

Form-genus *Retitricolpites* Van der Hammen 1956 ex Van der Hammen et Wijmstra 1964

(8) *Retitricolpites caquetanus* nov. sp.

Holotype: Mariñame 17'91-HdV18590; Location in slide: 100.7/58.3 (Plate II, 2).

Derivatio nominis: named after the Caquetá River. Diagnosis: Tricolpate, mesoreticulate pollen grain. Medium sized with subtriangular amb. Radially symmetrical. Isopolar; polar area large. Homobrochate. Lumina 1 µm. Short colpi.

Dimension in polar view: Lt, + = 47.5 µm; ex-M, + = 1.5 µm.

Variability in size: Lt, + = 40.5–49.5 µm.

Taxonomic affinity: Bombacaceae–Tiliaceae?

Remarks: resemblance with *Bombacacidites baumfalkii* (Lorente, 1986) and *Retitricolpites lorenteae* (Hoorn, 1993). Differs from the former in size and the lack of a pronounced margo; it differs from the latter in reticulum and also the lack of a margo. Differs from *R. brevis* (Dueñas, 1980) in size and the lack of an equatorial furrow.

(66) *Retitricolpites colpiconstrictus* nov. sp.

Holotype: Mariñame 15'91-HdV18589; Location in slide: 110.9/55.4 (Plate IV, 2).

Derivatio nominis: named after the characteristic constrictions at the colpi.

Diagnosis: Tricolpate, microreticulate pollen grain. Medium sized with subprolate shape. Radially symmetrical. Isopolar; polar area medium. Tectum relatively thick, columellae very close together. Constricticolpate. Exine slightly thicker at poles.

Dimensions: Lg, + = 29.5 µm; Lt, + = 23 µm; ex-M, + = 1–2 µm.

Variability in size: Lg, + = 23–29.5 µm; Lt, + = 13–23 µm.

Taxonomic affinities: unknown.

(16) *Retitricolpites tuberosus* nov. sp.

Holotype: Apaporis 8-HdV17196; Location in slide: 94.2/53.6 (Plate II, 3).

Derivatio nominis: named after the characteristic protuberances at the pollen surface.

Diagnosis: Tricolpate, microreticulate–verrucate pollen grain. Medium sized with circular amb. Radially symmetrical. Isopolar; polar area large. Costae colpi. Verrucae $3 \times 3 \mu\text{m}$.

Size in polar view: $\text{Lt}, + = 39 \mu\text{m}$; $\text{ex-M}, + = 1.5 \mu\text{m}$.

Variability in size: $\text{Lt}, + = 33\text{--}39 \mu\text{m}$.

Taxonomic affinity: Bombacaceae–Tiliaceae?

Remarks: resembles to *R. brevis* (Dueñas, 1980) but differs from this species in sculpture, size and the lack of equatorial furrow.

(93) *Retitricolpites wijningae* nov. sp.

Holotype: Caqueta III 11-HdV15893; Location in slide: 106.5/34 (Plate II, 6).

Derivatio nominis: named in honour to the Dutch palaeobotanist Vincent Wijninga

Diagnosis: Tricolpate, mesoreticulate pollen grain. Medium sized with prolate shape. Radially symmetrical. Isopolar; polar area medium. Homobrochate, simplibaculate. Coarse reticulum, lumina $1.5 \mu\text{m}$.

Dimensions: $\text{Lg}, + = 40.5 \mu\text{m}$; $\text{Lt}, + = 27.5 \mu\text{m}$; $\text{ex-M}, + = 1.5 \mu\text{m}$.

Variability in size: $\text{Lg}, + = 36.5\text{--}42 \mu\text{m}$; $\text{Lt}, + = 26.5\text{--}31 \mu\text{m}$.

Taxonomic affinity: unknown.

Remarks: resembles *R. maturus* (González Guzmán, 1967) but differs from this species in size and reticulum.

Form-genus *Retitricolporites* Van der Hammen 1956 ex Van der Hammen et Wijmstra 1964

(69) *Retitricolporites crassopolaris* nov. sp.

Holotype: Mariñame 15'91-HdV18582; Location in slide: 98.8/53.8 (Plate III, 4 and 5).

Derivatio nominis: named after the characteristic thickening at the poles

Diagnosis: Tricolporate, microreticulate pollen grain. Medium sized with subprolate shape.

Radially symmetrical. Isopolar; polar area small. Exine thicker at poles.

Dimensions: $\text{Lg}, + = 27.5 \mu\text{m}$; $\text{Lt}, + = 22 \mu\text{m}$; $\text{ex-M}, + = 1\text{--}2 \mu\text{m}$.

Variability in size: $\text{Lg}, + = 25.5\text{--}28.5 \mu\text{m}$; $\text{Lt}, + = 22\text{--}27.5 \mu\text{m}$.

Taxonomic affinity: unknown.

(105) *Retitricolporites oblatius* nov. sp.

Holotype: 3 Islas 72-HdV15957; Location in slide: 109.7/40 (Plate III, 11 and 12).

Derivatio nominis: named after the oblate shape of the pollen grain.

Diagnosis: Tricolporate, microreticulate pollen grain. Small sized with subspheroidal shape. Radially symmetrical. Isopolar; polar area medium. Costae colpi in part prolonged around the pore. Relatively thick exine and short columellae.

Dimensions: $\text{Lg}, + = 17.5 \mu\text{m}$; $\text{Lt}, + = 20 \mu\text{m}$; $\text{ex-M}, + = 1.5 \mu\text{m}$.

Variability in size: $\text{Lg}, + = 17.5\text{--}26.5 \mu\text{m}$; $\text{Lt}, + = 20\text{--}27.5 \mu\text{m}$.

Taxonomic affinities: unknown.

Remarks: resembles slightly to *R. solimoensis* (Hoorn, 1993) but has a different wall structure and the colpi are larger and costate.

(82) *Retitricolporites poriconspectus* nov. sp.

Holotype: 3 Islas 35-HdV17193; Location in slide: 98.9/48.7 (Plate III, 17).

Derivatio nominis: named after the noticeable pori of this grain.

Diagnosis: Tricolporate, microreticulate pollen grain. Medium sized with prolate shape. Radially symmetrical. Isopolar; polar area small. Columellae indistinct. Large equidimensional pori ($5 \times 5 \mu\text{m}$).

Dimensions: $\text{Lg}, + = 29.5 \mu\text{m}$; $\text{Lt}, + = 20 \mu\text{m}$; $\text{ex-M}, + = 1 \mu\text{m}$.

Variability in size: $\text{Lg}, + = 24\text{--}29.5 \mu\text{m}$; $\text{Lt}, + = 17.5\text{--}21 \mu\text{m}$.

Taxonomic affinity: Leguminosae.

(78) *Retitricolporites pygmaeus* nov. sp.

Holotype: Mariñame 35-HdV14992; Location in slide: 98.5/57 (Plate II, 9).

Derivatio nominis: named after the small size of this pollen grain.

Diagnosis: Tricolporate, microreticulate pollen grain. Small sized with prolate shape. Radially symmetrical. Isopolar; polar area small. Columellae indistinct. Colpi transversalis ($0.5 \times 2 \mu\text{m}$).

Dimensions: Lg, + = $17.5 \mu\text{m}$; Lt, + = $13 \mu\text{m}$; ex-M, + = $1 \mu\text{m}$.

Variability in size: Lg, + = $16.5\text{--}20 \mu\text{m}$; Lt, + = $12\text{--}13 \mu\text{m}$.

Taxonomic affinity: unknown.

(89) *Retitricolporites santaisabelensis* nov. sp.

Holotype: Agua Negra 76-HdV15966; Location in slide: 111.5/44.3 (Plate III, 7 and 8).

Derivatio nominis: named after the village of Santa Isabel (Amazonas).

Diagnosis: Tricolporate, microreticulate pollen grain. Medium sized with subspheroidal shape. Radially symmetrical. Isopolar; polar area medium. Short columellae. Pori $4 \times 5 \mu\text{m}$. Costae colpi and pori.

Dimensions: Lg, + = $35 \mu\text{m}$; Lt, + = $28.5 \mu\text{m}$; ex-M, + = $1.5 \mu\text{m}$.

Variability in size: Lg, + = $29.5\text{--}38.5 \mu\text{m}$; Lt, + = $22\text{--}28.5 \mu\text{m}$.

Taxonomic affinity: unknown.

(28) *Retitricolporites wijmstrae* nov. sp.

Holotype: Mariñame 15'91-HdV18589; Location in slide: 110.8/50.4 (Plate III, 13).

Derivatio nominis: named after the Dutch palynologist Tiete Alexander Wijmstra.

Diagnosis: Tricolporate, mesoreticulate pollen grain. Medium sized with subspheroidal shape. Radially symmetrical. Isopolar; polar area small. Homobrochate, simplibaculate. Costae colpi. Very large, lalongate pores, almond shaped ($7.5 \times 5.5 \mu\text{m}$). Lumina $1 \mu\text{m}$.

Dimensions: Lg, + = $46.5 \mu\text{m}$; Lt, + = $39.5 \mu\text{m}$; ex-M, + = $2 \mu\text{m}$.

Variability in size: Lg, + = $33\text{--}46.5 \mu\text{m}$; Lt, + = $33\text{--}39.5 \mu\text{m}$.

Taxonomic affinity: unknown.

Form-genus *Bombacacidites* Couper 1960

(114) *Bombacacidites araracuarensis* nov. sp.

Holotype: Mariñame 36-HdV 14993; Location in slide: 111/56 (Plate II, 11).

Derivatio nominis: named after the village of Araracuara (Caquetá).

Diagnosis: Tricolporate, macroreticulate pollen grain. Large sized with circular amb. Radially symmetrical. Isopolar, polar area medium. Short colpi. Homobrochate, duplibaculate. Very coarse reticulum, lumina $4.5 \mu\text{m}$.

Size in polar view: Lt, + = $50 \mu\text{m}$; ex-M, + = $1 \mu\text{m}$. Variability in size: Lt, + = $50\text{--}55 \mu\text{m}$.

Taxonomic affinity: Bombacaceae, *Ceiba*. Ecology: rain and marsh forests, especially along rivers and creeks.

Form-genus *Syncolporites* Van der Hammen 1954a

(106) *Syncolporites anibalii* nov. sp.

Holotype: Mariñame 40-HdV14997; Location in slide: 103.6/49.2 (Plate IV, 8).

Derivatio nominis: named in honour to the indian guide Aníbal Matapi.

Diagnosis: Syncolporate, microreticulate pollen grain. Small sized with triangular amb. Radially symmetrical. Polar area absent. Angulaperturate. Size in polar view: Lt, + = $22 \mu\text{m}$; ex-M, + = $1 \mu\text{m}$. Variability in size: Lt, + = $22\text{--}32 \mu\text{m}$.

Taxonomic affinity: Sapindaceae.

Form-genus *Psilastephanocolporites* Leidelmeyer 1966

(116) *Psilastephanocolporites marinamensis* nov. sp.

Holotype: Apaporis 8-HdV 17196; Location in slide: 108.5/48.3 (Plate III, 6).

Derivatio nominis: named after the Mariñame island in the Caquetá River.

Diagnosis: Stephanocolporate, psilate pollen grain. Medium sized with subspheroidal shape. Radially symmetrical. Isopolar; polar area medium. Columellae indistinct. Very short, inconspicuous colpi. Pori lalongate, oval shaped (3.5×6). Exine thicker in equatorial area.

Dimensions: Lg, + = 36.5 µm; Lt, + = 31 µm; ex-M, + = 1.5–2 µm.

Variation in size: Lg, + = 31–36.5 µm; Lt, + = 22–31 µm.

Taxonomic affinity: Sapotaceae.

(102) *Psilastephanocolporites matapiorum* nov. sp.
Holotype: 3 Islas 72-HdV15957; Location in slide: 96.4/38.9 Plate (Plate II, 13).

Derivatio nominis: named after the indian Matapí community of the Miriti River area.

Diagnosis: Stephanocolporate (4 colpi), psilate pollen grain. Medium sized with prolate shape. Radially symmetrical. Isopolar; polar area small. Columellae indistinct. Costae colpi. Pori lalongate, oval shaped (6.5 × 4.5 µm). Exine slightly thicker at poles.

Dimensions: Lg, + = 39.5 µm; Lt, + = 25.5 µm; ex-M, + = 0.5–1 µm.

Variability in size: Lg, + = 37.5–42 µm; Lt, + = 22–25.5 µm.

Taxonomic affinity: unknown.

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Fig. A1. Pollen percentage diagram of well 1AS-4a-AM. (This is the correct version of Fig. 5 from the paper "Mariri and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynological study," by C. Hoorn which was published in *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 105(3/4) on pp. 273-280.)

Elements included in the pollen sum

sandy clay

clay - silt

lignite

pyrite nodules

Scale

0 100 %

* Biostratigraphical markers

— Biostratigraphical boundary

Barren interval

+ = < 0.5 % @ = reworked

te incursions
stratigraphic

Legend

- *V. usmensis*
- *P. tibui*
- Indet. Pteridophyta
- Elements of the pollen sum
- Indet. Angiospermae

lements
luded from
pollen sum