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An environmental reconstruction of the palaeo-Amazon River system (Middle–Late Miocene, NW Amazonia)

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Abstract

New sedimentological and palynological data from the Tertiary sediments in the Upper Amazon River area suggest that these sediments are fluvio-lacustrine deposits of Middle to Late Miocene age. They were generated as a result of the uplift of the Eastern Cordillera (Andes) and constitute possibly the oldest relics of the Amazon River system. The palaeoenvironment in which these sediments were deposited is characterized by extensive wetlands environments formed by swamps, shallow lakes, crevasse splay channels and crevasse-delta lakes where the channel environment is poorly represented. The palaeovegetation was dominated by palms (e.g. *Mauritia* and *Grimsdalea*), riverine taxa (e.g. Bombacaceae, *Amanoa* and *Alchornea*), ferns and fern allies (e.g. Polypodiaceae and Selaginellaceae), floating meadows (Gramineae) and aquatic taxa (*Ceratopteris*, *Botryococcus* and *Azolla*). The relative abundance of Gramineae and the occurrence of Andean-type pollen taxa is related to the Andean origin of the fluvial system. The *varzeas* of the present Upper Amazon River flood-basin are probably the best analogue for the Middle to Late Miocene environment.

Intervals rich in marine palynomorphs, mangrove pollen, brackish tolerant molluscs and ostracods, and ichnofossils of the *Thalassinoides*–*Teichichnus* association suggest that the palaeoenvironment was characterized by brackish conditions and marine influence. These marine incursions are possibly related to the Langhian and the Serravallian global sea-level rise. Although in the Middle Miocene a global cooling is known to have occurred, no indicators of a cooler climate have been observed in the Miocene palynoflora of the Upper Amazon River area.

Finally, four new sporomorph species are described belonging to the form-genera *Psilatrilletes*, *Clavinaaperturites* and *Psilaperiporites*.

1. Introduction

The first indirect reference to the Miocene origin of the Amazon River system was made by Damuth and Kumar (1975) who estimated that the initiation of the Amazon Cone occurred between the Middle to Late Miocene. Campbell (1992) suggested that the Amazon River system fully evolved

as a transcontinental drainage system from Late Miocene time onwards when clastic detritus reached the Amazon Shelf covering the pre-existing carbonate platform. A first insight into the Miocene terrestrial record of NW Amazonia was provided by data from wells drilled when the coal potential of the Solimões Formation was being explored by the *Companhia de Pesquisas de Recursos Minerais* (CPRM) (Maia et al., 1977). Based on a study of well 1AS-4a-AM it has been showed that between the Early and Middle Miocene large geographical and environmental

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changes occurred in NW Amazonia. These changes were related to the genesis of the Andean river types and were caused by tectonic activity in the Eastern Cordillera (Hoorn, 1993a).

New sedimentological and palynological data of Middle to Late Miocene fluvio-lacustrine sediments from the Upper Amazon River area (Fig. 1) make possible a more detailed reconstruction of the history of the Amazon River system. Miocene sediments possibly represent the oldest deposits of Andean origin that are preserved in NW Amazonia and give an insight into the history of one of the worlds largest river systems. Furthermore, the palynological data allow us to reconstruct the vegetation history and to compare it with the present-day vegetation of the area.

The Middle to Late Miocene sediments extend over thousands of square kilometres (Fig. 1) and

will be referred to as Solimões/Pebas Formation since both names are currently used in Brazil and Peru/Colombia, respectively. The origin of these names is further explained in the section that deals with the Solimões/Pebas Formation. This paper will focus on the Colombian Amazonas Basin and the northeastern part of Peru, and the relation with the Solimões Basin (Brazil).

Many authors have written about the Tertiary sediments of Amazonia although most of the early studies were focused exclusively on mollusc taxonomy (Orton, 1867; Boettger, 1878; Steinmann, 1930; Katzer, 1903; Ruegg and Rozenzweig, 1949; De Greve, 1938; Nuttall, 1990). The first large-scale studies on the sediments of the Amazonian Tertiary were carried out in Brazil during the seventies by CPRM (Maia et al., 1977). Other detailed information was generated during explo-

Fig. 1. Generalized map showing the distribution of the Solimões/Pebas Formation and the study area. Basins: P=Putumayo, N=Napo, M=Marañon, CA=Colombian Amazonas, BA=Brazilian Amazonas, S=Solimões, A=Acre, U=Ucayali. MD=Madre de Dios. Arches: v=Vaupes, i=Iquitos, sm=Sierra do Moa, f=Fitzcarraldo, c=Caravari, p=Purus, ma=Monte Alegre, g=Garupa (modified after Räsänen et al., 1987).

ration studies by *Petrobras* and the large-scale governmental initiative *Radambrasil* (1977). At the same time, a multidisciplinary exploration study took place in Colombia (Proradam, 1979). However, no conclusive data were provided about the Tertiary depositional history of NW Amazonia. The present study forms part of a multidisciplinary project that was initiated in 1988 by *Tropenbos-Colombia* in Colombian Amazonia.

2. Geography

The study area forms part of the Amazon River drainage basin (Fig. 1). This is a highly dynamic area where tectonic perturbation of fluvial systems has taken place during Tertiary and Quaternary time, and still determines fluvial and lake patterns today (Salo et al., 1986; Räsänen et al., 1987; Dumont, 1992, 1993). An overview of the characteristics of the Amazon River system is given by Sioli (1984). The Amazon River flows eastwards, a few degrees south of the Equator and drains $7.05 \times 10^6 \text{ km}^2$ from which $5 \times 10^6 \text{ km}^2$ is covered by rain forest.

At present three river types are distinguished in Amazonia: the Andean 'white' water rivers, and the Amazonian 'clear' water and 'black' water rivers. The Andean rivers have a high pH, high suspended load and the catchment area is the Andean region. The 'clear' and 'black' water rivers have varying pH, a high bedload and drain the shield area (Sioli, 1984). Gibbs (1967) concluded that the Andean mountain environment controls the major part of the geochemistry of the Amazon River. Landim et al. (1983) and Franzinelli and Potter (1983) suggest that in the upper Amazon the sediments are dominated by unstable minerals, reflecting a purely Andean origin. In the lower Amazon, an increased maturity and a predominance of stable mineral content was observed due to the effects of tropical weathering and the admixing of sediments eroded from the Precambrian shields in Amazonia.

In the central part of the drainage basin, the Amazon River has an anastomosing pattern with an abundance of fluvial islands (Kalliola et al., 1992). In summer large channel bars are exposed.

These bars are composed of mainly pebbles and sand, but also include locally fossils, and coal blocks (e.g. Aramaça, Fig. 2). The pebbles are reworked from Pleistocene deposits, whereas the fossils and coal blocks are reworked from the Solimões/Pebas Formation.

Two main landscape units are distinguished: *terra firme*, land never flooded and the *varzea*, land permanently or temporarily flooded. *Igapos* are the flood-basin environments of the black and clear water rivers. The *varzea* covers around 5 to $6 \times 10^4 \text{ km}^2$ and is characterized by numerous lakes of riverine origin. Little deltas are formed within these lakes. Sediments are distributed by secondary channels of the Amazon River during stages of high discharge. Nutrients transported by this Andean river enrich the *varzea* environment and hypoxic conditions can result. The *varzea* is characterized by floating meadows, swamps and flood-basin forest. The Amazon River estuary is funnel shaped and the tidal influence reaches about 100 km inland (Sioli, 1984). No true delta has developed at the Amazon River mouth due to the Brazilian Current which drags the sediments northwards along the Atlantic coast. All these features of the present Amazon River system are important in interpreting the Miocene sediments of Amazonia since these were largely deposited by the ancestral Amazon River.

The main geologic units that dominate the landscape are the Precambrian basement, the Miocene Solimões/Pebas Formation, and fluvial terraces produced by the river system that dissects the aforementioned units. The terrace sediments are of Plio(?)–Pleistocene age and are partly composed of sands and gravels of Andean origin (Van der Hammen et al., 1992). The Miocene unit forms a gentle, hilly landscape. The Precambrian basement forms also gentle but larger hills, and where it crops out in the river it causes rapids (e.g. near La Pedrera, Fig. 2).

The best season for studying the outcrops of the Solimões/Pebas Formation along the Upper Amazon River (Fig. 2) is between September and November. The water level is then at its lowest which is about 20 m below the highest water level. Differences between high and low water stands tend to diminish eastwards (Sioli, 1984). Along

Fig. 2. Detailed map of the study area with the location of the sections and main outcrops.

the Caquetá River, however, best season for studying the outcrops is between January and March. At the outcrops care has to be taken with the phenomenon of the *terras caídas*. These are slices of outcrop that fall off, especially along the outer bends of the river, due to the action of the river waters and heavy rains. The outcrops of the Solimões/Pebas Formation locally have 'salt licks'. These are places where animals of the rain forest (e.g. monkeys, tapirs, rodents) lick the sediment to obtain mineral nutrients. It has been shown

that at the 'salt licks' the sediment is enriched in Ca, P, Mg, Na, K and Cl (Lips and Duivenvoorden, 1991).

3. Geological background

The sediments of the Solimões/Pebas Formation are part of the infill of several sedimentary basins. In Brazil the Solimões Formation is known from the Acre (foreland) Basin and the intracratonic

Solimões and Brazilian Amazonas Basins. In the latter it only appears in the most western edge of the basin. In Peru the Pebas formation occurs in the northeast of the country and in the Marañon and Madre de Dios (foreland) Basins (Guizado, 1975; Kronberg et al., 1989; W. Morales, pers. commun., 1992). Whether it occurs also in the Ucayali (foreland) Basin remains speculative. In Colombia the Pebas formation and its equivalent the La Tagua beds (Eden et al., 1982) form part of the intracratonic Colombian Amazonas Basin and the Putumayo (foreland) Basin.

The intracratonic basins are situated in and around the graben that subdivides the Amazon Craton into the Guyana Shield and the Brazilian Shield (Fig. 1). This graben is located along the Solimões megashear. The megashear divides the continent E–W from coast to coast and is of the transcurrent fault type (De Loczy, 1966; Grabert, 1983, 1991; Caputo, 1991). The intracratonic basins are subdivided and separated from the Andean foreland basins by structural highs in the basement (Fig. 1) which are the result of flexural lithospheric uplift in response to orogenic loading of the Andean belt (e.g., Iquitos Arch, Caputo, 1991). The earliest known uplift of the Andean belt occurred in the Paleocene (Van der Hammen, 1961; Kroonenberg et al., 1990; Sarmiento, 1993) and has continued since then with a climax during the Pliocene (Van der Hammen et al., 1973).

At outcrops the beds of the Solimões/Pebas Formation present gentle dips which are due to post-Miocene tectonics in the area.

4. The Solimões/Pebas Formation

The Solimões Formation was described in Brazil by Moraes Rego (1930; validated by Caputo et al., 1971) and the type locality is situated along the Solimões River. In Peru the name Pebas beds was first introduced in the 19th century. At a later stage it was named Pebas formation although a formal description is lacking. Gabb (1869), Orton (1876), Katzer (1903), Steinmann (1930), De Gréve (1938), Ruegg and Rosenzweig (1949), Sanz (1974), Pardo and Zúñiga (1976), Costa (1980, 1981) and Nuttall (1990) among others, make

reference to the Pebas beds or formation. The name is derived from the village Pevas situated along the Amazon River. It has been proposed that in Colombian Amazonia the names Pebas formation (Khobzi et al., 1980; Hoorn, 1990) and Mariñame sand unit (Hoorn, 1994) should be used where previously Galvis et al. (1979) suggested the name “Amazonian Tertiary”.

In Brazil the estimated maximum thickness of the Solimões Formation is 980 m (Maia et al., 1977). At the base the Solimões Formation contacts the Ramón Formation. This contact is a gradual transition from a reddish clay- and sand-dominated lithology (Ramón Formation) into finer clastics with a variety of colours (Solimões Formation). The top of the Solimões Formation is overlaid unconformably by the Pleistocene Içá Formation which consists mainly of sands and conglomerates (Maia et al., 1977). In the north the Solimões Formation onlaps on the basement and decreases in thickness from SW to NE.

Neither in Colombia nor Peru do precise data exist concerning the thickness and lower and upper contacts of the Pebas formation. However, a thickness of 200 and 600 m was suggested by Guizado (1975). The Pebas formation is overlaid by the Ipururo formation consisting mainly of sands and conglomerates and at the base it overlies the Chambira formation consisting of clay, sand and evaporites (Guizado, 1975).

The basal part of the Solimões Formation correlates with the Mariñame sand unit, whereas the upper part correlates with the Pebas formation (Fig. 3). Here the notion Solimões/Pebas Formation is applied in each of the three countries since the sediments of all the studied outcrops belong to the Pebas formation or upper part of the Solimões Formation.

The most significant outcrops of the Solimões/Pebas Formation are situated along the Upper Amazon River (e.g. Santa Sofia, Figs. 4 and 7) although in general they do not exceed heights of 30 m. Other localities where the formation crops out are situated along the Putumayo River (e.g. Arica and Indostan, J.V. Galvis, pers. commun., 1989) and along the Caqueta River (Puerto Remanso and Puerto Caimán). A stratigraphic

Fig. 3. Age, zones, formations and correlation between the different sections.

correlation between the field sections and well 1AS-4a-AM and is presented in Fig. 3.

In the study area the formation is characterized by blue-, turquoise- and olive-coloured clay and silty/sandy clay with fine-grained sand, lignite and black-grey clay intercalations. Noticeable is the abundance of molluscs, plant and vertebrates remains, purple mottling and bioturbation in the sediments. Dark-red clay intraclasts indicate reworking of oxidized material. The prevailing dark colours together with the preservation of the organic matter of plant and animal origin suggest anaerobic conditions and a high water table during deposition. However, periods of exposure also existed, as evidenced by mottling and bioturbation in lignites and dark clays. No red colours were observed in the outcrops of the study area although reddish sediments are known from the lower parts of the formation (Maia et al., 1977; Hoorn, 1993a).

Calcium-carbonate concretions and locally septarian nodules form the only solid rocks among the otherwise unconsolidated sediments. The local population uses these rocks for building since it is the only type of "hard rock" that is available in the area.

As will be supported below, the sediments of the Solimões/Pebas Formation are the result of dynamic environment of shallow lakes and swamps fed and interconnected by a fluvial system of Andean origin with episodic marine influence.

4.1. Lithofacies and sedimentary environments (Figs. 6–8)

A detailed overview of the lithology, sedimentary structures, bedding types and the depositional environments of the Solimões/Pebas

Fig. 4. Overview of the Santa Sofia section.

Formation is given below, accompanied by illustrations of some selected sections (Figs. 6–8).

(a) Channel/bank deposits

Sand bar deposits and crevasse splay channel deposits: The sand fraction represents only 5 to 15% of the total sediment composition in all described sections. The sandy sequences consist of yellow-brown, well sorted, fine and very fine-grained sand beds of several decimetres up to several metres in thickness. These sands have a clayey matrix. Sedimentary structures such as small and normal scale cross-bedding (Guanabara, 0–5.6 m, Fig. 8; Sta. Sofia, 15.0–15.4 m, Fig. 7), climbing ripples (Sururua, 3.2–4.4 m, Fig. 8) and flaser bedding (Indiana, 9.0–10.5 m, Fig. 6) were observed. In the rose diagrams in Fig. 9 measurements of the cross-bedding structures

of the Solimões/Pebas Formation (Middle–Late Miocene) are represented and show a predominantly eastward transport direction. This figure also shows a comparison with measurements made in the Mariñame sand unit (Early Miocene–early Middle Miocene) where transport directions were mainly northwestwards. It is clear that a drastic change in transport directions took place between the Early and Middle Miocene. The explanation for this is the incipient uplift of the Eastern Cordillera and a subsequent change in source area.

In Table 1 the heavy mineral suite of various sand samples is represented. The Middle to Late Miocene assemblage is dominated by unstable components such as garnet, chloritoid and epidote. These minerals are derived from rocks metamorphosed in the greenschist facies and considered to be of Andean origin (Hoorn, 1993a). This is in agreement with the results of Kronberg et al.

Fig. 5. Placer bone-beds, Los Chorros section.

(1989) who suggested (based on a geochemical study), that at least part of the sediments of the Solimões Formation had an Andean origin.

The southernmost sections (Benjamin Constant, Guanabara, and Sururua, Fig. 8) show the highest sand content. The base of the Guanabara section represents a series of sand bar deposits which are possibly within the realm of the main fluvial channel. Sandy sequences interbedded with clays (Santa Sofia, Fig. 7) or beds showing climbing ripples (Sururua, Fig. 8) are likely to be related to a crevasse splay channel environment. These crevasses broke into the flood-basin during high water. Flaser bedding such as in the Indiana section suggest tidal influence although no other tidal features such as herring-bone structures and double mud drapes were found.

(b) Flood-basin deposits

Shallow lake and crevasse-delta lake deposits: Blue-, turquoise- and olive-coloured sandy clay and clay represent the dominant lithology of the Solimões/Pebas Formation in the study area. These clays often contain millimetre-sized, organic or coaly fragments. Pyrite, vivianite crystals and gypsum are locally found scattered throughout the sediments. The gypsum is probably related to pyrite oxidation and subsequent reaction with Ca from carbonates. During palynological analysis it was noticed that the sandy clay and clay samples are relatively rich in Andean-type pollen taxa.

Planar, interlayered, and lenticular bedding types are common. Sediments and structures have locally been disturbed by loading, bioturbation,

Fig. 6. Lithostratigraphy of the Peruvian sections.

Fig. 7. Lithostratigraphy of the Colombian sections.

rooting and mottling due to pedogenic processes. Small nodular, carbonate fragments (<0.5 cm in diameter) accompany some of the mottled beds. The interlayered bedding presents a rhythmic alternation of sand/clays and/or organic matter (e.g. Santa Teresa 2.5–4.9 m; Los Chorros II, 14.3–18.1 m; Figs. 6 and 7) suggesting a cyclic deposition of tidal origin. The beds alternate at millimetre or centimetre scale and usually have a regular, non-erosional base; however, at Pijuayal (Fig. 6) lenticular shaped sediment bodies have been observed. The occurrence of lenticular and wavy bedding types could well be related to tidal

influence since periods of marine influence are known for the Miocene of Amazonia (Hoorn, 1993a,b). Moreover, mangrove pollen, brackish fauna (molluscs, ostracods, microforaminifera and dinoflagellate cysts) and trace fossils characteristic of the coastal realm occur in these sequences.

The sandy clay sequences with planar and lenticular bedding were deposited in shallow lakes in a flood-basin environment which received clastic fluvial input of Andean origin. These sediments were supplied to the lakes along crevasse splays. From time to time these lakes dried up and the sediments were exposed to pedogenesis. These pro-

Fig. 8. Lithostratigraphy of the Brazilian sections.

cesses still occurs in the present *varzea* lakes of the Amazon River system, although the brackwater aspect is lacking.

Backswamp deposits: Lignite and black, brown and grey, organic-rich clay are common in almost all the sections and occur as single beds or as a lignite–clay alternation (Pijuyal 3.8–7.5 m; Santa Sofia, 18.8–21.0 m; Mocagua, 23.9–24.8 m; Figs. 6 and 7). The lignite varies between several centimetres to a maximum of 1 m in thickness, but most common are beds of 0.5 m whereas the dark-coloured, organic-rich clay reaches thicknesses of 3 m (Indiana, 3.3–6.3 m, Fig. 6). Most of the palynological samples were taken from these lithologies.

The lignite is usually composed of fine organic material with a high content of sulphur and ashes (Maia et al., 1977). However, large botanical

remains were also found at Puerto Nariño and Paumari where large fossil tree trunks of several metres in length lay in the bedding plane. Leaves, stalks, seeds and vertebrate remains are also found in these beds. The lignite and the dark-coloured clay beds have regular, non-erosional bases and are sometimes laterally continuous for several hundreds of metres (e.g. Los Chorros and Pijuyal). In the aforementioned lithologies thin lenticular, light-coloured clay bodies occur which were formed during fluvial floodings.

These deposits originated in swamp and drowned swamp environments of the flood-basin which are occasionally incised by shallow swamp channels. Biogenic fragments of local origin accumulated in these environments although during floodings part of these organic deposits were eroded and redeposited elsewhere

Mariñame sand unit
(Early to early Middle Miocene)
 Mariñame & Tres Islas (Colombia)

Paleocurrent directions
 89 n
 15° interval
 radius = 25%
 frequency scaling

Solimões/Pebas Formation
(Middle to Late Miocene)

Pevas & Iquitos (Peru); Mocagua & Santa Sofia (Colombia);
 Guanabara, Sururua & Benjamin Constant (Brazil)

Paleocurrent directions
 41 n
 15° interval
 radius = 25%
 frequency scaling

Fig. 9. Rose diagram showing palaeocurrent directions measured in the Mariñame sand unit and the Solimões/Pebas Formation.

Swamp channel and crevasse splay channel deposits: Lenticular sediment bodies composed of sandy, dark-coloured, organic-rich clay or lignite, accompanied by reddish clay intraclasts, coprolites and large fossil fragments, are a noticeable feature. These sediment bodies contain at some places large vertebrate remains (Los Chorros I E, 15.0–15.4 m, Fig. 5; Santa Sofia 14.5–14.8 m, Fig. 7) and/or molluscs, Mocagua (23.9–24.8 m). The thickness of these intervals varies but does not usually exceed 0.5 m. Aepler and Reif (1971) refer to this kind of deposit as placer bone beds. The placer bone beds in the Solimões/Pebas Formation are thought to have been formed as lag deposits in a swamp and crevasse splay channel environment on the flood-basin during floods. In these channels all sorts of biogenic remains of the flood-basin accumulated, and were mixed with other sediment. A

local origin is inferred from the good preservation of these remains.

(c) Diagenetic products

Concretions, nodules and concretionary layers: Carbonate concretions are often the most obvious diagenetic feature in the mudstone and contain important information about the diagenetic evolution of the surrounding mudstone (Astin and Scotchman, 1988). In the study area concretions (regular shape), nodules (irregular shape) and concretionary layers were observed in most of the sections. The concretions and nodules are single, ellipsoidal bodies that vary from a few centimetres up to 1 × 0.5 m in diameter. The concretionary layers, instead, have a regular or intermittent character and follow bedding planes over several tens

Table 1
Heavy mineral composition of the Solimões/Pebas Formation (per cent of transparent heavy minerals based on counting an average of 300 grains per slide, excluding the opaques)

Location	Samples	opaque	Transparent heavy minerals (%)																
			tourmaline	zircon	garnet	rutile	anatase	staurolite	disthene	andalucite	chloritoid	epidote	aggregates	gr. hornbl.	pl. hornbl.	muscovite	chloritic matter	apatite	biotite
Pebas	P 1	47	1	9	6	-	3	-	-	-	72	4	-	-	-	-	1	1	2
	P 2	59	1	7	8	-	3	-	-	-	64	15	-	-	-	-	9	-	-
Chorros I W	LC 1	5	1	1	2	-	6	-	-	-	3	66	12	-	-	-	12	-	-
	LC 2	6	2	-	2	-	8	-	-	-	5	62	9	-	-	-	12	-	-
	LC 3	13	2	3	5	-	3	-	-	-	3	64	8	-	-	-	12	-	-
	LC 4	9	2	-	3	-	4	-	-	-	6	71	8	-	-	-	7	-	-
Chorros I E	LC 5	12	2	-	2	-	6	-	-	-	6	64	10	-	-	-	10	-	-
	LC 6	16	2	2	4	-	7	-	-	-	11	58	12	-	-	-	4	-	-
	LC 7	12	1	-	3	-	8	-	-	-	6	65	12	-	-	-	4	-	-
	LC 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	LC 9	9	2	2	3	-	6	-	-	-	7	60	11	-	-	7	2	-	-
	LC 10	18	1	-	4	-	5	-	-	-	6	66	8	-	-	2	7	-	-
Macedonia	M 1	10	4	-	-	-	3	-	-	-	4	84	5	-	2	-	-	-	-
	M 2	23	4	-	2	-	3	-	-	-	2	82	6	-	-	1	-	-	-
Sita Sofia	SS 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SS 2	6	-	1	4	-	6	-	-	-	6	68	8	-	-	-	6	-	-
B. Constant	BC 1	48	1	4	-	-	2	1	-	-	61	4	1	-	-	-	22	-	6
	BC 2	57	7	5	2	-	3	1	1	1	2	68	7	1	-	-	3	-	-
Sururua	S 1	6	2	2	8	-	-	-	-	-	5	75	8	-	-	-	1	1	1
	S 2	9	3	2	6	-	2	-	-	-	7	72	9	1	-	-	6	-	-
	S 3	11	-	2	10	-	1	-	1	-	6	70	6	-	-	-	1	2	1
	S 4	41	4	3	1	2	3	2	1	1	3	71	5	1	-	-	1	-	1
	S 5	16	3	2	8	-	2	-	-	-	8	62	9	2	-	-	4	-	-

of metres. These layers occur sometimes in rhythmic alternations (Chorros I W, 12.4–14.5 m, Fig. 7) or as lateral accretion beds such as at Benjamin Constant (a, 4–6 m, Fig. 8). At some places large-sized, septarian concretions also were found (e.g. Macedonia).

In general blue-grey colours prevail and the granulometry of the concretion or nodule ranges from clay to fine-grained sandy clay. Partially dissolved shell nuclei and sedimentary structures are occasionally preserved. The preservation of sedimentary structures in the concretions and the irregular pattern of concretionary layers suggest that these are secondary, diagenetic features. These concretions were never found in lag deposits where other intraclasts of this formation have been preserved, which suggests this is not a syn-sedimentary phenomenon.

The concretions have a calcium carbonate composition whereas the nodules of orange-brown colours are sideritic. The presence of siderite-like nodules suggests that at some stages iron reduction exceeded the sulphate reduction and the available iron could not be precipitated as FeS or pyrite (Pye et al., 1990 citing Curtis and Spears, 1968). Sandy clay can occasionally be cemented without necessarily being a concretionary layer. The abundance of calcium carbonate concretions can be explained by the abundance of carbonate available in the environment. The source of calcium is provided by dissolution of the shells in an acidic environment. The large amounts of humic acids from the surrounding swamps and forest are introduced in the aquatic environment and are responsible for the low pH that causes dissolution of the calcium.

5. Palaeontology

A special section is devoted here to the abundant occurrences of fossils other than spores and pollen in the Solimões/Pebas Formation. Although they do not form the main subject of this paper, their environmental and palaeogeographical implications are relevant to the general interpretation and are therefore reviewed.

5.1. Foraminifera

A monospecific assemblage of foraminifera was observed in a thin interval at Buenos Aires. These specimens were classified as *Protoelphidium* (S.R. Troelstra, pers. commun., 1993) and are indicative of low salinity conditions such as occur in estuarine systems. In these samples some reworked Eocene specimens were also observed. During the palynological study five different types of foraminiferal organic linings (Plate III) were observed in thin (10–15 cm) intervals of the Los Chorros and Mocagua sections. These linings show a resemblance to *Trochammina* (S.R. Troelstra, pers. commun., 1993), *Ammodiscus* and *Haplophragmoides* (H. Duque, pers. commun., 1993). However, in the inorganic fraction no trace of these genera was found. This is probably due to the fact that these genera are agglutinants which disintegrate easily leaving only the organic wall. *Trochammina* and *Haplophragmoides* are typical saltmarsh species. It is thought that the intervals of microforaminifera represent tempestites (i.e. storm deposits; Seilacher, 1982) and are related to marine incursions.

5.2. Ostracods

Ostracods are very abundant in the Solimões/Pebas Formation. Studies of these ostracods were carried out by Purper (1977), Purper and Pinto (1985), and Sheppard and Bate (1980). They suggest that the ostracod fauna indicates brackish as well as freshwater conditions. During the present study samples of ostracods were collected; D. van Harten (pers. commun., 1993) observed that the taxonomic diversity of the assemblage is low and that the abundance of specimens is high suggesting rather extreme conditions. The most common genus is *Cyprideis* which is indicative of an anomalo-haline environment. However, freshwater taxa also are present.

5.3. Molluscs

Molluscs (lamellibranchs, gastropods) are the most common type of macrofossils in the Solimões/Pebas Formation. They are very well

preserved and the bivalves often have their two valves still together indicating an in situ position. In other cases the molluscs have been transported and form part of the channel deposits. The molluscs occur in varying densities in the sediment, concentrated in beds or in lenticular bodies (0.5 m thick) with erosional bases, or as patches in clay, sandy clay and lignite. At Indiana they form cross-bedded layers in a black clay interval. They also can be mixed up in the sediment due to bioturbation.

An extensive compilation of the molluscs of the Pebas formation was presented by Nuttall (1990). More recently Wesselingh (1993) completed a study on the molluscs of the Los Chorrros sections. He also analyzed ^{13}C and ^{18}O ratios of some selected genera. Four ecological assemblages were distinguished: (1) a perimarine assemblage indicative of brachyhaline conditions (e.g., *Cymia*, *Nassarius*, *Corbula* and ?*Chrysallida*); (2) a fluvial assemblage dominated by large species, possibly tolerant to some degree of brackishness (e.g., *Dyris ortonii*, *Tryonia minuscula scalaroides*, *Aylacostoma browni* and *Anadontites*); (3) a lacustrine assemblage dominated by small species (e.g., *Dyris*, *Toxosoma eborea*, *Vitrinella*, *Pachydon*, *Pachydon trigonalis*, *Pebasia dispar*, *Ostomya papyria* and ?*Raetoma*) where true fresh water taxa such as *Sphaerium* are absent; and (4) a terrestrial assemblage composed of land snails (*Strophocheilus* and *Orthalicus*) and the amphibious genus *Asolene*. Assemblages 2 and 3 are the most common ones.

Nuttall (1990), pointed out that the presence of the genus *Pachydon* is a strong indication of a N to S migration of this genus, which is known to be endemic in the Neogene of NW South America. This supports the hypothesis that a marine incursion with an entrance from the Caribbean affected the study area (Hoorn, 1993a, 1994). Wesselingh (1993) additionally proposes a migration of Andean genera into the Amazon Basin and, as a possible third migration process, dispersion due to birdtrekking.

5.4. Other macrofossils

Large macrofossils of plant and animal origin are well preserved in most of the sections. At

Paumari and Puerto Nariño large tree trunks occur in the bedding plane of lignite layers. Plant remains such as seeds and leaves locally form part of swamp deposits. Most remarkable are the large vertebrate remains found in the swamp, swamp channel and crevasse splay channel deposits (Fig. 5). Among the vertebrate remains are fragments of crocodile, fish, tortoise, bird, and various others. Fish remains of the Carcharinidae (blue shark), Myliobatidae (sting ray), Callichthyidae (armored catfish), Chimaeridae (chimera), Sciaenidae (drums), Anastomidae, Erythrinidae, Serrasalminidae, and Characidae were identified (H. Nijssen and K. Monsch, pers. commun., 1993).

The fragmentary but well preserved character of the macrofossils suggests a short transport distance. Reworked Miocene fossils presently are accumulating on the channel bars of the Amazon River. Various studies on the vertebrate fossils of the Solimões Formation in the Acre region were presented by Frailey (1986), Bocquentin et al. (1989), Pereira and Bocquentin (1989), Bocquentin and Rodrigues (1989), and Campbell and Frailey (1991).

5.5. Ichnofossils

Two kinds of ichnofossils were observed: bioturbation by burrowing fauna and coprolites of various sizes. Most common is bioturbation of the *Thalassinoides*–*Teichichnus* association (?? Mangano and G. Buatois, pers. commun., 1993), indicating a brackish environment with marine influence. *Thalassinoides* is characterized by large, interconnected burrows (ca. 1 cm wide–15 cm long) of irregular shape which occur in organic-rich, black clay or lignite beds up to 1 m thick and are visible because of the turquoise blue clay that fills the burrows (Fig. 10). Crab fragments are present in some burrows. Mollusc beds and sedimentary structures have often been disturbed by bioturbation characterized by single, non-connected burrows. Coprolites with sizes of approximately 1 × 5 cm were found in the placer bone-beds. Less common are the clusters of small pellets of approximately 1 mm in diameter found

Fig. 10. Ichnofossils (*Thalassinoides* type), Los Chorros section.

in some of the clayey intervals (e.g., at Puerto Remanso).

6. Palynology

The abundance of organic-rich lithologies in the Solimões/Pebas Formation permitted a thorough palynological analysis, allowing the age of the sediments to be established, and providing an insight into the palaeovegetation of Miocene Amazonia. The palynological results are presented in 7 pollen percentage diagrams (Figs. 11 and 12a,b) which are subdivided into 8 ecological zones (A–H) based on the occurrence of ecologically significant taxa. A total 149 taxa were determined; full names, taxonomic affinities and the ecological significance of these taxa are presented in the systematic part. Each diagram is accompanied by a cumulative diagram representing the total sporo-

morph content counted per sample. These cumulative diagrams show the relation of the pollen sum with *Psilamonoletes tibui* and *Verrucatosporites usmensis* (rather common spores) and the indetermined Pteridophyta and Angiosperms. The sections presented here are dated using the biostratigraphical markers and zones presented in Hoorn (1993a). These pollen zones relate to the earlier defined Miocene zones in the Venezuelan basins (Lorente, 1986) with ages based on the Caribbean foraminifera zonations (Germeraad et al., 1968).

6.1. Materials and methods

In total 118 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 are treated with sodium pyrophosphate

Included in pollen sum ($\Sigma 100$)

[illegible]

Excluded from pollen

anbos
Bombacacidites spp.*
E. maristellae*
Verrucatosporites sp.-*Verruiletes* sp.
R. alsyae*
Cyperaceapollis sp.*

M. mulleri*
S. porcosatus*
P. vermicosus*
P. minutus
R. leticianus
C. microclavatus*
P. normalis
P. cyamus
Ssp.
redundans
E. cf. muelleri
Bacuriletes sp.*
R. poncospectus
B. muinaneorum*
Bacuricolpites sp.
R. dubiosus
P. marginalis
E. fenzenii
R. simplex*
Polauricolpites spp.*
P. dilatatus*
R. kaarsii*
E. barbeitoensis*
Pterip. minutus*
R. lewisii
R. medius
E. spinosus*
R. ante
Pr

from pollen sum

- Key**
- V. usmensis*
  - P. tibui*
  - Indet. Pteridophyta
  - Pollen sum
  - Indet. Angiosperms

ed

um

Fig. 12. (a) Pollen percentage diagrams of the Colombian sections.

finity

Included in pollen sum ($\Sigma 100$)

V. usmensis

P. tibui

Indet. Pteridophyta

Pollen sum

Indet. Angiosperms

Fig. 12. (b) Continued.

v = no samples   + = < 0.5 %   * = known taxonomic affinity

∅ = no samples   + = < 0.5 %   * = known taxonomic affinity

Included in pollen sum (Σ 100%)

oris sp.

Key

- *V. usmensis*
- *P. tibui*
- Indet. Pteridophyta
- Pollen sum
- Indet. Angiosperms

($\text{Na}_4\text{P}_2\text{O}_7 \cdot 10\text{H}_2\text{O}$) in a 10% solution with H_2O and lignites are oxidized with Schulze mixture (2HNO_3 , 60% KClO_3 , 7%). Finally, bromoform with density 2.0 g/cm^3 was used to separate the inorganic fraction. 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. Twenty four samples were barren or gave a sum lower than 100 specimens. The data were stored and processed in a spreadsheet programme (Excel 3.0™) and classified with TWINSPAN (Two-way indicator species analysis; Hill, 1979). The pollen percentage diagrams were constructed with 'Pollen diagram', created by J.J. Duivenvoorden at the Hugo de Vries-Laboratory, in combination with the drawing programme Macdraw II™.

The classification program TWINSPAN was used to group ecologically similar species together. A particular ordering was chosen for each of the two main biostratigraphic zones (the *Psiladi-porites/Crototricolpites* and *Crassoretitritiles* Zones considered as one zone). 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; Hoorn, 1994). 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. This matrix was used to arrange the individual curves in the diagrams, and as a base for ecological zonation.

6.2. Age (Fig. 3)

The Santa Teresa section belongs to the *Psiladi-porites/Crototricolpites* Zone (Early Miocene–early Middle Miocene) based on the presence of *Proxapertites tertiaria*, *Crototricolpites annemariae* and *Retimonocolpites absyae*. Species indicative of a younger age such as *Crassoretitritiles vanraadshoovenii*, *Grimsdalea magnaclavata* and an acme of Compositae (*Echitricolporites spinosus*) are absent. Neither are there indications for an older age such as a *Retricolporites guianensis* Acme or the presence of *Verrutricolporites rotundiporus* and *Cicatricosisporites dorongensis*. However, in the

biostratigraphical zonation of the Solimões Basin (Hoorn, 1993) it was shown that in the *Crassoretitritiles* Zone (Middle Miocene) there is an interval where *Crassoretitritiles vanraadshoovenii* is absent. It is possible that Santa Teresa belongs to this interval of the Middle Miocene zone. Additionally, the presence of biostratigraphical markers was checked in samples from La Tagua, San Vicente del Caguán (Putumayo Basin) and Indiana. Only one marker species of the *Psiladi-porites–Crototricolpites* Assemblage Zone was found. This indicates that an age of Early Miocene to early Middle Miocene is most likely for these samples.

The Iquitos and Pevas sections belong to the *Crassoretitritiles* Zone (Middle Miocene). This age is based on the presence of *Crassoretitritiles vanraadshoovenii* and the absence of *Grimsdalea magnaclavata* and other younger pollen marker species.

The Los Chorros, Mocagua and Santa Sofia sections belong to the *Grimsdalea* Zone (Middle–Late Miocene) because of the presence of *Grimsdalea magnaclavata* and *Crassoretitritiles vanraadshoovenii*. The absence of an *Echitricolporites spinosus* Acme and other marker species such as *Alnipollenites verus* and *Fenestrites spinosus* excludes a younger age. For samples of the Puerto Caimán section a similar age is suggested.

6.3. Description of the pollen percentage diagrams (Figs. 11 and 12a,b)

Eight ecological zones (A–H) were differentiated, and their main characteristics will be described briefly before considering the details of each individual section. Zones A–C are exclusive to the Peruvian sections and defined on the basis of the high percentages of *Mauritiidites franciscoi* (zone B), *Monoporites annulatus*, *Deltoidospora adriennis* and riverine taxa such as *Retitricolporites irregularis* and *Psilatricolporites operculatus* (zone A). Zone C is similar to the A and B but has large amounts of *Cyperaceapollis* sp. Zones D–H are exclusive to the Colombian sections. In Zone D large percentages of *Grimsdalea magnaclavata* are the main characteristic. Zone E includes large percentages of *Deltoidospora adriennis* and

Psilatricolporites silvaticus whereas zone F is characterized by the abundance of *Monoporites annulatus*. Zone G was differentiated because of the abundance of marine palynomorphs and zone H because of the high percentages of *Heterocolpites rotundus*.

Santa Teresa section (Peru); Psiladiporites–Crototricolpites Zone (early Miocene to early Middle Miocene)

The lower part of the diagram, zone A (1.4–3.8 m), is characterized by abundances of *Psilamonomolpites nanus* (Palmae), *Perisyncolporites pokornyi* (Malpigiaceae), *Psilatricolporites* cf. *varius*, *Deltoidospora adriennis* (*Acrostichum*), *Zonocostites ramonae* (*Rhizophora*) (5%), *Echiperiporites akanthos*, *Echitricolporites maristellae*, *Scabratrporites redundans* and *Echitriletes* cf. *muelleri*–*Bacutriletes* sp. (Selaginellaceae). In the upper part of the diagram, zone B (9.7–10.4 m), there is a large peak of *Mauritiidites franciscoi* (*Mauritia*) (65%). In both zones *Monoporites annulatus* (Gramineae) is common, oscillating from 5 to 20%. Furthermore, low abundances were observed of *Heterocolpites incomptus* (*Miconia*?), *Magnastriatites grandiosus* (*Ceratopteris*), *Retimonocolpites maximus* (Palmae), *Psilatricolporites operculatus* (*Alchornea*), *Psilatricolpites minutus*, *Retitricolpites simplex*. Taxa of probable Andean origin such as *Cyatheacidites* sp. (Cyatheaceae), *Verrutriletes* cf. *bullatus* (*Alsophila*), *Clavinaperturites microclavatus* (*Hedyosmum*), *Matonisorites mulleri* (*Hemitelia*), *Podocarpidites* sp. (*Podocarpus*) are also present.

Iquitos and Pevas sections (Peru); Crassoretitriletes Zone (Middle Miocene)

The Iquitos section belongs to zone A (1.6–3.1 m) and is characterized by peaks of *Psilatricolporites operculatus* (*Alchornea*) (50%), *Deltoidospora adriennis* (*Acrostichum*) (65%), and *Monoporites annulatus* (Gramineae) (25%). There are moderate peaks in the *Retitricolporites poriconspectus* and *Psilatricolporites costatus* curves. More constant throughout the diagram are *Mauritiidites franciscoi* (*Mauritia*) and *Retimonocolpites maximus* (Palmae). *Zonocostites ramonae* (*Rhizophora*) occurs in low percentages. Andean taxa such as

mentioned before are present with additionally *Kuylisporites waterbolkii* (*Hemitelia*).

The Pevas section is subdivided into three ecological zones. Zone A (2.2–3.3 m) is dominated by *Deltoidospora adriennis* (*Acrostichum*) (25%), *Crassoretitriletes vanraadshoovenii* (*Lygodium*) (20%), *Monoporites annulatus* (Gramineae) (20%). Peaks occur in the curves of *Mauritiidites franciscoi* (*Mauritia*), *Proxapertites tertiaria* (*Crematosperma*), *Retitricolporites lalongatus*, *Magnastriatites grandiosus* (*Ceratopteris*), and *Botryococcus* sp. (70%). Zone B (3.3–7.5 m) is dominated by *Mauritiidites franciscoi* (*Mauritia*) (35%), *Psilamonomolpites amazonicus* (*Euterpe*) (10%), *Retitricolporites irregularis* (*Amanoa*) (15%), *R. solimoensis* (30%), *R. milnei*, *Psilatricolporites crassoexinatus* and *P. devriesii*. At the top of this interval there is a little peak of *Zonocostites ramonae* (*Rhizophora*) (7%). Noticeable is the absence of Gramineae and the aquatic indicators. Zone C (11.6–19.5 m) is characterized by the presence of *Mauritiidites franciscoi* (*Mauritia*) (15–20%) and peaks in the curves of *Monoporites annulatus* (Gramineae) (15%), *Retimonocolpites maximus* (Palmae), *Perisyncolporites pokornyi* (Malpigiaceae), *Bombacidites bellus* (Bombacaceae) and *Psilatricolporites costatus*. At 12.7 m there is a noticeable peak in the curve of *Cyperaceae* sp. (Cyperaceae) (80%) followed at 13.7 m by a peak of *Botryococcus* sp. Other relevant species to the diagram are *Heterocolpites incomptus* (*Miconia*?), *Psilatricolporites operculatus* (*Alchornea*) and *P. cf. varius*. Taxa of probable Andean origin are present although not abundant.

Santa Sofia, Mocagua and Los Chorros sections (Colombia); Grimsdalea Zone (Middle–Late Miocene)

The Santa Sofia section is subdivided into three ecological zones. Zone D (3.1–10.8 m) is characterized by abundances of *Grimsdalea magnaclavata* (Palmae) (35%), *Monoporites annulatus* (Gramineae) (20%), *Cyatheacidites* sp. (Cyatheaceae) (20%) and *Azolla* sp. (20%). Zone E (14.1–14.5 m) is a lignite layer dominated by *Deltoidospora adriennis* (*Acrostichum*) (25%), *Polypodiaceisporites* cf. *potoniei* (15%), *Retimonocolpites maximus* (Palmae) (12%), *Heterocolpites incomptus*

(*Miconia*?) (17%) and taxa of the Sapotaceae type such as *Psilatricolporites* spp., *Psilatricolporites transversalis* and *P. silvaticus* (15%). This interval is followed by sandy clay (14.5–17.4 m) representing again zone D with *Grimsdalea magnaclavata* (Palmae) (30%) as the main species. Zone F (17.4–20.2 m) is dominated by *Monoporites annulatus* (Gramineae) (35%) including an interval with high percentages of *Azolla* sp. (15%) and peaks of *Psilamonocolpites amazonicus* (*Euterpe*) (20%), *Psilatricolporites* cf. *varius*, *P. operculatus* (*Alchornea*), *Retitricolpites lorentae* (Bombacaceae) (20%), *Echiperiporites estelae* (Malvaceae) (20%), *Heterocolpites verrucosus* (Melastomataceae), *Psilatricolporites costatus*, *Bombacacidites baculatus* (*Pachira*) and *Psilatricolporites crassoexinatus*. An interval with abundant Andean taxa (each curve around 8%) overlaps zone D and E, coinciding with a lithology of sandy clay. From the entire diagram the following taxa were observed: *Magnastriatites grandiosus* (*Ceratopteris*), *Psilamonocolpites amazonicus* (*Euterpe*), *Mauritiidites franciscoi* (*Mauritia*), *Psilamonocolpites* spp. (Palmae) and *Echitriteles* cf. *muelleri*–*Bacutriteles* sp. (Selaginellaceae).

The Mocagua section is subdivided into three ecological zones. Zone F (2.3–6.1 m) shows abundant *Monoporites annulatus* (Gramineae) (12%), *Psilatricolporites* cf. *varius* (12%), *Heterocolpites rotundus*, *Verrucatosporites* sp.–*Verrutriteles* sp., *Echitriteles* cf. *muelleri*–*Bacutriteles* sp. (Selaginellaceae), *Psilatriletes peruanus*, *Perinomonoletes* sp.–*Echinosporis* sp., *Pediastrum* sp. and, an assemblage of taxa of probable Andean origin. Zone G (6.1–7.1 m) is dominated by *Grimsdalea magnaclavata* (Palmae) (45%) accompanied by *Mauritiidites franciscoi* (*Mauritia*) (15%), *Echidiporites barbeitoensis* (*Korthalsia*). There are peaks in the marine palynomorphs (20%) curve and a minor peak in the *Zonocostites ramonae* (*Rhizophora*) (1.5%) curve. Zone D (15.1–21.1 m) is characterized by abundant *Grimsdalea magnaclavata* (Palmae) (10–50%) and peaks in the curves of *Magnastriatites grandiosus* (*Ceratopteris*) (20%), *Psilamonocolpites amazonicus* (*Euterpe*), *P. nanus* (Palmae), *Psilatricolporites operculatus*, (*Alchornea*), *Retitricolpites lorentae* (Bombacaceae) and *Bombacacidites baumfalkii* (Bombacaceae). In the

upper part of this interval taxa of probable Andean origin prevail. The top of the section belongs to zone F (23.9–24.8 m) which is defined by abundant *Monoporites annulatus* (Gramineae) (25%) and *Psilatricolporites* cf. *varius* (25%). In general, all zones present prominent curves of *Deltoidospora adriennis* (*Acrostichum*), *Monoporites annulatus* (Gramineae) and *Azolla* sp.

The two Los Chorros I sections are about 300 m apart. The symbol ($\approx$) indicates the correlation level. The western section is subdivided into two ecological zones. Zone D (2.9–8.5 m) is characterized by fluctuating amounts of *Grimsdalea magnaclavata* (Palmae) (5–32%), *Monoporites annulatus* (Gramineae) (0–15%), *Deltoidospora adriennis* (*Acrostichum*) (2.5–30%), *Mauritiidites franciscoi* (*Mauritia*) (2.5–30%), *Echidiporites barbeitoensis* (*Korthalsia*) (0–30%), *Retimonocolpites maximus* (Palmae), *Heterocolpites incomptus* (*Miconia*?) and *Retitricolporites irregularis* (*Amanoa*). Zone F–G (8.5–15 m) is dominated by *Monoporites annulatus* (Gramineae) (30%), and peaks in the curves of *Grimsdalea magnaclavata* (Palmae), *Retitricolpites* cf. *maledictus* and *Botryococcus* sp. At the top of this interval there is a peak of marine palynomorphs (60%) accompanied by a small peak in the *Zonocostites ramonae* (*Rhizophora*) curve.

The eastern section is subdivided into three ecological zones. Zone G (9.7–15.4 m) overlaps with zone F–G of the western section. This zone is dominated by *Grimsdalea magnaclavata* (Palmae) (5–30%) and variable amounts of *Monoporites annulatus* (Gramineae) (2.5–60%), *Deltoidospora adriennis* (*Acrostichum*) (2.5–30%), *Mauritiidites franciscoi* (*Mauritia*) (15%), *Echidiporites barbeitoensis* (*Korthalsia*) and marine palynomorphs (30%). Zone E (19.4–20 m) is dominated by *Deltoidospora adriennis* (*Acrostichum*) (80%), and taxa of the Sapotaceae type such as *Psilatricolporites transversalis* and *P. silvaticus*. Zone H (20–26.6 m) is characterized by *Psilamonocolpites amazonicus* (*Euterpe*) (10%), *Grimsdalea magnaclavata* (Palmae) (5–15%), and fluctuating amounts of *Retimonocolpites maximus* (Palmae) (15%), *Polypodiaceisporites* cf. *potonie* (*Pteris*), *Heterocolpites rotundus* (35%) and *H.*

verrucosus (Melastomataceae). At the base of the zone there is a moderate peak of marine palynomorphs accompanied by *Zonocostites ramonae* (*Rhizophora*). Andean taxa, and *Botryococcus* sp. and *Azolla* sp. show fluctuating values in the both diagrams.

6.4. Interpretation of the diagrams

The Miocene sections of the Upper Amazon River represent a highly dynamic flood-basin environment where swamps, drowned swamps, shallow lakes and swamp and crevasse splay channel deposits alternate with each other. The pollen percentage diagrams present an erratic pattern where a sustained succession can rarely be detected.

In general the palaeovegetation is dominated by palms. The most common palm types are *Mauritia*, *Grimsdalea*, *Euterpe*, *Psilamonocolpites nanus*, *Korthalsia* and *Retimonocolpites maximus*. However, there is an important difference between the palm composition of the Peruvian and the Colombian sections. In the the Peruvian sections *Mauritia* is the dominant species whereas in the Colombian sections *Grimsdalea* (an extinct palm type) dominates. This suggests that the palm vegetation changed in character during the Middle to Late Miocene and that *Grimsdalea* took over the dominant role from *Mauritia*. *Mauritia* is a palm type that grows on poorly drained soils. For *Grimsdalea* no ecological affinity is known although it is thought to form part of the coastal backswamps (Germeraad et al., 1968). The *Grimsdalea* peaks are common in the lacustrine deposits. They probably formed the dominant vegetation that surrounded the shallow flood-basin lakes.

An important characteristic of all diagrams is the fluctuating percentage of Gramineae which represent floating meadows in the fluvial environment. The Gramineae can occur together with other aquatic taxa such as *Ceratopteris*, *Azolla* sp., *Botryococcus* sp. and *Pediastrum* sp. which are prolific during periods of high water stands. In the Santa Sofia section (17.4–21 m, Fig. 12a) there is an apparent succession of *Acrostichum*/Sapotaceae – *Grimsdalea*-Gramineae – *Azolla*-Gra-

mineae. Peaks of the planktonic algae *Botryococcus* sp. represent episodic lacustrine phases.

Spores such as *Verrucatosporites usmensis* and *Psilamonoletes tibui* form a very important part of the total sporomorph content of all samples. The ecological implications of these spores remain speculative. They are possibly related to a semi-aquatic environment.

Taxa common in the mountainous Andean region such as *Podocarpus*, *Hedyosmum*, Cyatheaaceae, *Hemitelia* and *Alsophila* were observed mainly in the sandy clay intervals (e.g. Santa Sofia, 14.5–18.5 m, Fig. 12a). These taxa reached Amazonia by river transport and were deposited together with the sediments in shallow lakes of the flood-basin. The Andean assemblage is occasionally accompanied by reworked Cretaceous palynomorphs.

Taxa related to riparian vegetation such as Bombacaceae, *Amanoa*, *Alchornea* and *Crematosperma* are abundant only in certain intervals. In the Pevas section *Crematosperma* and *Retitricolpites lalongatus* seem to be the main components of a swamp deposit (Pevas, 2.4 m; Fig. 11) which at a later stage was inundated by clastic sediments where ferns (*Acrostichum* and *Lygodium*) dominated followed by the riverine taxa *Mauritia*, *Amanoa* and *Retitricolporites solimoensis* (Pevas, 2.4–7.5 m; Fig. 11). In the upper part of this section there is a thin swamp interval which is dominated by local stands of Cyperaceae (Pevas, 14.8 m; Fig. 11).

Occasional low abundances of *Rhizophora* suggest an influence of coastal waters on the depositional environment. In the Colombian Mocagua and Los Chorros sections (Fig. 12b), marine incursions are reflected by abundant marine palynomorphs in the organic matter (microforaminifera and dinoflagellate cysts). The large amounts of *Acrostichum*, an indicator of coastal conditions, in combination with *Rhizophora*, confirm this view.

7. Miocene, Holocene and Present palynological and vegetational data compared

At present, the composition of swamp vegetation in Amazonia differs according to the water type that invades the site (Junk, 1983). Floating meadows are restricted to the Amazon River (and

other white water affluents) and do not occur along the rivers of Amazonian origin (black water). The genesis of Middle Miocene wetland deposits is related to a white, Andean river type and therefore the recent and subrecent wetland systems of the present Amazon River system might be the best analogues.

Absy (1979) presents a detailed palynological study of the Holocene Terra Nova section (Brazilian Amazonia). She concludes that the most common taxa in the Holocene section are *Alchornea*, *Symmeria*, *Myrthaceae*, *Miconia*, *Cecropia* and *Gramineae* and that vegetation fluctuations are largely determined by the changes in water level. The water level also forms the basis of the swamp classification by Kalliola et al. (1992). Kalliola et al. (1992) distinguish four present-day swamp vegetation types in Peruvian Amazonia. These are (1) herbaceous swamps with permanent lakes, characterized by free floating aquatic taxa with grass mats followed by a shallow water association of *Azolla*–*Gramineae*–*Ludwigia*/Cyperus, (2) shrub swamps, characterized by *Alchornea*–*Annona*–*Palmae* which surround the herbaceous vegetation, (3) palm swamps, dominated by *Mauritia*–*Ficus*–*Virola*, and (4) a combined forest swamp. They conclude that the Maraon wetlands are highly unstable and transitional in nature.

The Miocene diagrams do not show a very close resemblance to the Holocene Terra Nova section (Absy, 1979). For instance, there is no characteristic riverbank genus such as *Cecropia* in the Miocene sections. Also Cyperaceae and Compositae are relatively rare in the Miocene sediments. However, indications of a riverine environment with flood plain lakes which are eventually invaded by floating meadows exist in both Holocene and Miocene sections. Also Andean taxa such as *Podocarpus* and montane ferns are present in both sections. The ecological zones that were distinguished in the Middle to Late Miocene sections seem to relate best to the present swamp types described by Kalliola et al. (1992).

8. Amazonia and the Miocene global climate

Kennett (1982) presented a review of the Neogene palaeoclimatic history as inferred from

palaeoceanographic studies. These studies show that the evolution of Miocene climate was strongly dependant on changes in the deepwater circulation patterns caused by plate tectonic readjustments. A global cooling in the Middle Miocene (from ca. 14 Ma onwards) resulted in a significant expansion of the East Antarctic ice sheets. The growth of these ice sheets is related to the thermal isolation of Antarctica due to the creation of the Circum-Antarctic Current in the Oligocene. Since the expansion of the East Antarctic ice sheet, global climates have not returned to the temperatures of the Early Miocene and the early part of the Middle Miocene. This cooling episode initiated a major change in the terrestrial plant assemblage over wide areas. More recently it has been suggested that the Miocene cooling trend was a relatively gradual process (Woodruff and Savin, 1991) and occurred through 2–3 glacial–interglacial cycles (Wright et al. 1992).

In Amazonia the Pleistocene climatic changes have been recorded palynologically in the form of vegetation changes from forest or woodland into open savannah (Absy and Van der Hammen, 1976; Van der Hammen, 1972; Van der Hammen et al., 1992; Van der Hammen and Absy, 1994). The change to the savannah vegetation was recognized by these authors in the form of increasing percentages of *Gramineae* accompanied by taxa such as *Byrsonima*, *Didymopanax* and *Curatella*.

The Miocene sediments of NW Amazonia present no evidence for a vegetational change related to the Middle Miocene (14.8–12.6 Ma) cooling event. However, the Middle to Late Miocene polynoflora of the palaeo-Amazon River environments differs considerably from that found in the Early Miocene fluvial sediments (Hoorn, 1993a, 1994). The Early Miocene fluvial sediments have an Amazonian origin and are characterized by a rather diverse assemblage of palm and forest taxa. The Middle Miocene to Late Miocene fluvio-lacustrine sediments are dominated by palms, *Gramineae*, ferns, fern allies, aquatic taxa and an assemblage of transported Andean taxa. However, no taxa of the savannah vegetation were observed. It is thought that large-scale environmental changes triggered by uplift of the Eastern Cordillera and the marine incursions played a

decisive role in the change in composition of the palaeovegetation during the Miocene. The increase of Gramineae in the *Crassoretitriletes* Zone represents the appearance of floating meadows in a lake and swamp environment of a white water river system and not a feature of grasslands in a drier climate.

9. Discussion

The fluvio-lacustrine deposits of the Miocene Amazon River system present a strong brackish component. This was concluded on the basis of sedimentological, palaeontological and palynological evidence. It is thought that the Miocene marine incursions that affected Amazonia were due to a transgression from the north via the present Maracaibo Lake area in Venezuela. This is supported by the occurrence of marine intervals in the Llanos Basin (NELL, 1992) and by the absence of marine sediments of Miocene age between the Purus High (Fig. 1) and the River Xingu, to the east, in Brazil (Caputo, 1984). In addition, marine deposits such as the Early Miocene Pirabas Formation (Garrafiello and de Araujo, 1990) and the partially marine Middle Miocene Barreiras Formation (Arai et al., 1988) extend no more than ± 300 km inland from the Atlantic coast (?? Machado, pers. commun., 1991). It seems unlikely, therefore, that a direct connection existed between the Atlantic and NW Amazonia before the Late Miocene. Moreover, terrigenous clastic sediments of the Amazon River cover the carbonate sequences of the Atlantic shelf from Late Miocene onwards (Campbell, 1992).

Nuttall (1990) suggested that the presence of the bivalve *Pachydon* in NW Amazonia is an indication for this northern connection since this genus is known only in the Neogene from the Caribbean region. Additionally, the presence of the fossil fish *Colossoma* and *Arapaima* in the Miocene Honda Group (Magdalena Valley) gives further indication of a connection between Amazonia and the north (Lundberg et al., 1986; Lundberg and Chernoff, 1992). At present, *Colossoma* and *Arapaima* are exclusively known from the Amazon and Orinoco Rivers. Nuttall (1990) and Lundberg et al. (1986) suggest that

this northern connection went through the Magdalena Valley prior to completion of the uplift of the Eastern Cordillera.

Sedimentological evidence in the Honda Group (Magdalena Valley) indicates a strong affect of an uplift phase of the Eastern Cordillera at the beginning of the Middle Miocene (Van der Wiel, 1991; Guerrero, 1993). Sedimentological and palaeomagnetic data from the Villavieja Formation suggest that a significant uplift pulse of the Andes occurred between 12.9 and 11.5 Ma (Guerrero, 1992). At 11.8 Ma a continuous mountain range is thought to have existed, isolating the Magdalena Valley, and a new river system originated in the Magdalena Valley (Magdalena River = Neiva Formation) at 10.13 ± 0.18 Ma with an E to W transport direction (Guerrero, 1993). The genesis of the Amazon River system seems related to the same tectonic event. This is supported by the sediment composition and palaeocurrent directions of Middle to Late Miocene sediments in Amazonia described above, which suggest an Andean origin and an eastward transport direction.

10. Conclusions

The Middle to Late Miocene sediments of NW Amazonia are the first deposits of the incipient Amazon River system. This river system originated as a result of uplift of the Eastern Cordillera and bears a strong resemblance to the present Upper Amazon River system. Initially, during Middle Miocene time, no connection existed between the palaeo-Amazon and the Atlantic. However, from the beginning of the Late Miocene, clastic deposits from the Amazon River in the Atlantic proves the existence of such a connection.

In NW Amazonia the Middle to Late Miocene environment was dominated by a fluvio-lacustrine, moderately anastomosing system with eastward transport directions. Sedimentological, palynological and palaeontological characteristics suggests brackish conditions that point towards an estuarine character for the system.

Transport directions, heavy mineral composition and pollen taxa of probable Andean origin are the most important evidence for the Andean provenance of this fluvio-lacustrine system which

is dominated by suspended load transport. Sedimentary environments of the wetlands such as shallow lakes, crevasse splay channels, crevasse-delta lakes and backswamps were common, but there is no evidence of a true fluvial channel. The paleo-vegetation was characterized by floating meadows in shallow lakes which were fringed by palm swamps, ferns, fern allies and riverine forest. The Miocene lake/swamp environment is comparable to the present *varzeas* of the Amazon River flood-basin.

There is a pronounced difference in pollen composition between the Early Miocene and the Middle Miocene sediments. In the Early Miocene the vegetation was dominated by palm swamps and riverine forest (Hoorn, 1994). In the Middle to Late Miocene deposits Gramineae, ferns, fern allies, and Andean taxa (*Podocarpus*, *Hedyosmum*, *Hemitelia*, *Alsophila*, and Cyatheaceae) occur frequently. It is thought that this change in pollen composition reflects a major environmental change related to the genesis of the Amazon River and subsequent invasion of this river into Amazonia.

Although a global climatic cooling began in the Middle Miocene (Kennett, 1982), no evidence of savannah development was detected in the Middle to Late Miocene of Amazonia as is known from the cooler periods in the Quaternary (Absy, 1979; Van der Hammen, 1972; Van der Hammen and Absy, 1994).

Throughout the Miocene, marine influxes occurred in NW Amazonia (Hoorn, 1993a,b, 1994). The Solimões/Pebas Formation contains molluscs (lamellibranchs, gastropods), ostracods, trace fossils (*Thalassinoides*–*Teichichnus* association), marine palynomorphs, mangrove pollen, and sedimentological indications of tidal influence (e.g., flaser bedding, interlayered bedding) which all point to a brackish environment and marine influence. However, the overall continental character of the deposits and the lack of unambiguous tidal and coastal features exclude a shallow marine environment and suggest solely episodic marine influence. The episodes of marine influence are possibly linked with the Langhian and Serravallian global sea-level rise and are thought to have a Caribbean origin (Hoorn, 1993a, 1994).

Relatively rapid subsidence and possibly also an

increasing base level due to global sea-level rise were the main parameters that determined sediment aggradation in NW Amazonia. In general the sediment input did not hold pace with the subsidence rates and therefore drowning and the formation of extensive wetlands occurred.

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Appendix: Species list

All species and genera from the pollen diagram are listed, and accompanied by references. Additionally, taxonomic

affinity and ecology are presented. Suprageneric categories are after Iversen and Troels-Smith (1950), Potonié (1956) and Germeraad et al. (1968). When possible, taxonomic affinities are suggested based on Germeraad et al. (1968), Lorente (1986), Dueñas (1980) and Hoorn (1993a). The ecological significance of some of the present related species is based on the previously mentioned authors and, on Lindeman (1953), Van der Hammen (1963), Van Roosmalen (1985) and Graham (1988). The list includes 4 new sporomorphs formally described in the Systematics section. Three plates illustrate the holotypes of the new species and other specimens.

Pollenites

Inaperturatae

Clavainaperturites microclavatus nov. sp., Plate I, 9

Taxonomic affinity: Chlorantaceae, *Hedyosmum*. Ecology: common in montane forests and occasional occurrences in the lowland forests.

Cyperaceapollis sp. Krutzsch 1970

Taxonomic affinity: Cyperaceae. Ecology: common in herbaceous swamps and lowland savannahs.

Grimsdalea magnaclavata Germeraad et al. 1968, Plate I, 3

Taxonomic affinity: unknown, possibly an extinct palm type of the coastal vegetation.

Ephedripites sp. Bolkhovitina 1953

Ephedripites renzonii Dueñas 1986

Taxonomic affinity: Araceae, *Spathiphyllum*.

Monocolpatae

Clavamonocolpites sp. González Guzmán 1967, Plate I, 11

Taxonomic affinity: Palmae, *Iriarte*. Ecology: common in the lowland and premontane forests.

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

Taxonomic affinity: Palmae, *Mauritia*. Ecology: grows on poorly drained soils in permanently inundated, swampy areas. *Proxapertites tertiaria* Van der Hammen et García de Mutis 1965

Taxonomic affinity: Annonaceae, *Crematosperma*. Ecology: the Annonaceae are known from the floodplains of the present day Caqueta River.

Psilamonocolpites spp. Van der Hammen et García de Mutis 1965, Plate I, 1

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

Psilamonocolpites amazonicus Hoorn 1993aa

Taxonomic affinity: Palmae, *Euterpe*

Psilamonocolpites nanus Hoorn 1993a

Taxonomic affinity: Palmae

Psilamonocolpites rinconii Dueñas 1986

Taxonomic affinity: Palmae

Retimonocolpites absyae Hoorn 1993a

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

Retimonocolpites longicolpatus Lorente 1986

Taxonomic affinity: Palmae

Retimonocolpites maximus Hoorn 1993a

Taxonomic affinity: Palmae

Retimonocolpites retifossulatus Lorente 1986

Taxonomic affinity: Palmae

Trichotomosulcites sp. Couper 1953

Remark: pollen grains of this form-genus with a taxonomic affinity to *Bactris* (Palmae) are here included. Ecology: *Bactris* is common in the lowlands.

Monoporatae

Monoporites annulatus Van der Hammen 1954

Taxonomic affinity: Gramineae. Ecology: forms part of open vegetations in a range of environments from humid to dry.

PLATE I

1000 ×

1. *Psilamonocolpites* spp.
2. *Echidiporites barbeitoensis*.
3. *Grimsdalea magnaclavata* (with little echinae).
4. *Stephanocolpites* sp.
5. *Echitricolporites spinosus*.
6. *Polyadipollenites* spp. (*Inga* type).
7. *Psilaperiporites multiporatus* (holotype).
8. *Multimarginites vanderhammenii*.
9. *Clavainaperturites microclavatus* (holotype).
10. *Echiperiporites* spp. (500 ×).
11. *Clavamonocolpites* sp. (*Iriarte* type).
12. *Echiperiporites* spp. (*Hibiscus* type) (500 ×).

PLATE I

Some members of this family act as pioneer vegetation in open water habitats (floating meadows) and on mud and sand flats.

Diporatae

Psiladiporites minimus Van der Hammen et Wijmstra 1964

Taxonomic affinity: Moraceae, *Ficus*–*Artocarpus*–*Sorocea*

Psiladiporites redundantis González Guzmán 1967

Remarks: although the form-genus was formally named *Psilodiporites* (Varma et Rawat, 1963), at a later stage it was also 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), for discussion purposes, preference was given here to the latter in order to avoid confusion.

Taxonomic affinity: Moraceae

Echidiporites barbeitoensis Muller et al. 1987, Plate I, 2

Taxonomic affinity: Palmae, *Korthalsia ferox*.

Dicolporatae

Multimarginites vanderhammenii Germeraad et al. 1968, Plate I, 8

Remark: an orthographical correction has been introduced. In the original publication the species name was written as *M. vanderhammeni*. Taxonomic affinity: Acanthaceae, *Trichantera gigantea* or *Bravaisia integerrima*. Ecology: *Bravaisia* grows in tropical forests.

Tricolpatae

Bacutricolpites spp. Van der Hammen 1956a

Remarks: pollen grains corresponding to *Bacutricolpites* were not identified at species level. The name is invalid and is used here in an informal way since no well preserved pollen grains were available for validation.

Crototricolpites annemariae Leidelmeyer 1966

Taxonomic affinity: Euphorbiaceae, *Croton*

Perfotricolpites digitatus González Guzmán 1967

Taxonomic affinity: Convolvulaceae, *Merremia*

Psilatricolpites acerbus González Guzmán 1967

Psilatricolpites anconis Hoorn 1994

Psilatricolpites minutus González Guzmán 1967

Psilatricolpites simplex González Guzmán 1967

Retitricolpites antonii González Guzmán 1967

Retitricolpites caquetanus Hoorn 1994

Taxonomic affinity: Bombacaceae–Tiliaceae?

Retitricolpites colpiconstrictus Hoorn 1994

Retitricolpites depressus Wijmstra 1971

Retitricolpites lalongatus Wijmstra 1971

Retitricolpites lewisii Wijmstra 1971

Retitricolpites lorentae Hoorn 1993a

Taxonomic affinity: Bombacaceae

Retitricolpites cf. maledictus González Guzmán 1967

Retitricolpites cf. maturus González Guzmán 1967

Retitricolpites simplex González Guzmán 1967

Remarks: this species was originally described as tricolpate.

Lorente 1986, observed that this species also can appear as tricolporate. Taxonomic affinity: Anacardiaceae?

Retibrevitricolpites catatumbus González Guzmán 1967

Retibrevitricolpites yavarensis Hoorn 1993a

Striatricolpites catatumbus González Guzmán 1967

Remarks: in the species are included some specimens which present oval pori. Dueñas 1980 distinguished these porate pollen grains as *Striatricolpites melenae*. However, following the example of Lorente (1986) and Germeraad et al. (1968), here these specimens are included in *Striatricolpites catatumbus*. Taxonomic affinity: Leguminosae, Caesalpinioideae, *Crudia*–*Macrolobium*–*Isobertlinia*. Ecology: Caesalpinioideae are common in the lowlands. *Macrolobium* occurs on the riverbanks at poorly drained sites.

Triporatae

Cricotriporites guianensis Leidelmeyer 1966

Corsinipollenites oculusnoctis (Thiergart 1940) Nakoman 1965

Taxonomic affinity: Onagraceae, *Ludwigia*. Ecology: common in herbaceous, swamps with fresh or slightly brackish water.

Proteacidites spp. Cookson 1950 ex Couper 1953

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

Proteacidites cf. triangulatus Lorente 1986

Taxonomic affinity: Sapindaceae–Proteaceae

Psilatriporites sarmientoi Hoorn 1993a

Retitriporites sp. 1 (Van der Hammen 1956a) Ramanujam 1966

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

Retitriporites dubiosus González Guzmán 1967

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

Scabratriporites redundans González Guzmán 1967

Tricolporatae

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. Ecology: trees and large shrubs of the tropical lowlands which grow on the river banks.

Bombacacidites araracuarensis Hoorn 1994

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

Bombacacidites baculatus Muller et al. 1987

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

Bombacacidites baumfalkii Lorente 1986 O.C.

Remark: an orthographical correction has been introduced. Originally the name was published as *B. baumfalki*. Taxonomic affinity: Bombacaceae.

Bombacacidites bellus Frederiksen 1983

Taxonomic affinity: Bombacaceae, *Bombax*.

Bombacacidites muinaeorum Hoorn 1993a

Taxonomic affinity: Bombacaceae, *Bombacopsis*.

Crassieoapertites columbianus Dueñas 1980

Remarks: this pollen grain presents sometimes 4 apertures

instead of 3. Taxonomic affinity: Leguminosae, Papilionoideae, *Carnalia eurocarpa*–*Dioclea virgata*

Echitricolporites maristellae Muller et al. 1987

Taxonomic affinity: Bombacaceae–Malvaceae

Echitricolporites spinosus Van der Hammen 1956a ex Germeraad et al. 1968, Plate I, 5

Taxonomic affinity: Compositae.

Ilexpollenites sp. Thiergart 1937 ex Potonié 1960

Taxonomic affinity: Aquifoliaceae, *Ilex*. Ecology: swamp, marsh and rain forests.

Margocolporites vanwijhei Germeraad et al. 1968

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

Psilatricolporites spp. Van der Hammen 1956a ex Van der Hammen et Wijmstra 1964

Remark: species which show a taxonomic affinity with Sapotaceae, are included in this form-genus.

Psilatricolporites atalayensis Hoorn 1993a

Psilatricolporites costatus Dueñas 1980

Psilatricolporites crassoexinatus Hoorn 1993a

Psilatricolporites cyanus Van der Hammen et Wijmstra 1964

Psilatricolporites devriesii Lorente 1986 O.C.

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

Psilatricolporites divisus Regali et al. 1974

Taxonomic affinity: Sapotaceae

Psilatricolporites exiguus Hoorn 1993a

Psilatricolporites garzonii Hoorn 1993a

Psilatricolporites labiatus Hoorn 1993a

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

Psilatricolporites magniporatus Hoorn 1993a

Taxonomic affinity: Leguminosae?

Psilatricolporites normalis González Guzmán 1967

Psilatricolporites obesus Hoorn 1993a

Taxonomic affinity: Sapotaceae

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

Psilatricolporites cf. *operculatus* Van der Hammen et Wijmstra 1964

Psilatricolporites silvaticus Hoorn 1993a

Taxonomic affinity: Burseraceae–Sapotaceae

Psilatricolporites transversalis Dueñas 1980

Taxonomic affinity: Sapotaceae

Psilatricolporites triangularis Van der Hammen et Wijmstra 1964

Psilatricolporites cf. *varius* Dueñas 1983

Psilatricolporites venezuelanus Lorente 1986

Retitricolporites sp. 1 Van der Hammen 1956a 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.

Retitricolporites sp. 2 Van der Hammen 1956a ex Van der Hammen et Wijmstra 1964

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

Retitricolporites caputoi Hoorn 1993a

Retitricolporites crassicosatus Van der Hammen et Wijmstra 1964

Taxonomic affinity: Rubiaceae

Retitricolporites crassopolaris Hoorn 1994

Retitricolporites ellipticus Van Hoeken-Klinkenberg 1966

Retitricolporites guianensis Van der Hammen et Wijmstra 1964

Taxonomic affinity: Sterculiaceae–Tiliaceae. Ecology: dry and moist forest, premontane and lower montane forests

Retitricolporites hispidus Van der Hammen et Wijmstra 1964

Retitricolporites irregularis Van der Hammen et Wijmstra 1964

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

Retitricolporites kaarsii Hoorn 1993a

Taxonomic affinity: Euphorbiaceae, *Dalechampia*

Retitricolporites leticianus Hoorn 1993a

Retitricolporites medius González Guzmán 1967

Retitricolporites milnei Hoorn 1993a

Retitricolporites oblatum Hoorn 1994

Retitricolporites poriconspectus Hoorn 1994

Taxonomic affinity: Leguminosae

Retitricolporites pygmaeus Hoorn 1994

Retitricolporites solimoensis Hoorn 1993a

Retitricolporites ticuneorum Hoorn 1993a

Rugutricolporites arcus Hoorn 1993a

Taxonomic affinity: Chrysobalanaceae, *Licania*

Syncolporites cf. *incomptus* Van Hoeken-Klinkenberg 1964

Taxonomic affinity: Lorantheae?

Syncolporites sp. Van der Hammen 1954

Syncolporites poricostatus Van Hoeken-Klinkenberg 1966

Taxonomic affinity: Myrtaceae

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

Zonocostites duquei Dueñas 1980 O.C.
Remarks: this species was first published with the name *Z. duquensis*. The name was at a later stage changed by Dueñas into *Z. duquei* (1981). 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

Syncolpatae

Spirosyncolpites spiralis González Guzmán 1967

Stephanocolpatae

Psilastephanocolpites marginatus Wijmstra 1971

Stephanocolpites sp. Van der Hammen 1954 ex Potonié 1960, Plate I, 4

Taxonomic affinity: Passifloraceae?

Stephanocolpites evansii Muller et al. 1987

Stephanoporatae

Retistephanoporites crassiannulatus Lorente 1986

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

Psilastephanoporites herngreenii Hoorn 1993a

Taxonomic affinity: Apocynaceae

Stephanocolporatae

Jandufouria saemrogiformis Germeraad et al. 1968

Taxonomic affinity: Bombacaceae, *Catostemma*. Ecology: marsh and rain forests.

Psilastephanocolporites fissilis Leideimyer 1966

Taxonomic affinity: Polygalaceae

Psilastephanocolporites marinamensis Hoorn 1994

Taxonomic affinity: Sapotaceae

Psilastephanocolporites schneideri Hoorn 1993a

Taxonomic affinity: Rhizophoraceae?

Periporatae

Echiperiporites spp. Van der Hammen et Wijnstra 1964 Plate I, 10 and 12

Remarks: two species which show a taxonomic affinity with Malvaceae are grouped in this form-genus. One of these species probably represents *Hibiscus* (Plate I, 12), the other one is a unknown Malvaceae.

Echiperiporites akanthos Van der Hammen et Wijnstra 1964

Echiperiporites estelae Germeraad et al. 1968

Taxonomic affinity: Malvaceae (*Thelespia populnea*–*Hibiscus tiliaceus*) or Convulvulaceae (*Ipoema*). Ecology: tropical, coastal vegetation.

Psilaperiporites minimus Regali et al. 1974

Taxonomic affinity: Amarantaceae–Chenopodiaceae

Psilaperiporites multiporatus nov sp. Plate I, 7

Pericolporatae

Perisyncolporites pokorny Germeraad et al. 1968

Taxonomic affinity: Malpighiaceae.

Heterocolpatae

Heterocolpites incomptus Van der Hammen 1956a ex Hoorn 1993a

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.

Heterocolpites rotundus Hoorn 1993a

Taxonomic affinity: Combretaceae–Melastomataceae

Heterocolpites verrucosus Hoorn 1993a

Taxonomic affinity: Melastomataceae

Polyadeae

Polyadopollenites spp. Pflug et Thomson 1953, Plate I, 6

Taxonomic affinity: Leguminosae, Mimosoideae (*Inga*?).

Ecology: in dry lands from sea level up to 1500 m. *Inga* is common today along fresh water creeks in the Lower Magdalena Valley.

Vesiculatae

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. Locally *Podocarpus* is also found in lowland tropical vegetation (e.g., Iquitos and Araracuara).

PLATE II

1000 ×

1. *Polypodiaceisporites* sp.
2. *Matonisporites mulleri*.
3. *Echinosporis* sp.
4. *Bacutritiles* sp.
5. *Psilatritiles lobatus* (holotype).
6. *Kuylisporites waterbolckii*.
7. *Perinomonoletes* spp.
8. *Foveotritiles ornatus*.
9. *Verrutritiles* sp.
10. *Psilatritiles peruanus* (holotype).
11. *Crassoretitritiles vanraadshoovenii* (with spore attached) (500 ×).
12. *Verrucatotritiles* cf. *bullatus*.
13. *Polypodiaceisporites* cf. *potoniei*.

PLATE II

Sporites**Triletes**

Bacutrilletes sp. Van der Hammen 1956a ex Potonié 1956, Plate II, 4

Taxonomic affinity: Selaginellaceae

Crassoretitrites vanraadshoovenii Germeraad et al. 1968, Plate II, 11

Remarks: this species was first published with the name *Crassoretitrites vanraadshoovenii*. An orthographical correction has been introduced. Taxonomic affinity: Schizaeaceae, *Lygodium microphyllum*. Ecology: a climbing fern, common of the humid marshes and swamps forests of West Africa and Indo-Malaysia. This species is also related to the coastal swamps (Germeraad et al. 1968). At present absent from South America.

Cyatheacidites sp. Cookson 1947 ex Potonié 1956

Taxonomic affinity: Cyatheaceae. Ecology: montane forest.

Deltoidospora adriennis (Potonié et Gelletich 1933) Frederiksen 1983

Taxonomic affinity: Polypodiaceae, *Acrostichum aureum*. Ecology: halophytic fern associated with the mangrove vegetation. This species is here used as environmental indicator in association with *Zonocostites*.

Echitrites cf. *muelleri* Regali et al. 1974

Taxonomic affinity: Selaginellaceae?

Foveotrites ornatus Regali et al. 1974, Plate II, 8

Taxonomic affinity: Lycopodiaceae.

Kuylisporites waterbolckii Potonié 1956 O.C., Plate II, 6

Remark: this species was first published with the name *Kuylisporites waterbolckii*. An orthographical correction has been introduced. Taxonomic affinity: Cyatheaceae, *Cyathea horrida* type. Ecology: montane forest

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

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

Matonisporites mulleri Playford 1982, Plate II, 2

Taxonomic affinity: Matoniaceae or Dicksoniaceae, also resemblance to Cyatheaceae, *Hemitelia*. Ecology: montane forest

Polypodiaceoisporites sp. Lorente 1986, Plate II, 1

Taxonomic affinity: Pteridaceae

Polypodiaceoisporites cf. *potoniei* Kedves 1961, Plate II, 13

Taxonomic affinity: Pteridaceae, *Pteris*.

Psilatrites sp. Van der Hammen 1956a

Taxonomic affinity: Vittariaceae, *Polytaenium*

Psilatrites lobatus nov. sp., Plate II, 5

Psilatrites peruanus nov. sp., Plate II, 10

Taxonomic affinity: *Jamesonia* or *Pteris*?

Rugotrites sp. Van der Hammen 1956a ex Potonié 1956

Verrucatotrites cf. *bullatus* Van Hoeken-Klinkenberg 1964, Plate II, 12

Taxonomic affinity: Cyatheaceae, *Alsophila*. Ecology: montane forest

Verrutrites sp. Van der Hammen 1956a ex Potonié 1956, Plate II, 12

Monoletes

Echinosporis spp. Krutzsch et al. 1967, Plate II, 3

Taxonomic affinity: Thelypteraceae or Athyriaceae?

Perinomonoletes spp. Krutzsch et al. 1967, Plate II, 7

Taxonomic affinity: Aspleniaceae (*Asplenium*) or Thelypteraceae (*Thelypteris*).

Laevigatosporites catanejensis Germeraad et al. 1968

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

Psilamonoletes tibui Van der Hammen 1956a

Verrucatosporites sp. Pflug 1952 ex Potonié 1956

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

Taxonomic affinity: Polypodiaceae, *Stenochlaena palustris*

Other palynomorphs**Marine palynomorphs**

Dinoflagellate cysts (Plate III, 7) and 5 types of foraminiferal organic linings (Plate III, 1–5).

Aquatic taxa

Botryococcus sp. (Chlorophyta). Ecology: a lacustrine planktonic alga tolerant to salt.

Pediastrum sp. (Chlorophyta) (Plate III, 8). Ecology: a planktonic alga of fresh, stagnant water and tolerant to a degree of brackishness.

Azolla sp. (Salvinaceae, Pteridophyta), a fern common in stagnant, eutrophic or oligohaline water.

Fungi

Tetraploa cf. *aristata* (Plate III, 4), a saprophytic fungus very common on grasses and usually found on leaf bases and stems just above the soil.

Systematic part

The new species recognized in the studied samples are placed within the form-genera *Clavinaaperturites*, *Psilaperiporites* and *Psilatrites* and described according to the norms of the International Code of Botanical Nomenclature (ICBN). For each species, structure, sculpture, shape, size, variability of size (measured on 5 different grains) was described. 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 (Mocagua etc.) followed by the sample number; the residue

PLATE III

1000 ×

1, 2, 3 and 5. Microforaminifera (500 ×).

4. *Tetraploa* cf. *aristata*.

6. Microforaminifera.

7. Dinoflagellate cyst.

8. *Pediatrum* sp. (500 ×).

number at the Hugo de Vries-Laboratory and the location of the pollen grains on the slides. Coordinates were measured with Leitz microscope PO 6 in the Hugo de Vries-Laboratory. The following abbreviations have been used in the descriptions: Lg, + longitude; Lt, + transverse longitude; ex-M, + thickness of the exine.

Clavainaperturites Van der Hammen et Wijmstra 1964

Clavainaperturites microclavatus nov. sp., Plate I, 9

Derivatio nominis: the name is derived from the very small size of the clavae.

Holotype: Mocagua-7 HdV18210, Colombia. Location in slide: 104.9/57.8. Plate I, 9

Diagnosis: Inaperturate, microclavate pollen grain. Medium sized with subspheroidal shape. Apolar, asymmetric. Tectum perforate. Clavae thin and very small (1–1.5 μm).

Dimensions: Lt, + = 23 μm ; ex-M, + = 1 μm

Variability in size: Lt, + = 22–26 μm ; ex-M, + = 1–1.5 μm

Taxonomic affinity: Chlorantaceae, *Hedyosmum*. Ecology: common in montane forests and occasional occurrences in the lowland forests.

Remark: this species differs from the type-species, *Clavainaperturites clavatus* Van der Hammen et Wijmstra 1964, because of its subspheroidal shape and the smaller size of the clavae.

Form-genus *Psilaperiporites* Regali et al. 1974

Psilaperiporites multiporatus nov. sp. Plate I, 7

Derivatio nominis: the name is derived from the large amount of pores.

Holotype: Santa Sofia-23HdV 18183, Colombia. Location in slide: 96.3/51. Plate I, 7

Diagnosis: Periporate, psilate pollen grain. Apolar, asymmetric. Medium sized with subspheroidal shape. The diameter of the pores ranges between 2 and 4 μm . An annulus of 2–3 μm thick surrounds these pores. The amount of pores ranges from 9 to 16.

Dimensions: Lt, + = 33 μm ; ex-M, + = 1 μm

Variability in size: Lt, + = 33–38 μm ; ex-M, + = 1–1.5 μm

Taxonomic affinity: unknown.

Remarks: this species differs from the type-species, *Psilaperiporites robustus* Regali et al. 1974, because of the smaller size and amount of pores.

Form-genus *Psilatrilletes* Van der Hammen 1956a

Psilatrilletes lobatus nov. sp. Plate II, 5

Derivatio nominis: the name is derived from lobed sclerine.

Holotype: Mocagua-58 HdV18222, Colombia. Location in slide: 60.7/105.1. Plate II, 5

Diagnosis: Trilete, psilate spore. Radially symmetrical. The sclerine forms at the equator, interrational, lobe-shaped thickenings. The laesura is thin lined and almost reaches the equator.

Dimensions: Lt, + = 33 μm ; scl-M, + = 5.5 μm

Variability in size: Lt, + = 27–35 μm ; scl-M, + = 4.5–7.5 μm

Taxonomic affinity: unknown.

Remark: this species differs from the type-species, *Psilatrilletes guaduensis* Van der Hammen 1956b, because of the thickness of the sclerine and lobe-shaped thickenings at the equator. This species is named as type 290 by Hooghiemstra (1984).

Psilatrilletes peruanus nov. sp. Plate II, 10

Derivatio nominis: name after the country Peru.

Holotype: Santa Sofia 26-HdV18184, Colombia. Location in slide: 101.5/62. Plate II, 10

Diagnosis: Trilete, psilate spore. Radially symmetrical. Sclerine thickened at the equator. The laesura is bordered by thick ridges (2 μm) and reaches the equator forming there little protrusions.

Dimensions: Lt, + = 45 μm ; scl-M, + = 5.5 μm

Variability in size: Lt, + = 39–45 μm ; scl-M, + = 4.5–7.5 μm

Taxonomic affinity: *Jamesonia* or *Pteris rangiferina*?

Remarks: this species differs from the type-species, *Psilatrilletes guaduensis* Van der Hammen 1956b, because of the thickness of the sclerine and the protrusions at the laesura.

References

- Absy, M.L., 1979. A palynological study of Holocene sediments in the Amazon basin. Ph.D. Dissert., Univ. Amsterdam.
- Absy, M.L. and Van der Hammen, T., 1976. Some paleoecological data from Rondonia, southern part of Amazon basin. *Acta Amazonica*, 6: 293–299.
- Aepler, R. and Reif, W.E., 1971. Origin of bonebeds. *Abstr. 8th Int. Sedimentol. Cong. Heidelberg*, p. 1.
- Arai, M., Ucsugui, N., De Fatima, D. and Goes, A.M., 1988. Considerações sobre a idade do Grupo Barreiras no Nordeste do estado do Para. *Anais XXXV Cong. Bras. Geol.*, (2), Belem, Para, pp. 738–752.
- Astin, T.R. and Scotchman, I.C., 1988. The diagenetic history of some septarian concretions from Kimmeridge Clay, England. *Sedimentology*, 35: 349–368.
- Bocquentin, J. and Rodrigues, J.C., 1989. Ocorrência do *Chelus colombianus* (*Chelonii*, Chelidae) no Mioceno Superior do Acre, Brasil. *Anais XI Cong. Bras. Paleontol.*, Curitiba, pp. 439–446.
- Bocquentin, J., Pereira, J., Buffetaut, E. and Negri, F.R., 1989. Nova interpretação do gênero *Purussaurus* (Crocodylia, Alligatoridae). *Anais XI Cong. Bras. Paleontol.*, Curitiba, pp. 427–438.
- Boettger, O., 1878. Die Tertiärfaua von Pebas am oberen Marañon. *Jahrb. d.k.k. Geol. Reichsanst.*, 28(3): 485–504.
- Bolkhovitina, N.A., 1953. Spore-pollen characteristic of Cretaceous deposits of central regions of the USSR. *Akad. Nauk SSSR Geol. Inst. Trudy*, 145: 1–184 (in Russian).
- Campbell, A.E., 1992. Carbonate and siliciclastic shelf geometry in response to changes in relative sea level in the Guyana Basin. In: *Unconformities in seismic records and outcrop*. Ph.D. Dissert., Free Univ. Amsterdam.

- Campbell, K.E. and Frailey, C.D., 1991. Uncovering the mysteries of the Amazon. Vertebrate paleontology reveals creatures great and small. *Terra*, 29: 36–50.
- Caputo, M.V., 1984. Stratigraphy, tectonics, palaeoclimatology and palaeogeography of Northern basins of Brazil. Ph.D. Thesis, California Univ., Santa Barbara, 586 pp.
- Caputo, M.V., 1991. Solimões megashear: intraplate tectonics in Northwestern Brazil. *Geology*, 19: 246–249.
- Caputo, M.V., Rodrigues, R. and De Vasconcelos, D.N.N., 1971. Litoestratigrafia da bacia do rio Amazonas. *Rel. Tec. Int.* 641-A, Petrobras-Renor, Belem, pp. 35–46.
- Costa, E.V., 1980. Gasteropodos Cenozoicos do Alto Amazonas (Estado de Amazonas) Brasil. *An. Acad. Bras. Cienc.*, 52: 867–891.
- Costa, E.V., 1981. Revisão de gastropodes fosseis da localidade de Tres Unidos, Formação Pebas, Plioceno do Alto Amazonas, Brasil. *Anais II Cong. Latino-Americano Paleontol.*, Porto Alegre, pp. 635–649.
- Couper, R.A., 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. *N. Z. Geol. Surv. Paleontol. Bull.*, 22: 1–77.
- Couper, R.A., 1960. New Zealand Mesozoic and Cainozoic plant microfossils. *N. Z. Geol. Surv. Paleontol. Bull.*, 32: 1–87.
- Curtis, C.D. and Spears, D.A., 1968. The formation of sedimentary iron minerals. *Econ. Geol.*, 63: 257–270.
- Damuth, J.E. and Kumar, N., 1975. Amazon Cone: morphology, sediments, age, and growth pattern. *Geol. Soc. Am. Bull.*, 86: 863–878.
- De Gréve, L., 1938. Eine molluskenfauna aus dem Neogen von Iquitos am oberen Amazonas in Peru. *Abh. Schweiz. Palaeontol. Ges.*, 61, 133 pp.
- De Loczy, L., 1966. Contribuições a paleogeografia e história do desenvolvimento geológico da bacia do Amazonas. *Bras. Div. Geol. Mineral.*, Rio de Janeiro, 223, 96 pp.
- Dueñas, H., 1980. Palynology of Oligocene–Miocene strata of borehole Q-E-22, Planeta Rica, Northern Colombia. *Rev. Palaeobot. Palynol.*, 30: 313–328.
- Ducñas, H., 1986. Geología y Palinología de la Formación Cienaga de Oro, Región Caribe Colombiana. *Bol. Geol. Ingeominas, Publ. Esp.*, Bogotá, 18, 51 pp.
- Dumont, J.F., 1992. Rasgos morfoestructurales de la llanura Amazónica del Perú: efecto de la neotectónica sobre los cambios fluviales y la delimitación de las provincias morfológicas. *Bull. Inst. Fr. Et. Andines*, 21: 801–833.
- Dumont, J.F., 1993. Lake patterns as related to neotectonics in subsiding basins: the example of the Ucamara Depression, Peru. *Tectonophysics*, 222: 69–78.
- Eden, M.J., McGregor, D.F.M. and Morelo, J.A., 1982. Geomorphology of the middle Caqueta basin of eastern Colombia. *Z. Geomorphol. N.F.*, 26: 343–364.
- Frailey, C.D., 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Rio Acre region, Western Amazonia. (Contrib. Science, 374.) *Nat. Hist. Mus.*, Los Angeles, 46 pp.
- Franzini, E. and Potter, P.E., 1983. Petrology, chemistry, and texture of modern river sands, Amazon river system. *J. Geol.*, Univ. Chicago, 91: 23–39.
- Frederiksen, N.O., Carr, D.R. and Lowe, G.D., 1983. Middle Eocene palynomorphs from San Diego, California. Part I. Introduction, Spores and Gymnosperm pollen. *AASP Contrib. Ser.*, 12: 1–31.
- Frederiksen, N.O., 1983. Middle Eocene palynomorphs from San Diego, California. Part II. Angiosperm pollen and Miscellaneous. *AASP Contrib. Ser.*, 12: 32–154.
- Gabb, W.M., 1869. Descriptions of fossils from the clay deposits of the Upper Amazon. *Am. J. Conch.*, 4: 197–200.
- Galvis, J.V., Huguett, A. and Ruge, P., 1979. Geología de la Amazonia Colombiana. *Bol. Geol. Ingeominas, Bogotá*, 22: 1–86.
- Garraffelo, J.M. and De Araujo, V., 1990. *Anais XXXVI Cong. Bras. Geol.*, Natal, 1, pp. 470–474.
- Germeraad, J.H., Hopping, C.A. and Muller, J., 1968. Palynology of Tertiary sediments from tropical areas. *Rev. Palaeobot. Palynol.*, 6: 189–348.
- Gibbs, R.J., 1967. The geochemistry of the Amazon River system: Part 1. The factors that control the salinity and the composition and concentration of the suspended solids. *Geol. Soc. Am. Bull.*, 78: 1203–1232.
- González Guzmán, A.E., 1967. A palynological study on the Upper Los Cuervos and Mirador Formations (Lower and Middle Eocene; Tibu area, Colombia). Ph.D. Dissert., Univ. Amsterdam, 68 pp.
- Grabert, H., 1983. The Amazon shearing system. *Tectonophysics*, 95: 329–336.
- Grabert, H., 1991. Der Amazonas. Geschichte und Probleme eines Stromgebietes zwischen Pazifik und Atlantik. Springer, Berlin, 235 pp.
- Graham, A., 1988. Studies in Neotropical Palaeobotany, V. The Lower Miocene communities of Panama—The Culebra Formation. *Ann. Miss. Bot. Gard.*, 75: 1440–1466.
- Guerrero, J., 1993. Magnetostratigraphy of the upper part of the Honda Group and Neiva Formation. Miocene uplift of the Colombian Andes. Ph.D. Dissert., Duke Univ., 108 pp.
- Guizado, J., 1975. Las molasas del Plioceno–Cuaternario del Oriente Peruano. *Bol. Soc. Geol. Peru*, 45: 25–44.
- Hill, M.O., 1979. TWINSPLAN—a FORTRAN Program for arranging Multivariate Data in an Ordered Two Way Table by Classification of the Individuals and the Attributes. Cornell Univ., Dep. Ecol. Systematics, Ithaca, N.Y.
- Hooghiemstra, H., 1984. Vegetational and climatic history of the High Plain of Bogotá, Colombia. A continuous record of the last 3.5 million years. *Diss. Bot.*, 79, 368 pp.
- Hoorn, C., 1990. Evolución de los ambientes sedimentarios durante el Terciario y el Cuaternario en la Amazonia Colombiana. *Colombia Amazonica*, Bogotá, 4: 97–126.
- Hoorn, C., 1993a. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 105: 267–309.

- Hoorn, C., 1993b. Geología del Nororiente de la Amazonia Peruana: la formación Pebas. In: R. Kalliola, M. Puhakka and W. Danjoy (Editors), *Amazonia Peruana—Vegetación Húmeda Tropical en el Llano Subandino*. Paut and Onern, Jyväskylä, pp. 69–85.
- Hoorn, C., 1994. Fluvial palaeoenvironments in the Amazonas Basin (Early Miocene–early Middle Miocene, Colombia). *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 109: 1–54.
- Iversen, J. and Troels-Smith, J., 1950. Pollenmorfologiske definitioner of typer. *Dan. Geol. Unders., Række IV*, 3, 52 pp.
- Junk, W.J., 1983. Ecology of swamps on the middle Amazon. In: A.J.P. Gore (Editor), *Ecosystems of the World 4B*. Mires: Swamp, Bog, Fen, and Moor. Elsevier, Amsterdam, pp. 269–94.
- Kalliola, R., Puhakka, M., Salo, J., Tuomisto, H. and Ruokolainen, K., 1991. The dynamics, distribution and classification of swamp vegetation in Peruvian Amazonia. *Ann. Bot. Fennici*, 28: 225–329.
- Kalliola, R., Salo, J., Puhakka, M., Rajasilta, M., Häme, T., Neller, R.J., Räsänen, M.E. and Danjoy Arias, W.A., 1992. Upper Amazon channel migration. Implications for vegetation perturbation and succession using bitemporal Landsat MSS images. *Naturwissenschaften*, 79: 75–79.
- Katzer, F., 1903. *Grundzüge der Geologie des unteren Amazonasgebietes*. Leipzig, pp. 258–260.
- Kedves, M., 1961. *Etudes palynologiques dans le bassin de Dorog*, II. *Pollen Spores*, 3: 101–153.
- Kennett, J.P., 1982. *Marine Geology*. Prentice-Hall, Englewood Cliffs, NJ, 812 pp.
- Khobzi, J., Kroonenberg, S.B., Faivre, P. and Weeda, A., 1980. Aspectos geomorfológicos de la Amazonia y Orinoquia Colombianas. *Rev. CIAF*, Bogotá, 5: 97–126.
- Kronberg, B.I., Franco, J.R., Benchimol, R.E., Hazenberg, G., Doherty, W. and Vandervoet, A., 1989. Geochemical variations in Solimões Formation sediments (Acre basin, Western Amazonia). *Acta Amazonica*, 19: 319–333.
- Kroonenberg, S.B., Bakker, J.G.M. and Van der Wiel, A.M., 1990. Late Cenozoic uplift and paleogeography of the Colombian Andes: constraints on the development of high-andean biota. *Geol. Mijnbouw*, 69: 279–290.
- Krutzsch, W., 1970. Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen—sowie der Mikroplanktonformen des nördlichen Mitteleuropas, VII. VEB Gustav Fischer, Jena, 170 pp.
- Krutzsch, W., Pacltova, B. and Sontag, E., 1967. Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen—sowie der Mikroplanktonformen des nördlichen Mitteleuropas, IV und V. VEB Gustav Fischer, Jena.
- Landim, P.M.B., Bosio, N.J., Wu, F.T. and Castro, P.R.M., 1983. Minerais pesados provenientes do leito do rio Amazonas. *Acta Amazonica*, 13: 51–72.
- Leidelmeyer, P., 1966. The Paleocene and Lower Eocene pollen flora of Guyana. *Leidse Geol. Meded.*, 38: 49–70.
- Lindeman, J.C., 1953. The vegetation of the coastal region of Suriname. Ph.D. Dissert., Univ. Utrecht, 135 pp.
- Lips, J.M. and Duivenvoorden, J.F., 1991. Características morfológicas y químicas de Salados en la cuenca del Medio Caquetá (Amazonia Colombiana). *Colombia Amazonica*, Bogotá, 5: 119–130.
- Lorente, M.A., 1986. Palynology and palynofacies of the Upper Tertiary in Venezuela. *Diss. Bot.*, 99, 222 pp.
- Lundberg, J.G., Machado-Allison, A. and Kay, R.F., 1986. Miocene Characid fishes from Colombia: Evolutionary stasis and extirpation. *Science*, 234: 208–209.
- Lundberg, J.G. and Chernoff, B., 1992. A Miocene fossil of the Amazonian fish *Arapaima* (Teleostei, Arapaimidae) from the Magdalena River region of Colombia—Biogeographic and evolutionary implications. *Biotropica*, 24: 2–14.
- Maia, R.G., Godoy, H.K., Yamaguti, H.S., De Moura, P.A., Da Costa F.S., De Holanda, M.A. and Costa, J., 1977. Projeto de carvão no Alto Solimões. Relatório Final. CPRM-DNPM, 137 pp.
- Moraes Rego, L.F., 1930. Notas sobre a Geologia do território de Acre e da bacia do Javari. Cezar and Cavalcante, Manaus, 45 pp.
- Muller, J., de Di Giacomo, E. and Van Erve, A.W., 1987. A palynological zonation for the Cretaceous, Tertiary, and Quaternary of Northern South America. *AASP Contrib. Ser.*, 19: 7–76.
- Nakoman, E., 1965. Description d'un nouveau genre de forme, *Corsinipollenites*. *Soc. Geol. Nord Ann.*, 85: 155–600.
- NELL, 1992. Estado del conocimiento de la cuenca de los Llanos. Vicepresidencia de exploración y producción. Gerencia de exploración. Inst. Colombiano Petróleo. 2 volumes. Inter. Rep.
- Nuttall, C.P., 1990. A review of the Tertiary non marine molluscan faunas of the Pebasian and other inland basins of north-western South America. *Bull. Br. Mus. Nat. Hist. Geol.*, 45: 165–371.
- Orton, J., 1876. The Andes and the Amazon, or, Across the Continent of South America. Harper, New York, 3rd ed., 645 pp.
- Pardo, A.A. and Zuñiga, F., 1976. Estratigrafía y evolución tectónica de la región de la selva del Perú. (I) Paleozoico y (II) Mesozoico y Cenozoico. *Memorias Segundo Congreso Latinoamericano de Geología*. Bol. Geol., Caracas, Publ. Esp., 7: 588–608.
- Pereira, J. and Bocquentin, J., 1989. *Brasilosuchus mendesi*, n. g., n. sp., un novo representante da Família Gavialidae do Neogeno do Acre, Brasil. *Anais XI Cong. Bras. Paleontol.*, Curitiba, pp. 457–463.
- Playford, G., 1982. Neogene palynomorphs from the Huon Peninsula, Papua New Guinea. *Palynology*, 65: 29–54.
- Pflug, H. and Thomson, P.W., 1953. Pollen und Sporen des mitteleuropäischen Tertiärs. *Palaeontographica*, Abt. B, 94: 1–138.
- Potonié, R., 1956–60. Synopsis der Gattungen der Sporae dispersae, 1–3. *Geol. Jahrbuch. Beih.*, 23 (1956): 1–103; 31 (1958): 1–114; 39 (1960): 1–189.
- Proradam, 1979. La Amazonia Colombiana y sus recursos. Inst. Geogr. Agustín Codazzi, Bogotá. Several volumes.
- Purper, I., 1977. Some ostracodes from the Upper Amazon Basin, Brazil. *Environment and age*. In: H. Löffler and D.

- Danielopol (Editors), Aspects of Ecology and Zoography of Recent and Fossil Ostracoda. Junk, The Hague, 521 pp.
- Purper, I. and Pinto, I.D., 1985. New data and new ostracodes from Pebas Formation—Upper Amazon basin. *Coletanea de trabalhos paleontológicos*. Ministerio das minas e energia, departamento nacional da producao mineral. Brasilia. *Paleontol. Estratigr.*, 2: 427–434.
- Pye, K., Dickson, J.A.D., Schiavon, N. Coleman, M.L. and Cox, M., 1990. Formation of siderite–Mg–calcite–iron sulphide concretions in intertidal marsh and sandflat sediments, north Norfolk, England. *Sedimentology*, 37: 325–343.
- Radambrasil, 1977. Diverse authors. *Geologia. Levantamento de recursos naturais*. Ministerio das minas e energia departamento nacional da producao mineral. 14: 17–123.
- Ramanujam, C.G.K., 1966. Palynology of the Miocene lignite from South Arcot District, Madras, India. *Pollen Spores*, 8: 149–203.
- Räsänen, M., Salo, J. and Kalliola, R.J., 1987. Long-term fluvial perturbation in the western Amazon basin: Regulation by sub-andean tectonics. *Science*, 238: 1398–1401.
- Reif, W.E., 1982. Muschelkalk/Keuper bone-beds (Middle Triassic, SW Germany)—Storm condensation in a regressive cycle. In: G. Einsele and A. Seilacher (Editors), *Cyclic and Event Stratification*. Springer, Berlin, pp. 299–325.
- Regali, M.S., Uesugui, N. and Santos, A., 1974. Palinología dos sedimentos Meso-Cenozoicos do Brasil (II). *Bol. Téc. PETROBRAS*, Rio de Janeiro, 17: 263–362.
- Ruegg, W. and Rosenzweig, A., 1949. Contribución a la geología de las formaciones modernas de Iquitos y la Amazonia superior. Vol. Jub. Soc. Geol. Peru, (II), 3: 1–24.
- Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, P., Niemelä, P., Puhakka, M. and Coley, P.D., 1986. River Dynamics and the diversity of Amazon lowland forest. *Nature*, 322: 254–258.
- Sanz, V., 1974. Geología preliminar del área Tigre–Corrientes en el Nor Oriente Peruano. *Bol. Soc. Geol. Peru*, 44: 106–127.
- Sarmiento, G., 1993. Estratigrafía, palinología y paleoecología de la Formación Guaduas (Maastrichtiano–Paleoceno; Colombia). Ph.D. Dissert., Univ. Amsterdam.
- Seilacher, A., 1982. General remarks about event deposits. In: G. Einsele and A. Seilacher (Editors), *Cyclic and Event Stratification*. Springer, Berlin, pp. 161–174.
- Sheppard, L.M. and Bate, R.H., 1980. Plio-Pleistocene ostracods from the upper Amazon of Colombia and Peru. *Palaeontology*, 23: 97–124.
- Sioli, H., 1984. The Amazon and its main affluents: Hydrography, morphology of the river courses, and river types. In: H. Sioli (Editor), *The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin*. Junk, The Hague.
- Steinmann, G., 1930. *Geología del Peru*. Carl Winters Universitätsbuchhandlung, Heidelberg, 448 pp.
- Van der Hammen, T., 1954. El desarrollo de la flora Colombiana en los periodos geológicos; I. Maastrichtiano hasta Terciario mas inferior. *Bol. Geol. Bogotá*, 2: 49–106.
- Van der Hammen, T., 1956a. Description of some genera and species of fossil pollen and spores. *Bol. Geol. Bogotá*, 4: 111–117.
- Van der Hammen, T., 1956b. A palynological systematic nomenclature. *Bol. Geol. Bogotá*, 4: 63–101.
- Van der Hammen, T., 1961. Late Cretaceous and Tertiary stratigraphy and tectogenesis of the Colombian Andes. *Geol. Mijnbouw*, 40: 181–188.
- Van der Hammen, T., 1963. A palynological study on the Quaternary of British Guyana. *Leidse Geol. Meded.*, 29: 125–180.
- Van der Hammen, T., 1972. Changes in vegetation and climate in the Amazon Basin and surrounding areas during the Pleistocene. *Geol. Mijnbouw*, 51: 641–643.
- Van der Hammen, T. and Absy, M.L., 1994. Amazonia during the Last Glacial. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 109: 247–261.
- Van der Hammen, T. and García de Mutis, C., 1965. The Paleocene pollen flora of Colombia. *Leidse Geol. Meded.*, 35: 105–16.
- Van der Hammen, T. and Wijmstra, T.A., 1964. A palynological study on the Tertiary and the Upper Cretaceous of British Guyana. *Leidse Geol. Meded.*, 30: 183–241.
- Van der Hammen, T., Werner, J.H. and Van Dommelen, H., 1973. Palynological record of the upheaval of the Northern Andes: a study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its High-Andean biota. *Rev. Palaeobot. Palynol.*, 16: 1–122. [Also published as *The Quaternary of Colombia*, 2, Amsterdam (T. van der Hammen, Editor).]
- Van der Hammen, T., Urrego, L.E., Espejo, N., Duivenvoorden, J.F. and Lips, J.M., 1992. Late-glacial and Holocene sedimentation and fluctuations of river water level in the Caquetá River area (Colombian Amazonia). *J. Quat. Sci.*, 7: 57–67.
- Van der Wiel, A.M., 1991. Uplift and volcanism of the SE Colombian Andes in relation to Neogene sedimentation in the Upper Magdalena Valley. Ph.D. Dissert., Univ. Wageningen, 208 pp.
- Van Hoeken-Klinkenberg, P.M.J., 1964. A palynological investigation of some Upper Cretaceous sediments in Nigeria. *Pollen Spores*, 6: 209–31.
- Van Hoeken-Klinkenberg, P.M.J., 1966. Maastrichtian, Paleocene and Eocene pollen and spores from Nigeria. *Leidse Geol. Meded.*, 38: 37–48.
- Van Roosmalen, M.G.M., 1985. Fruits of the Guyanan flora. *Inst. Syst. Bot. Utrecht and Sylviculture Dep. Wageningen Agric. Univ.*, 483 pp.
- Varma, C.P. and Rawat, M.S., 1963. A note on some diporate grains recovered from Tertiary horizons of India and their potential marker value. *Grana Palynologica*, 4: 130–139.
- Wesselingh, F., 1993. On the systematics of Miocene aquatic molluscs from Los Chorros (Dept. Amazonas, Colombia) and Nuevo Horizonte (Dept. Loreto, Peru) with comments on palaeoenvironment and palaeogeography. M.Sc. Thesis, Free Univ., Amsterdam, 123 pp.
- Woodruff, F. and Savin, S.M., 1991. Mid-Miocene isotope stratigraphy in the deep sea: High resolution correlations,

- paleoclimatic cycles, and sediment preservation. *Paleoceanography*, 6: 755–806.
- Wright, J.D., Miller, K.G. and Fairbanks, R.G., 1992. Early and Middle Miocene stable isotopes: Implications for deepwater circulation and climate. *Paleoceanography*, 7: 357–389.
- Wijmstra, T.A., 1971. The palynology of the Guiana coastal basin. Ph.D. Dissert., Univ. Amsterdam, 62 pp.