

Environmental changes in Amazonia as evidenced by geological and paleontological data

Dilce de Fátima Rossetti¹ and Peter Mann de Toledo¹

¹Instituto Nacional de Pesquisas Espaciais-INPE, Rua dos Astronautas 1758-CP 515, 12245-970 São José dos Campos-SP, Brazil

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RESUMO. Mudanças ambientais na Amazônia evidenciadas por dados geológicos e paleontológicos. Discussões focalizando a biodiversidade Amazônica poderiam melhorar substancialmente se uma abordagem multidisciplinar fosse considerada. Além de influências biológicas, a divergência de espécies parece ser fortemente motivada por tensões no ambiente físico. Conseqüentemente, a reconstrução da história geológica, fornecida pela análise de dados sedimentológicos e paleontológicos, é crucial para se reconstituir os cenários de evolução de paleopaisagens, bem como compreender seus mecanismos controladores e a sucessão da biota associada através do tempo. Informações desta natureza para a região Amazônica são ainda escassas, pontuais e dispersas na literatura, pouco contribuindo para a análise dos mecanismos que influenciaram a evolução das espécies. Neste trabalho, apresenta-se uma visão geral referente aos registros sedimentares e paleontológicos disponíveis para a Amazônia. Apesar da documentação de florestas tropicais já em tempos pelo menos miocênicos, os dados aqui reunidos levam à conclusão de que seria impossível conceber um modelo de floresta tropical estável e com acúmulo progressivo das espécies desde então. Pelo contrário, os dados sedimentares e paleontológicos suportam um cenário muito mais complexo para o teatro evolucionário amazônico, caracterizado por modificações sucessivas no ambiente físico e na biota associada em consequência de mudanças no nível relativo do mar, no clima e no comportamento tectônico. Embora o impacto dos primeiros dois fatores tenha sido destacado em muitas publicações, são necessárias informações adicionais a fim de ressaltar a importância destas mudanças ambientais no tempo geológico. Em particular, trabalhos recentes vêm demonstrando cada vez mais a grande influência de reativações tectônicas no desenvolvimento dinâmico dos paleoambientes cenozóicos da Amazônia. Manifestações tectônicas são registradas até mesmo em tempos presentes, tendo forte controle no estabelecimento de bacias da drenagem e na distribuição de áreas inundadas e de terra firme. Conseqüentemente, este fator, ainda não enfatizado previamente em modelos biogeográficos, deve ser um ponto de grande interesse para estudos futuros enfocando a evolução e distribuição moderna de espécies amazônicas.

PALAVRAS-CHAVE: biodiversidade amazônica, registro sedimentar e fóssil, paleopaisagem, geologia histórica, tectônica.

ABSTRACT. Discussions focusing on the Amazon biodiversity might be significantly improved if a multidisciplinary approach is considered. In addition to biological influences, species divergence seems to be strongly motivated by stress in the physical environment. Therefore, the reconstruction of the geological history, provided by sedimentary and paleontological data, is crucial to provide different scenarios of paleolandscape evolution, and understand their controlling both mechanisms and the succession of the associated biota through geological times. For the particular case of the Amazonia, these data are still scarce, spotty and dispersed in the literature, limiting the reconstruction of the mechanisms that might have influenced species evolution. In this paper, an overview concerning the sedimentary and paleontological records available for Amazonia is provided. Although rainforests seem to have been established in Amazonia since at least the Miocene, this compilation leads to defend the hypothesis that would be impossible to envision a stable environment with progressive species accumulation through time. Sedimentary and paleontological data support an Amazonian evolutionary theater that appears to be much more complex, being characterized by successive changes of the physical environment and of the associated biota as a result of changes in relative sea level, climate and tectonics. Although the impact of the first two factors has been highlighted in many publications, further information must be collected in order to fully characterize the importance of these changes over time. In particular, recent studies have increasingly demonstrated the great significance of tectonic reactivations in Amazonia as a major control on development of paleoenvironments through the Cenozoic. Tectonics seems to be acting even at the present, having a strong control on the establishment of drainage basins and on the distribution of flooded and *terra firme* areas. Therefore, this factor, not emphasized by previous biogeographic models, should be a point of a main concern for future studies focusing on the evolution and modern distribution of Amazonian species.

KEY-WORDS: Amazon biodiversity, sedimentary and fossil record, paleolandscape, geological history, tectonics.

The highly complex nature of the Amazonian biodiversity is an unquestionable issue that has been increasingly stressed out on numerous regional and international fora and publications (e.g., several papers in Vieira *et al.* 2001 and references therein). This complexity arises from the fact that the influencing mechanisms are variable, as are rates and modes of speciation when different taxonomic groups are contrasted (Endler 1977, Patton and Silva 2001). Additionally, the still inadequate mapping of the biota has been of great concern, as it precludes conclusive answers for the construction of speciation events (Tuomisto *et al.* 2003). Despite these major biases,

the challenge now is to discuss the processes involved on the origin and evolution of the Amazonian biodiversity applying a more interdisciplinary approach.

In addition to biological influences (e.g., Patton and Silva 2001), many speciation hypotheses have claimed changes in physical environments as one of the most important mechanisms to motivate speciation events in many taxonomic groups (Rüegg and Rosenzweig 1949, Räsänen *et al.* 1987, 1990, 1995, Webb 1995, Humphries 2000, Patton *et al.* 2000, Patton and Silva 2001, Renaud and Dam 2002). To test this theory, one must look back into the past and analyze the sedi-

mentary and paleontological records in order to provide elements for reconstructing the evolution of ancient landscapes, their controlling mechanisms, as well as the succession of the contemporaneous biota.

For the particular instance of the Brazilian Amazonian biota, there have been many authors defending important speciation processes over the last million years (Absy *et al.* 1991, Van der Hammen *et al.* 1992, Webb and Rancy 1996, Behling and Costa 2000, Behling and Hooghiemstra 2000, Freitas *et al.* 2001, Pessenda *et al.* 2001, Sifeddine *et al.* 2001). Approaching this hypothesis is highly problematic taking into account the overall lack of detailed studies emphasizing the sedimentary successions and their associated fossil record. These are essential tools for reconstructing past environments and, thus, to hypothesize coherent evolutionary scenarios.

Studies focusing on Cretaceous and Cenozoic sedimentary strata are of particular interest for biodiversity analyses. According to phylogeographers (e.g., Avise 2000), these geological periods, in particular the Cenozoic, witnessed the origin and evolution of most of modern species (Aleixo e Rossetti in press). Sedimentary rocks of these ages are widespread in Amazonia, but their study is difficult due to the abundant vegetation cover and low relief, which result in a paucity of exposures. In addition, the huge size of the area and its still inaccessible nature, have precluded more widespread and systematic investigations. Furthermore, the available geological information concerning these deposits remains to be synthesized in order to be useful for discussing the influence of environmental factors on the origin and evolution of the Amazonian biodiversity.

This paper aims to provide an overview of the main geological events since the Cretaceous that might have contributed to the establishment of the Amazon evolutionary theater, with direct impacts on the development its associated biota. Rather than providing a full discussion of geological processes, this review will introduce aspects concerning past physical environments that these authors consider crucial to be brought into a biological perspective when discussing the factors that might have influenced the development of the Amazonian biodiversity. Data from the fossil record will be integrated, as much as possible, with geological information in order to discuss species evolution within the context of paleoenvironmental changes. This approach attempts to help demonstrating the dynamic nature of Amazonian landscape through time, and consequent impacts on the evolution of its associated biota. It is our goal to introduce geological and paleontological information in a language that can be understood by specialists from other field areas, in particular biologists and biogeographers.

GEOLOGIC FRAMEWORK

The oldest and more stable terrains of Brazilian Amazonia are located in two large (*i.e.*, 430,000 km²) areas of the

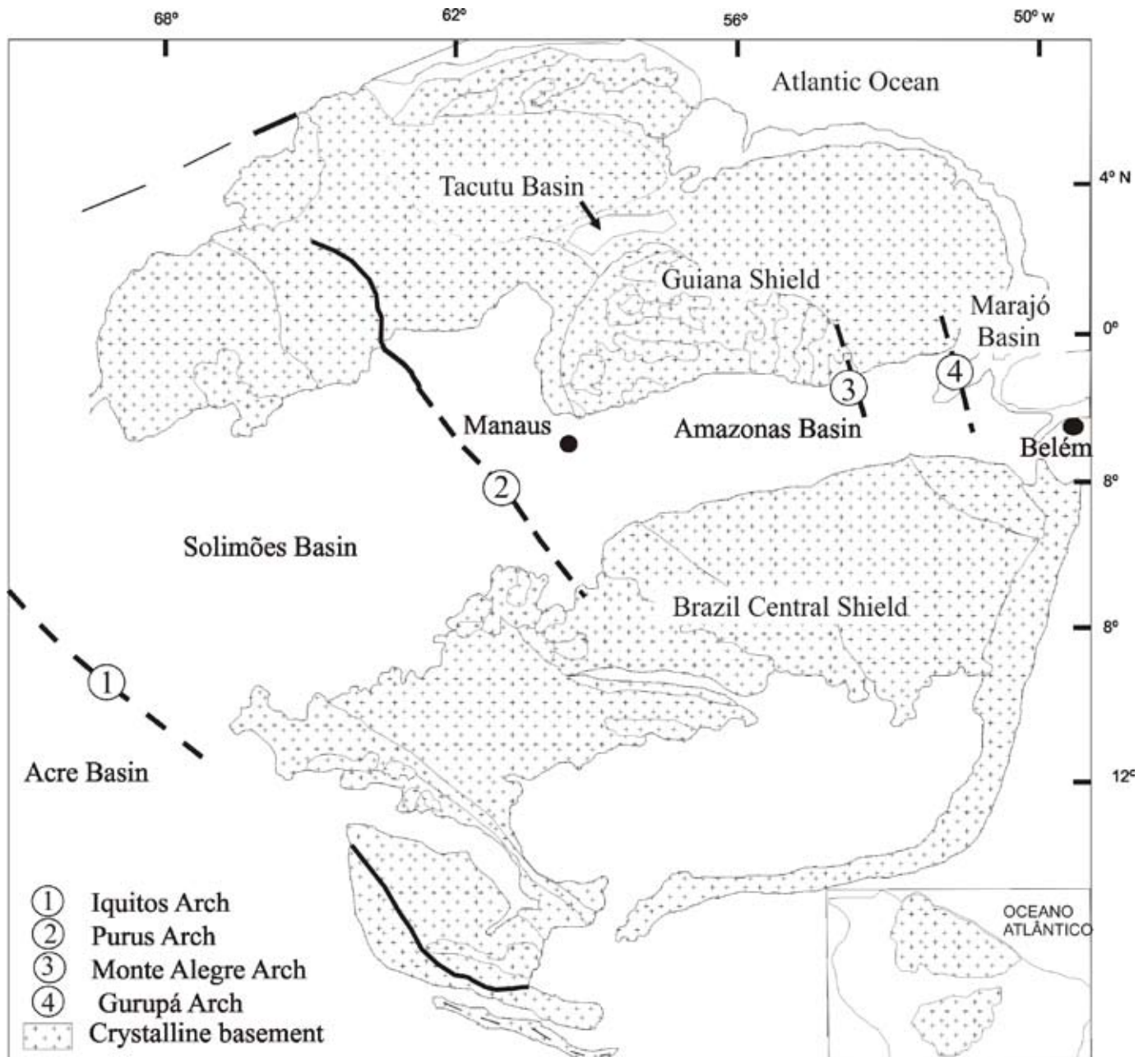
Amazonian Craton, represented by the Guiana and Brazil Central Shields (Fig. 1), whose ages range from 2.6 to 0.5 billion years. These areas are cut by depressions that served as sites for sediment deposition since approximately 500 million years ago. These depressions are represented by the Amazonas, Solimões and Acre sedimentary basins, which are defined by structural arches formed by ancient folding or faulting. Hence, the Amazonas Basin consists of an east-west elongated area nearly 500,000 km² and 6,500 m deep, bounded by the Gurupá (east) and Purus (west) arches. The Solimões Basin is up to 600,000 km² and more than 4,000 m deep, and is formed in the adjacency of the Amazonas Basin, between the Purus and Iquitos arches. The Acre Basin, located to the west of Iquitos Arch, comprises more than 7,000 m of sedimentary fill.

The Amazonian sedimentary basins were reactivated in the Cretaceous and Tertiary due to opening of the South Atlantic Ocean, a process that led to separation of South American and African tectonic plates. This tectonic process formed the Marajó Basin (also named Marajó Graben System) to the east of the Gurupá Arch (Fig. 1), which encompasses an area up to 1.5x10⁶ km² and about 10,000 m deep. It also led to the establishment of the Tacutu Basin (Fig. 1), a northeast-southwest elongated trough up to 7,000 m deep established in a central area of the Guiana Shield. The meso-Atlantic sea floor spreading caused a compression of the South American plate against the Nazca plate, producing several episodes of reactivation along the Andes. Tectonics was active even through the end of Tertiary. For instance, reactivations during Miocene produced compression in a large area near Manaus, as well as numerous faults eastward up to the coast (Igreja 1992, Bemerguy 1997, Costa and Hasui 1997, Góes and Rossetti 2001, Costa *et al.* 1993, 1995, 2002, Bemerguy *et al.* 2002). It has been proposed that several Upper Cretaceous and Miocene estuarine paleovalleys became established in northeastern Pará and along the Maranhão coastline as a result of tectonics (Rossetti 2006). Tectonics remained active even during the Quaternary, controlling the establishment of many of the major Amazonian river systems and of their tributaries (RADAM 1974, Costa *et al.* 1996, 1997, 2001, Bemerguy 1981, Bemerguy *et al.* 2002, Bezerra 2003). An incredible record of tectonic activity during Late Quaternary to Holocene has been provided for Marajó Island, northeastern Amazonia, which resulted in important reorganizations of drainage systems, well documented by an exceptionally well preserved complex network of abandoned channels (Rossetti and Valeriano 2006, Rossetti *et al.* in press a,b).

RECONSTRUCTING LANDSCAPES FROM THE SEDIMENTARY RECORD SINCE THE CRETACEOUS

Analysis of the sedimentary record provides key elements for reconstructing landscape evolution through the interpretation of past physical environments that represent sites for sediment deposition. A succession of historically related sedi-

Figure 1. Location of the main sedimentary basins, arches and shields in the Amazonian region.



mentary settings defines a depositional system, which characterizes a particular landscape developed during a certain period of time as a reflex of a combination of factors including tectonics, climate, sedimentation rate, sea level, topography, among others. All these parameters that dictate the type of physical environment can be inferred from the study of the sedimentary record.

Many further efforts are required in the future to gather round information and reveal adequately the succession of depositional systems in Brazilian Amazonia, as well as their controlling mechanisms. Despite incomplete records, the available information suggests many landscape changes over the past million years taking place as a response of tectonics linked to the Andean rise and the opening of the South Atlantic Ocean, as briefly summarized above. In addition to intense

tectonism, climate changes and sea level fluctuations were important factors to have influenced the sedimentary patterns during several geological periods in Amazonia.

At the end of Paleozoic, the Amazonian sedimentary basins experienced a long period of erosion, following a phase of intense magmatism and tectonic reactivations. Renewed deposition took place, forming the Alter do Chão Formation (Eiras *et al.* 1994, Cunha *et al.* 1994) during the mid to late Cretaceous (Price 1960, Daemon 1975). In sub-surface, this lithostratigraphic unit is recorded throughout the Amazonas and Solimões basins, while in surface it is widespread only to the east of Manaus, forming an elongated belt sandwiched between the Guiana and the Brazil Central Shields. This is because these portions of the basin remained, in general, more stable relatively to other areas, where tectonic reactivations

took place later on in the Cenozoic, promoting new subsidence, and the return to sediment deposition.

The Alter do Chão Formation encompasses a sedimentary pile that reaches more than 500 m thick. This unit comprises feldspathic, medium- to coarse-grained sandstones attributed to high energy, braided to anastomosed fluvial depositional systems and, secondarily, muddy lacustrine deltaic depositional systems (Daemon 1975). By the time the Alter do Chão Formation was deposited, the drainage flew in a main westward direction. The Andes was only in its early stages of development and, as a consequence, the channels could discharge their sediment load directly into the Pacific Ocean.

Despite the traditional view that the Alter do Chão Formation contains deposits formed on entirely continental environments, sedimentological data available for this unit are still inadequate to fully reconstruct their depositional settings. In fact, there is a great possibility that these deposits had also a contribution of marine processes, at least during sometime in their later evolution. This is suggested with basis on their comparison with many other temporally equivalent rocks formed in adjacent basins located to the east of the Amazonas Basin. For instance, deposits of the Itapecuru Group (Rossetti and Truckenbrodt 1997) that crop out in the São Luís-Grajaú Basins and Cametá Sub-basin, located respectively in most of Maranhão and northeastern Pará states, bear great similarity with the Alter do Chão Formation. Likewise this unit, the Itapecuru Group contains a large volume of deposits formed on continental environments, mainly fluvial, deltaic and lacustrine. However, an important part of this sedimentary succession contains an abundance of sandstones and mudstones formed on tidal estuarine and storm-influenced marine environments linked to shallow epicontinental seas (Rossetti 1997, 1998, Lima and Rossetti 1999, 2001, Rossetti *et al.* 2000, Rossetti 2001). Furthermore, a recent study focusing on the Alter do Chão Formation in an area located a few km to the east of the city of Manaus has led to the recognition of a variety of paleoenvironments also influenced by coastal processes (Rossetti and Netto 2006). According to these authors, these deposits formed in a wave-dominated deltaic depositional system that would have prograded into a marine-influenced basin. As opposed to previous interpretations, it appears that a significant part of Cretaceous deposits, in particular those formed during the Albian to Cenomanian periods in northern Brazilian basins, was influenced by widespread marine transgressions. These events would have resulted in submergence of large and shallow continental areas, affecting sediment deposition even in innermost portions of the intracratonic Amazonas Basin. Many other correlatable Cretaceous deposits located in sub-andian basins, such as the Llanos in Venezuela, the Maranhão in Colômbia, the Madre de Dios-Beni in Bolívia, and the Ucayali in Peru, also display a sedimentary record resulting from marine incursion derived from the Caribbean Sea (Sempere *et al.* 1997). It is interesting to recall that during this period of the geological time large areas of the United States Western Interior and of the African

continent were submerged, forming shallow epicontinental seaways, as a result of a worldwide trend for high sea level.

At the end of Cretaceous and beginning of Tertiary, sea retreat led to a prolonged regressive phase. This process would have exposed large Amazonian areas to subaerial processes, with development of a widespread surface of erosion marked by lateritic paleosols (King 1962, Wijmstra 1971, Lucas *et al.* 1989, Prasad 1983 Truckenbrodt *et al.* 1995). This phase of non-deposition and erosion, which might have lasted as much as 40 million years (Rossetti 2004), is correlated throughout many Amazonian areas, and has probably also correspondence with many other surfaces recorded in Gondwanan continents (Aleva 1981, Grandin and Thiry 1983, Firman 1994, Valetton 1999). The maintenance of prevailing subaerial conditions in Amazonia during this prolonged time length is not due solely to an overall drop in sea level, but to a combination with a major phase of tectonic stability. In the absence of tectonics, there is a smaller chance to create space for accommodating and preserving a sedimentary pile. The presence of lateritic paleosols denotes strong seasonality, with fluctuation between well defined dry and wet periods.

Following the sea level retreat, a renewed phase of tectonics took place during Miocene, as a reflex of Andean reactivations. This process would have shut a possible connection with the Pacific Ocean, favoring the creation of a large basin with mostly lacustrine sedimentation in western Amazonia, recorded by the Solimões Formation. A westward oriented drainage would have fed this lake, with sands sourced from the Purus Arch. Sediment inflows derived from the Caribbean Sea would have reached the lake time to time, being particularly significant during the later stages of deposition of the Solimões Formation (e.g., Nutall 1990, Hoorn, 1993, 1994, Monsch 1998). In addition, there is a proposal that even fully marine conditions might have been established during this time (Räsänen *et al.* 1995).

A rise in relative sea level is well documented in the northeastern Amazonia during the early to middle Miocene, as revealed by deposition of the Pirabas and Barreiras formations (Petri 1957, Ferreira 1966, Urdininea 1977, Góes *et al.* 1990, Rossetti 2001, Netto and Rossetti 2003). By that time, coastal areas of the Brazilian states of Pará and Maranhão were dominated by extensive but shallow carbonatic shelves that were connected to estuarine depositional systems, where sandstones and mudstones were formed under the influence of tidal currents (Rossetti *et al.* 1989, 1990, Arai *et al.* 1988, Góes *et al.* 1990). Estuarine deposits during the Miocene are recorded in areas located circa 200 km inland from the modern coastline. There seems to have no equivalent deposits entering westward into central areas of Amazonia, where temporally equivalent deposits are thin and fluvial in nature (Rossetti *et al.* 2005).

The end of Miocene was marked by a phase of widespread subaerial exposure, recorded by erosion and establishment of an expressive lateritic paleosol (Rossetti 2001, 2004). This resulted in an unconformity that is correlatable throughout a

distance of up to 1000 km along several basins of northeastern Amazonia. This surface, which is possibly equivalent to the unconformity recognized at the top of Solimões Formation in western Amazonia (Rossetti *et al.* 2004), denotes the prevalence of well defined, alternating dry and wet seasons attributed to climates relatively more arid than the present one (Rossetti 2001).

Following this period of sea level drop and soil development, a renewed phase of sedimentation is documented in Amazonia during an uncertain time between Pliocene and Pleistocene. To the west, this phase is represented by the Içá Formation, which consists mostly of reddish sandstones formed in fluvial systems. That drainage would have been different than the modern ones, being characterized by shallow, energetic, highly migrating, braided to anastomosed channels, probably also related to climates drier than today's (Rossetti *et al.* 2005). Deposits temporally equivalent to the Içá Formation in northeastern Amazonia and several areas in central Amazonia are inserted in the sedimentary succession known generically as Post-Barreiras (Mörner *et al.* 2001, Rossetti 2001, 2004). This unit, dominantly sandy, overlies the Miocene succession, and includes fluvial and eolian sedimentation.

After deposition of the Içá and Post-Barreiras units, no sedimentation is recorded in Amazonia until late Pleistocene. If in one hand this lack of record might be due to the absence of detailed studies, it is also plausible to propose that this region might have experienced another period of erosion. This is suggested with basis on the presence of several areas where late Pleistocene and younger deposits unconformably overlie Plio-Pleistocene units. In part, this implies in the lack of new space for sediment accommodation related to a relatively stable tectonic scenario, and probably low relative sea level.

Several pulses of sediment deposition are recorded in Amazonia, however, during the last 40,000 yr BP. Sedimentation seems to have been particularly active to the west of Manaus, where progressively less energetic alluvial deposits developed through time (Rossetti *et al.* 2005). Unpublished data reveal that this paleoenvironmental scenario seems to have also prevailed in areas located further eastward, near the Amazon mouth. There are many studies showing changes in the distribution of vegetation cover during this time interval, with several records of open vegetation suggestive of drier climates even in central Amazonian areas (Rossetti *et al.* 2004). Increased humidity during the last 6,000 to 5,000 yr BP (Turcq *et al.* 1998, Behling and Costa 2000, Behling and Hooghiemstra 1998, 1999, 2000, Baker *et al.* 2001, Mayle *et al.* 2000) might have contributed for expansion of the rain forest as seen today.

CHANGES IN PHYSICAL ENVIRONMENT AS INDICATED BY THE FOSSIL RECORD

As shown above, modern Amazonia should not be regarded as a stable environment, but rather as a transitory landscape

representative of a momentum within a dynamic evolutionary history. Any regional change on physical conditions might cause disequilibrium in this system and, as a consequence, an impact on the evolutionary trends of the associated biota. This is because the organisms will be under selective pressure, being forced to adapt to new environmental characteristics.

In general, vegetation is the first to respond to changes in physical environment (Crowling *et al.* 2001, Foody 2003, Kerr and Ostrovsky 2003), and the paleoflora record should reflect these changes. Unfortunately, the Cretaceous record of plant fossils is almost inexistent in Amazonia. Palynological assemblages of Cretaceous strata from extreme northeastern Amazonia contain representatives of a paleoflora dominated by conifers and gymnosperms (Lima *et al.* 1980, Lima 1982), suggestive of cool and arid climates. These data are consistent with information obtained from other areas in Brazil (e.g., Lima 1980, Falkenheim *et al.* 1981, Lima 1983, Petri 1983), which might be an indicative that this climatic condition might have prevailed throughout the Brazilian territory.

Despite the scarcity of fossil information, there is no reason to invoke a much different climatic condition in Amazonia during this time. The prevalence of feldspathic deposits attributed to high energy, braided to anastomosed fluvial systems, as observed in the Alter do Chão Formation, is favored under climates tending to aridity. It would be unconceivable to have a vegetation type similar to the present one covering Amazonia developing under such environmental conditions.

Despite indications of semi-arid climatic patterns in some marginal Amazonian areas (e.g., Rossetti *et al.* 2001), an increased humidity toward the end of Cretaceous, as recorded in many Brazilian areas (e.g., Lima 1983, Petri 1983, Suguio and Barcelos 1983a,b, Petri 1998), might have contributed to forest development. A paleofauna adapted to this ecosystem is well recorded up to Paleocene (Estes and Wake 1972). During the Eocene, several lines of evidence point to the presence of neotropical rainforests in South America (Burnham and Johnson 2004; Jaramillo *et al.* 2006). Unfortunately, there is no sedimentary record from this period exposed in Amazonia. On the other hand, as mentioned above, the development of a widespread surface of non-deposition marked by paleosols denoting high seasonality throughout Amazonia during this time leads to suggest the prevalence of subtropical forests.

Following a period of expansion of the Antarctic ice sheet during Oligocene, humid forests became amplified again in South America (Behrensmeyer *et al.* 1992). Pollen record indicates tropical forests in Amazonia during Miocene, with many modern plant genera with taxonomic diversity similar to modern ones already present at the end of this period (Van der Hammen 2001, Colinvaux and Oliveira 2001). Fossil leaves from Pirabas Formation, northeastern Amazonia, demonstrate that many plant species similar to modern ones might have been established even in Early Miocene. This is particularly suggested by an assemblage of paleoflora with up to 20 species that hold a close phylogenetic similarity with endemic families present in modern Amazonian areas (Duarte

2001). Likewise Amazonia, a study based on evolutionary rate analysis points to great species diversification in seasonally dry neotropical forests during Late Miocene to Pliocene (Pennington *et al.* 2004).

Despite the record of Miocene forests bearing plant groups bearing similarity to modern neotropical forests, sedimentary strata from this age in the Acre Basin display paleovertebrate representatives with morphological adaptations for open habitats, such as large rodents with cursorial habitats (Mones and Toledo 1989), and phororacoid birds. Furthermore, Miocene strata from western Amazonia bear a faunal assemblage consisting of primates (Kay and Cozzuol 2006) and a highly diverse ground sloth population (e.g., Rancy 2000) within a same stratigraphic horizon. A similar faunal association was recently recorded in Miocene deposits from Colombia (Meldrum and Kay 1997). These occurrences may point to a mosaic environment with gallery forests and open vegetation in Amazonia, similarly to what has been documented for several other areas in South America (e.g., Paula Couto 1979, Pascual 1996). Such landscape records a new scenario for development of co-evolutionary processes involving a widespread area of tropical forest in northern South America, with the emergence of frugivorous faunal elements in a prevailing hypsodonty and cursorial community (Pascual 1996, Behrensmeier *et al.* 1992).

The rapid expansion of mixed forest and open vegetation was probably favored by the establishment of a homogeneous geomorphologic pattern characterized by lowland areas (Irion *et al.* 1995), abundance of water, and higher humidity than most of the previous Oligocene period. As a consequence, large bodies of water developed, probably as seen in the modern Pantanal ecosystem in central South America. This habitat would have promoted the arrival of large faunal elements, with Miocene deposits from Acre Basin in western Amazonia documenting the largest diversity of giant extinct crocodiles found so far (e.g., Souza Filho *et al.*, 1989, 1993; Vilanueva and Souza Filho, 1990).

Relatively to Miocene, the Pliocene became progressively cooler worldwide, a tendency that continued throughout Pleistocene, favoring the replacement of forests by savannas (Hooghiemstra and Van der Hammen 1998, Van der Hammen and Hooghiemstra, 2000, Van der Hammen 2001). This climatic change was accompanied by a modification on the physical system in South America, which became connected to North America after almost 50 million years of complete isolation (Stehli and Webb 1985). This geological period in Amazonia is recorded by Içá Formation to the west and Post-Barreiras Formation to the east of Amazonia. Unfortunately, no fossil has been documented in these units but, as discussed previously, the sedimentary record gives indications of prevailing climates drier than today's. In addition to climate, the ecosystem in this region might have been affected by the Panama land bridge, which allowed migratory trends of terrestrial paleofauna between the Americas. Although questionable (Heads 2005), molecular studies of modern vertebrate

groups suggest the origin of many living species during this time (Bates 2001, Patton and Silva 2001).

Although still spotty, there are several pollen data from Amazonia supporting remarkable changes in vegetation cover since Pleistocene, with periods cooler/drier than today's in late Quaternary (Latrubesse and Franzinelli 1988, Behling and Hooghiemstra 1999, Behling *et al.* 1999, Mayle *et al.* 2000, Behling *et al.* 2000, Behling and Costa 2000, 2001, Absy *et al.* 1991, Behling *et al.* 2001, Baker *et al.* 2001, Freitas *et al.* 2001, Haffer 2001, Sifeddine *et al.* 2001, Bush *et al.* 2004, Pessenda *et al.* 2004). This is particularly shown by expansion of the genus *Podocarpus* during this time and in early Holocene (e.g., Hoorn 1997).

Additionally, a megafauna typical of open habitats is recorded in Pleistocene strata from western Amazonia (Rancy 2000). Furthermore, the mastodont *Stegomastodon waringi* and the ground sloth *Eremotherium laurillardii* displaying late Pleistocene radiocarbon ages were recorded for a central Amazonian site (Rossetti *et al.* 2004). These data are consistent with analysis of Andean glaciers, which reveals a volume of dust accumulation during Holocene that is much greater (i.e., 200 times greater) than the present one, which is related to drier periods over Amazonas Basin (Van der Hammen 2001). The Holocene has experienced an increased humidity, with a pulse between 10,000-8,000 years, 6,000 and 5,000 years and after 4,000 years, when the rainforest as seen today fully developed (Sifeddine *et al.* 2001).

FINAL COMMENTS

The foregoing presentation serves to show the importance of integrating the sedimentary and fossil records in order to reconstruct paleolandscapes. Even where data are incomplete, as in Brazilian Amazonia, this type of information provides elements for understanding how the Amazonian vegetation and the associated fauna might have responded to modifications in environmental conditions through time. Despite many controversies about how and when these changes took place, a dynamic Amazonian system is becoming a scenario of increased acceptance. The presence of rainforests similar to modern ones since early Tertiary times is unquestionable. This cannot be used, though, to claim an ancient Amazonian forest system that would have uniformly persisted stable up to present (Fischer 1960, Colinvaux and Oliveira 2001, Hoorn 2006), which would conflict with all other databases pointing to fluctuating landscapes through time. Likewise many other regions in the world (Culver and Rawson 2000), Amazonia seems to have responded to environmental changes acting at a global and regional scale, which have controlled the distribution of forested areas and the associated biota. The major challenge for future projects is to increase the efforts to adequately gather a larger volume of information from the sedimentary and fossil records, which will be used to provide a more precise reconstruction of the Amazonian geological

history. This advance is essential to approach issues concerning to decipher the origin, evolution, and modern species.

Despite the importance of geological history for analyzing the Amazonian biodiversity, one must be aware of inappropriate uses of geological data. For instance, although already extensively addressed in previous publications (Haffer 2001, Rossetti 2004), it is important to highlight the lack of geological support for some speciation hypotheses that have been broadly applied in order to explain the Amazonian biodiversity. For instance, the use of structural arches as biogeographic barriers for modern species (e.g., Räsänen *et al.* 1987, 1990, Patton *et al.* 2000, Patton and Silva 2001) is not sustained, as these are features that became buried long ago. Even considering that some arches might have experienced reactivations in younger geologic periods, many other tectonic events unrelated to these arches took place in Amazonia that might have larger implications for the species distribution. Likewise, the presence of major marine transgressions (p.e., Rëgg and Rosenzweig 1949, Webb 1995, Bates 2001) over the region, even during Quaternary (Irion 1984, Frayley *et al.* 1988, Campbell 1990), as the cause for species isolation, was never proved with basis on geological data (see for instance Hoorn 1996, Marshall and Lundberg 1996, Paxton and Crampton 1996). A rise in sea level in the order of up to 150 m, as proposed by some authors (e.g., Nores 2004), would have caused the submergence of most of the Amazonian lowlands, which is not demonstrated by the available geological data. Furthermore, the fluvial barrier hypothesis (e.g., Wallace 1853, Bates 1863, Ayres 1986, Capparella 1988, Ayres and Clutton-Brock 1992), already questioned by some authors (Haffer 2001, Haffer and Prance 2001), might work solely for those Amazonian rivers developed over geologically stable areas (Aleixo 2004). This, however, is far from being a rule for many rivers of the Amazon drainage basin, which might have had a very dynamic development, changing many times their position through time (e.g., Rossetti *et al.* 2005).

An important geological aspect to be brought into the biogeographic perspective is the neotectonic history of Amazonia. Despite traditionally considered as a stable terrain, many works, as previously mentioned, have increasingly shown that this region has experienced important fault reactivations even during the Quaternary. Seismic activity is going on even at the present, as revealed by the occurrence of several epicenters concentrated in eight seismogenic zones, where earthquakes of magnitudes up to 6.0 in the Richter scale have been reported (Mito 1993). Considering the prevailing lowland nature of the area, fault displacement, even at a small scale, might have tremendous impact in terrain configuration and development of drainage basins (RADAM 1974, Costa *et al.* 1996, 1997, 2001, Bemerguy 1981, Bemerguy *et al.* 2002, Bezerra 2003, Rossetti and Valeriano, 2006, Rossetti *et al.* 2005a, in press a,b, Silva 2005). This process dictates the distribution of flooded and *terra firme* areas, and seems to affect species development (Rossetti *et al.* 2005b, Aleixo and Rossetti in press). Despite the great importance of tectonics during the

Quaternary evolution of Amazonia, this factor has never been considered on biogeographic models, and should be, together with climate change, one point of major concern in future studies. Analysis of the sedimentary record is the key to reconstruct such events through geological times, as tectonic instabilities might determine the styles of both depositional environments and sedimentary structures.

Studies attempting to analyze the influence of geological events on development of Amazonian biodiversity must be undertaken in conjunction with investigations aiming to determine the timing of species divergences. In more recent years, many species phylogenies have been reconstructed with the aid of DNA sequence data (e.g., Richardson *et al.* 2001, Pennington *et al.* 2004, Erkens *et al.* 2007, Aleixo and Rossetti in press). Several of these studies point to genetic speciation in rainforest animals predating Pleistocene (e.g., Moritz *et al.* 2000, Glor *et al.* 2001), being probably related to Miocene (Aleixo 2004, Patton and Silva 2004) or even Oligocene (George 1993). Taking into account South American mammals, application of this hypothesis might be sustained considering the autochthonous groups marsupials, caviomorph rodents and edentates, but some questions are still raised in the case of the evolutionary scenario for all murid genera. The latter group, as well as a significant portion of the remaining modern tropical mammal fauna, derives from North American ancestors, being part of the inter-American biotic exchange, initiated at the end of Pliocene about 3 million years ago (Marshall *et al.* 1994). The time and mode of arrival of each group in South America is still open to intense debate on the basis of incomplete and even controversial evidences related to the contrast between molecular and geological / paleontological data. Therefore, a genetic divergence pre-dating the Miocene certainly cannot be applied to all mammalian genera (Costa 2003), and distinct groups should be analyzed under sound hypotheses of biogeographical and speciation events (Galewski *et al.* 2005, Tuomisto 2007, Koepfli *et al.* 2007), including different times of arrival in South America (Stephan *et al.* 2004). The most likely is to consider that speciation within the various groups was not synchronous, as seen by relationships among South American edentates, but strongly linked to distinct geological events (Delsuc *et al.* 2004). Therefore, the use of molecular studies aiming to test geological hypothesis as mechanisms for species divergence must be undertaken comparing results from various groups.

Finally, it is essential to address issues related to the modern distribution of Amazonian biodiversity within a historical perspective. This procedure might contribute to a better understanding of species distributions in the modern ecosystem (Tuomisto and Ruokolainen 1997, Ruokolainen *et al.* 2005). For instance, the presence of open habitats within the tropical rainforest matrix might be related to historical factors. In this regard, it has been claimed that areas of *cerrados* in Amazonia represent remains of Holocene vegetation developed in connection with central Brazilian areas during past drier climates, which became constrained to small spots as a result of

increased seasonality (Ledru 2002, Pennington 2004, Ledru *et al.* 2006). Taking into account the mid-Holocene expansion of Amazon rainforest as the most likely scenario (Mayle 2004, Vivo and Carmignotto 2004), it would be expected to find relics of such past environments in modern habitats. A further example is provided by modern distributions of forest trees suggestive of past biogeographic patterns of fauna that would have acted as seed dispersals. There are several plant species in tropical rainforest of Central South America with large seeds that do not have modern dispersers (Barlow 2000). Ground sloths, toxodonts and mastodonts, which are well recorded in sedimentary deposits from several areas in Amazonia, are potential candidates as feeders and dispersal agents (Galetti 2002). Many of the fruiting trees that have their dispersal capability restricted to long distance are naturally more suitable for extinctions or constraints on their biogeographic ranges.

Therefore, historical and geological data must be combined with studies of Amazonian biodiversity, not only to approach the origin and evolution of species, but also as the key to understand their modern distribution and predict their possible changes upon future modifications on the physical environment, such as global warming.

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REFERENCES

- Absy, M. L., A. Cleef, M. Fournier, L. Martin, M. Servant, A. Sifeddine, M. F. Ferreira-Silva, F. Soubiès, K. Suguio, B. Turcq and T. Van der Hammen (1991) Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de l'Amazonie au cours des 60.000 dernières années. Première comparaison avec d'autres régions tropicales. *Comptes Rendus de l'Académie des Sciences Paris* 312: 673-678.
- Aleixo, A. (2004) Historical diversification of a terra-firme forest bird superspecies: a phylogeographic perspective on the role of different hypotheses of Amazonian diversification. *Evolution* 38:1303-1317.
- _____ and D. F. Rossetti (In press) Avian gene trees, landscape evolution, and geology: towards a modern synthesis of Amazonian historical biogeography? *Journal of Ornithology*.
- Aleva, G. J. J. (1981) Bauxitic and other duricrusts on the Guiana Shield, South America, p. 261-269. In: P. K. Barnerji (ed.) *Laterisation Processes, Proceeding of International Seminar on Laterisation Processes*. New Delhi: Oxford and IBH Publishers.
- Aweise, J. C. (2000) *Phylogeography: the history and formation of species*. Harvard: Harvard University Press.
- Ayres, J. M. (1986) *Uakaris and Amazonian flooded forests*. PhD Thesis. Cambridge: University of Cambridge.
- _____ and T. H. Clutton-Brock (1992) River boundaries and species range size in Amazonian primates. *American Naturalist* 140: 531-471.
- Baker, P. A., G. O. Seltzer, S. C. Fritz, R. B. Dunbar, M. J. Grove, P. M. Tapia, S. L. Cross, H. D. Rowe and J. P. Broda (2001) The history of South American tropical precipitation for the past 25,000 years. *Science* 291: 640-643.
- Barlow, C. (2000) *The ghosts of evolution: nonsensical fruit, missing partners, and other ecological anachronisms*. New York: Basic Books.
- Bates, H. W. (1863) *The Naturalist on the River Amazon*. London: Murray.
- Bates, J. (2001) Avian diversification in Amazonia: evidence for historical complexity and a vicariance model for a basin diversification pattern, p. 119-139. In: I. C. Vieira, J. M. C. Silva, D. C. Oren and M. A D' Incao (eds.) *Diversidade biológica e cultural da Amazônia*. Belém: Museu Paraense Emílio Goeldi.
- Behling, H. and M. L. Costa (2000) Holocene environmental changes from the Rio Curuá record in the Caxiuana region, eastern Amazon Basin. *Quaternary Research* 53: 369-377.
- _____ and _____ (2001) Holocene vegetational and coastal environmental changes from the Lago Crispim record in northeastern Pará State, eastern Amazonia. *Review of Palaeobotany and Palinology* 114: 145-155.
- _____ and H. Hooghiemstra (1998) Later Quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 139: 251-267.
- _____ and _____ (1999) Environmental history of the Colombian savannas of the Llanos Orientales since the last glacial maximum from lake records El Pinal and Carimagua. *Journal of Paleolimnology* 21: 461-476.
- _____ and _____ (2000) Holocene Amazon rainforest-savanna dynamics and climatic implications: high resolution pollen record from Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Science* 15: 687-695.

- _____, J. C. Berrio and H. Hooghiemstra (1999) Late Quaternary pollen records from the middle Caquetá river basin in central Colombian Amazon. *Palaeogeography, Palaeoclimatology, Palaeoecology* 145:193-213.
- _____, H. W. Arz, J. Pätzold and G. Wefer (2000) Late Quaternary vegetational and climate dynamics in northeastern Brazil, inferences from marine core GeoB 3104-1. *Quaternary Sciences Reviews* 19: 981-994.
- _____, G. Keim, G. Irion, W. Junk and J. Nunes de Melo (2001) Holocene environmental changes in the Central Amazon Basin inferred from Lago Calado, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 173: 87-101.
- Behrensmeyer, A. K., J. D. Damuth and W. A. Di Michele (1992) *Terrestrial ecosystems through time*. Chicago:University of Chicago Press.
- Bemerguy, R. L. (1997) *Morfotectônica e evolução paleogeográfica da região da calha do rio Amazonas*. Doctoral Thesis. Belém: Universidade Federal do Pará.
- _____. (1981) *Estudo sedimentológico dos paleocanais da região do Rio Paracauari, Soure, Ilha do Marajó, Estado do Pará*. M.Sc. Thesis. Belém: Universidade Federal do Pará.
- _____, J. B. S. Costa, Y. Hasui, M. S. Borges and A. V. Soares Jr. (2002) Structural geomorphology of the Brazilian Amazon region, p. 245-258. In: E. L. Klein, M. L. Vasque and L. T. Rosa Costa (eds.) *Contribuições à geologia da Amazônia*. Belém: Sociedade Brasileira de Geologia (Núcleo Norte).
- Bezerra, P. E. L. (2003) *Compartimentação morfotectônica do interflúvio Solimões-Negro*. M.Sc. Thesis. Belém: Universidade Federal do Pará.
- Burnham, R. J. and K. R. Johnson (2004) South American palaeobotany and the origins of neotropical rainforests. *Philosophical Transactions of the Royal Society B: Biological Sciences* B 359: 1595-1610.
- Bush, M. B., P. E. Oliveira, P. A. Colinvaux, M. C. Miller and J. C. Moreno (2004) Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214: 359-393.
- Campbell, K. E. (1990) The geologic basics of biogeographic patterns in Amazonia, p. 33-43. In: G. Peters and R. Hutterer (eds.) *Vertebrates in the tropics*. Bonn: Museum Alexander Koenig.
- Capparella, A. (1988) Genetic variation in Neotropical birds: implications for the speciation process. *International Ornithological Congress*, 19. Acta Ottawa 2: 1658-1664.
- Colinvaux, P. A. and P. E. Oliveira (2001) Amazon plant diversity and climate through the Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166: 51-63.
- Costa, L. P. (2003) The historical bridge between the Amazon and the Atlantic forest of Brasil: a study of molecular phylogeography with small mammals. *Journal of Biogeography* 30: 71-86.
- Costa, J. B. S. and Y. Hasui (1997) Evolução geológica da Amazônia, p. 15-19. In: M. L. Costa and R. S. Angélica (eds.) *Contribuições à geologia da Amazônia*. Belém: Sociedade Brasileira de Geologia.
- _____, M. S. Borges, R. L. Bemerguy, J. M. G. Fernandes, J. R. Costa and M. L. Costa (1993) A evolução cenozóica da região de Salinópolis, nordeste do Estado do Pará. *Geociências* 12: 373-396.
- _____, Y. Hasui, M. S. Borges and R. L. Bemerguy (1995) Arcabouço tectônico mesozóico-cenozóico da região da calha do Amazonas. *Geociências* 14: 77-83.
- _____, R. L. Bemerguy, Y. Hasui, M. S. Borges, C. R. P. Ferreira Jr., P. E. L. Bezerra, M. L. Costa and J. M. G. Fernandes (1996) Neotectônica da região amazônica-aspectos tectônicos, geomorfológicos e deposicionais. *Geonomos* 4: 23-44.
- _____, E. L. Moraes, H. Behling, J. C. V. Melo, N. V. M. Siqueira, and D. C. Kern (1997) Os sedimentos de fundo da Baía de Caxiuanã, p. 121-137. In: P. L. B. Lisboa (ed.) *Caxiuanã*. Belém: Museu Paraense Emílio Goeldi.
- _____, D. C. Kern, H. Behling and M. Borges (2002) Geologia, p. 179-206. In: P. L. B. Lisboa (ed.) *Caxiuanã: populações tradicionais, meio físico e diversidade biológica*. Belém: Museu Paraense Emílio Goeldi.
- Crowling, S. A., M. A. Maslin and M. T. Sykes (2001) Paleovegetation simulations of Lowland Amazonia and implications for neotropical allopatry and speciation. *Quaternary Research* 55: 140-149.
- Cunha, P. R. C., F. G. Gonzaga, L. F. C. Coutinho and F. J. Feijó (1994) Bacia do Amazonas. *Boletim de Geociências da Petrobrás* 8: 47-55.
- Culver, S. J. and P. F. Rawson (2000) *Biotic response to Global Change. The last 145 million years*. Cambridge: Cambridge University Press.
- Daemon, R. F. (1975) Contribuição à datação da Formação Altér do Chão, Bacia do Amazonas. *Revista Brasileira de Geociências* 5: 58-84.
- Delsuc F., S. F. Vizcaino and E.J.P. Douzery (2004) Influence of Tertiary paleoenvironmental changes on the diversification of South American mammals: a relaxed mo-

- lecular clock study with xenarthrans. *BMC Evolutionary Biology* 4:11-14.
- Duarte, L. (2001) Paleoflórula, p. 169-196. In: D. F. Rossetti and A. M. Góes (eds.) *O Neógeno da Amazônia Oriental*. Belém: Museu Paraense Emílio Goeldi, Coleção Friedrich Katzer.
- Eiras, J. F., C. R. Becker, E. M. Souza, F. G. Gonzaga, J. G. F. Silva, L. M. F. Daniel, N. S. Matsuda and F. J. Feijó (1994) Bacia do Solimões. *Boletim de Geociências da Petrobras* 8: 17-45.
- Ekerns, R. H. J., L. W. Chatrou, J. W. Maas, T. van der Niet and V. Savolainen (2007) A rapid diversification of rainforest trees (*Gutteria*: Annonaceae) following dispersal from Central into South America. *Molecular Phylogenetics and Evolution* 44: 399-411.
- Endler, J. A. (1977) *Geographic variation, Speciation and Clines*. Princeton: Princeton University Press.
- Estes, R. and M. H. Wake (1972) The first fossil record of caecilian amphibians. *Nature* 239: 228-239.
- Ferreira, C. S. (1966) Características lito-paleontológicas na Formação Pirabas, Estado do Pará. *Conferência Geológica das Guianas*, Anais, CNPq, 6: 101-111.
- Firman, J. B. (1994) Paleosols in laterite and silcrete profiles. Evidence from the South East Margin of the Australian Precambrian Shield. *Earth-Science Reviews* 36: 149-179.
- Fischer, A. G. (1960) Latitudinal variations in organic diversity. *Evolution* 14: 64-81.
- Foody, G. M. (2003) Remote sensing of tropical forest environments: towards the monitoring of environmental resources for sustainable development. *International Journal of Remote Sensing* 24: 4035-4046.
- Freitas, H. A., L. C. R. Pessenda, R. Aravena, S. E. M. Gouveia, A. S. Ribeiro and R. Boulet (2001) Late Quaternary vegetation dynamics in the southern Amazon Basin inferred from carbon isotopes in soil organic matter. *Quaternary Research* 55: 39-46.
- Faljenheim, F. U. H., M. R. Franke and A. V. Carozzi (1981) Petroleum geology of the Macaé Formation (Albian-Cenomanian), Campos Basin, Brazil- Carbonate microfacies, depositional and diagenetic models, natural and experimental porosity. *Petrobras Ciênc. Técn., Seção Exploração Petrolífera* 1: 1-140.
- Frailey, C. D., E. L. Lavina, A. Rancy and J. P. Souza Filho (1988) A proposed Pleistocene/Holocene lake in the Amazon Basin and its significance to Amazonian geology and biogeography. *Acta Amazonica* 18: 119-143.
- Galetti, M. (2001) Frutos dispersos por mamíferos extintos. *Ciência Hoje* 29: 83-85.
- Galewski, T., J-F Mauffrey, Y. L. R. Leite, J. L. Patton and E. J. P. Douzery (2005) Ecomorphological diversification among South American spiny rats (Rodentia; Echimyidae): a phylogenetic and chronological approach. *Molecular Phylogenetics and Evolution* 34: 601-615.
- George, W. (1993) The strange rodents of Africa and South America, p. 119-141. In: W. George and R. Lavocat (eds.) *The Africa-South America connection*. Oxford: Clarendon Press.
- Glor, R. E., L. J. Vitt and A. Larson (2001) A molecular phylogenetic analysis of diversification in Amazonian *Anolis* lizards. *Molecular Ecology* 10: 2661-2668.
- Góes, A. M., D. F. Rossetti, A. C. R. Nogueira and P. M. Toledo (1990) Modelo deposicional preliminar da Formação Pirabas no nordeste do estado do Pará. *Boletim do Museu Paraense Emílio Goeldi, Série Ciências da Terra* 2: 3-15.
- _____ and D. F. Rossetti (2001) Gênese da Bacia de São Luís-Grajaú, p. 15-29. In: D. F. Rossetti, A. M. Góes and W. Truckenbrodt (eds.) *O Cretáceo na Bacia de São Luís Grajaú*. Belém: Museu Paraense Emílio Goeldi, Coleção Friedrich Katzer.
- Grandin, G. and G. Thiry (1983) Les grandes surfaces continentales tertiaires des regions chaudes. Successions des types d'altération. *Cahiers ORSTOM Série Géologie* 12: 3-18.
- Haffer, J. (2001) Hypotheses to explain the origin of species in Amazonia, p. 45-118. In: I. C. Vieira, J. M. C. Silva, D. C. Oren and M. A. D' Incao (eds.) *Diversidade biológica e cultural da Amazônia*. Belém: Museu Paraense Emílio Goeldi.
- _____ and T. Prance (2001) Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* 16: 579-607.
- Heads, M. (2005) Dating nodes on molecular phylogenies: a critique of molecular biogeography. *Cladistics* 21: 62-78.
- Hooghiemstra, H. and T. Van der Hammen (1998) Neogene and Quaternary development of the Neotropical rainforest. *Earth-Science Reviews* 44: 147-183.
- Hoorn, C. (1993) Marine incursion and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynological study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105: 267-309.

- _____ (1994) *Miocene palynostratigraphy and paleoenvironments of northwestern Amazonia*. Doctoral Thesis. Amsterdam: University of Amsterdam.
- _____ (1996) Miocene deposits in the Amazonian foreland basin-Discussion. *Science* 273: 122-123.
- _____ (1997) Palynology of the Pleistocene glacial/interglacial cycles of the Amazon Fan (holes 940A, 944A, and 946A), p. 397-409. In: R. D. Flood, D. J. W. Piper, A. Klaus and L. C. Peterson (eds.) *Proceedings of the Ocean Drilling Program*, Scientific Results 155.
- _____ (2006) A formação do Amazonas. *Scientific American Brasil* 5: 40-45
- Humphries, C. J. (2000) Form, space and time: which comes first? *Journal of Biogeography* 27: 11-15.
- Igreja, H. L. S. (1992) *Aspectos tectono-sedimentares do fanerozóico do nordeste do Estado do Pará e noroeste do Maranhão*. Doctoral Thesis. Belém: Universidade Federal do Pará.
- Irion, G. (1984) Sedimentation and sediments of Amazonian rivers and evolution of the Amazonian landscape since Pliocene times, p. 201-214. In: H. Sioli (ed.) *The Amazon limnology and landscape ecology of a mighty tropical river and its basin*. Dordrecht: Junk Publishers.
- _____, J. Muller, J. N. Mello and W. J. Junk (1995) Quaternary geology of the Amazonian Lowland. *Geo-Marine Letters* 15: 267-309.
- Jaramillo, C., M J. Rueda and G. Mora (2006) Cenozoic plant diversity in the neotropics *Science* 311: 1893-1896.
- Kay, R. F. and M. A. Cozzuol (2006) New platyrrhine monkeys from the Solimões Formation (late Miocene, Acre State, Brazil). *Journal of Human Evolution* 50: 673-686.
- Kerr J. T. and M. Ostrovsky (2003) From space to species: ecological applications for remote sensing. *Trends in Ecology and Evolution* 18: 299-305.
- King, L. C. (1962) *The morphology of the Earth*. Edinburgh: Oliver and Boyd.
- Koepfli, K-P, M. E. Gompper, E. Eizirik, C-C Ho, L. Linden, J. E. Maldonado and R. K. Wayne (2007) Phylogeny of the Procyonidae (Mammalia: Carnivora): Molecules, morphology and the Great American Interchange. *Molecular Phylogenetics and Evolution* 43: 1076-1095.
- Latrubesse, E. M. and E. Franzinelli (1998) Late Quaternary alluvial sedimentation in the Upper Rio Negro Basin, Amazônia, Brazil: paleohydrological implications, p. 261-271. In: G. Benito, V. R. Baker and K. J. Gregory (eds.) *Paleohydrology and environmental change*. Germany: John Wiley and Sons Ltd.
- Ledru, M.-P. (2002) Late Quaternary history and evolution of the cerrados as revealed by palynological records, p. 33-52. In: P. S. Oliveira and R. J. Marquis (eds.) *The Tropical Cerrados of Brasil: Ecology and Natural History of a Neotropical Savanna*. New York: Columbia University Press.
- _____, G. Ceccantini, S. E. M. Gouveia, J. A. López-Sáez, L. C. R. Pessenda and A. S. Riberito (2006) Millennial-scale climatic and vegetation changes in a northern Cerrado (Northeast, Brazil) since the Last Glacial Maximum. *Quaternary Science Reviews* 25: 1110-1126.
- Lima, M. R. (1980) Considerações palinológicas a respeito de correlação estratigráfica entre as formações cretáceas do nordeste do Brasil: *1º Congresso Latinoamericano de Paleontologia*. Buenos Aires 5: 227-233.
- _____ (1982) Palinologia da Formação Codó, Maranhão. *Boletim do Instituto de Geociências-USP* 13: 116-128.
- _____ (1983) Paleoclimatic reconstruction of the Brazilian Cretaceous based on palynological data. *Revista Brasileira de Geociências* 13: 223-228.
- _____, V. J. Fulfaro and A. Bartorelli (1980) Análise palinológica de sedimentos cretáceos da região de Marabá, estado do Pará. *Boletim do Instituto de Geociências-USP* 11: 55-161.
- _____ and D. F. Rossetti (1999) Depositional facies in late Cretaceous-early Tertiary deposits in northwestern Maranhão State, Brazil. *Revista Brasileira de Geociências* 29: 237-244.
- _____ and _____ (2001) Análise faciológica e seqüencial de depósitos de delta de baía (Neocretáceo), leste da Bacia do Grajaú, MA, p. 151-190. In: D. F. Rossetti, A. M. Góes and W. Truckenbrodt (eds.) *O Cretáceo da Bacia de São Luís-Grajaú*. Belém: Museu Paraense Emílio Goeldi.
- Lucas, Y., B. Kobilsek and A. Chauvel (1989) Structure, genesis and present evolution of Amazonian bauxites developed on sediments. *Travaux ICSOBA* 19: 81-94.
- Marshall, L. G. and J. G. Lundberg (1996) Miocene deposits in the Amazonian foreland basin-Discussion. *Science* 273: 123-124.
- _____, A. L. Berta, R. Hoffstetter, R. Pascual, O. Reig, M. Bombim and A. Mones (1994) Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. *Paleovertebrata* 1: 176.
- Mayle, F. A., R. Burbridge and T. J. Killeen (2000) Millennial-scale dynamics of southern Amazonian rain forests. *Science* 290: 2291-2294.

- Meldrum, D. J. and R. F. Kay (1997) *Nuciraptor rubricae*, a new Pitheciin seed predator from the Miocene of Colombia. *American Journal of Physical Anthropology* 102: 407-427.
- Mioto, J. A. (1993) *Sismicidade e zonas sismogênicas do Brasil*. Doctoral Thesis. Rio Claro: Universidade Estadual Paulista.
- Mones, A. and P. M. Toledo (1989) Primer hallazgo de *Euphilus Ameghino*, 1889 (Mammalia:Rodentia:Neopiblemidae) em el Neogeno del Estado do Acre, Brasil. *Contribuciones Paleontológicas Museu Historia Natural de Montevideo* 21: 1-15.
- Monsch, K. A. (1998) Miocene fish faunas from the north-western Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143: 31-50.
- Mörner, N.-A., D. F. Rossetti and P. M. Toledo (2001) The Amazonian rainforest: only some 6-5 million years old, p. 3-18. In: I. C. Vieira, J. M. C. Silva, D. C. Oren and M. A. D'Incao (eds.) *Diversidade biológica e cultural da Amazônia*. Belém: Museu Paraense Emílio Goeldi.
- Moritz, C., J. L. Patton, C. J. Schneider and T. B. Smith (2000) Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics*. 31: 553-563.
- Netto, R. G. and D. F. Rossetti (2003) Ichnology and salinity fluctuations: a case study in the Early Miocene (Lower Barreiras succession) of São Luís Basin, Maranhão, Brazil: *Revista Brasileira de Paleontologia* 6: 5-18.
- Nores, M. (2004) The implications of Tertiary and Quaternary sea level rise events for avian distribution patterns in the lowlands of northern South America. *Global Ecology and Biogeography* 13: 149-161.
- 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. *British Museum of Natural History and Geology Bulletin* 45: 165-371.
- Pascual, R. (1996) Late-Cretaceous-Recent land-mammals na approach to south american geobiotic evolution. *Mastozoologia Neotropical* 3: 133-152.
- Patton, J. L. and M. N. Silva (2001) Molecular phylogenetics and the diversification of Amazonian mammals, p. 139-166. In: I. C. Vieira, J. M. C. Silva, D. C. Oren and M. A. D'Incao (eds.) *Diversidade biológica e cultural da Amazônia*. Belém: Museu Paraense Emílio Goeldi.
- Patton, J.L., M. N. Silva and J. R. Malcolm (2000) Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bull. Am. Mus. Nat. Hist.* 244: 1-306.
- Paula Couto, C. (1979) *Tratado de paleomastozoologia*. Rio de Janeiro: Academia Brasileira de Ciências.
- Paxton, C. G. M. and W. G. R. Crampton (1996) Miocene deposits in the Amazonian foreland basin-Discussion. *Science* 273: 123.
- Pennington, R. T., D. E. Prado and C. A. Pendry (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27: 261-273.
- _____, M. Lavin, D. E. Prado, C. A. Pendry, S. K. Pell and C. A. Butternworth (2004) Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosophical Transactions of the Royal Society B: Biological Sciences* B 359: 515-538.
- Pessenda, L. C. R., R. Boulet, R. Aravena, V. Rosolen, S. E. M. Gouveia, A. S. Ribeiro and M. Lamotte (2001) Origin and dynamics of soil organic matter and vegetation changes during the Holocene in a forest-savanna transition zone, southern Amazon state, Brazilian Amazon region. *The Holocene* 11: 250-254.
- _____, A. S. Ribeiro, S. E. Gouveia, R. Aravena, R. Boulet and J. A. A. Bendassoli (2004) Vegetation dynamics during the late Pleistocene in the Barreirinhas region, Maranhão State, Northeastern Brazil, based on carbon isotopes in soil organic matter. *Quaternary Research* 62: 183-193.
- Petri, S. (1983) Brazilian Cretaceous paleoclimates: evidence from clay-minerals, sedimentary structures and palynomorphs. *Revista Brasileira de Geociências* 13: 215-222.
- _____, (1998) Paleoclimas da Era Mesozóica no Brasil- evidências paleontológicas e sedimentológicas. *Revista de Geociências da Universidade de Guarulhos* 6: 22-38.
- _____, (1957) Foraminíferos miocênicos da Formação Pirabas. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo (Geologia)* Special Publication 216.
- Prasad, G. (1983) A review of the early Tertiary bauxite event in South America, Africa and India. *Journal of African Earth Sciences* 1: 305-313.
- Price, L. I. (1960) Dentes de Theropoda num testemunho de sonda no Estado do Amazonas. *Anais da Academia Brasileira de Ciências* 32: 79-84.
- RADAM (1974) Folha SA.22 Belém. Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.
- Rancy, A. (2000) *Paleoecologia da Amazônia. Megafauna do Pleistoceno*. Florianópolis: Universidade Federal de Santa Catarina, Editora UFSC.

- Räsänen, M. E., J. S. Salo and R. J. Kalliola (1987) Fluvial perturbation in the western Amazon Basin: regulation by long-term sub-Andean tectonics. *Science* 238: 1398-1401.
- _____, J. S. Salo, H. Jungner and L. Romero-Pittman (1990) Evolution of the Western Amazon lowland relief: impact of Andean foreland dynamics. *Terra Nova* 2: 320-332.
- _____, A. M. Linna, J. C. R. Santos and F. R. Negri (1995) Late Miocene tidal deposits in the Amazonian foreland basin. *Science* 269: 386-390.
- Renaud, S. and J. V. Dam (2002) Influence of biotic and abiotic environment on dental size and shape evolution in a Late Miocene lineage of murine rodents (Teruel basin, Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 184: 163-175.
- Richardson, J. E., R. T. Pennington, T. D. Pennington and P. M. Hollingsworth (2001) Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science* 293: 2242-2245.
- Rossetti, D. F. (1997) Internal architecture of mixed tide and storm-influenced deposits: an example from the Alcântara Formation, northern Brazil. *Sedimentary Geology* 114: 163-188.
- _____. (1998) Facies architecture and sequential evolution of an incised-valley estuarine fill: the Cujupe Formation (Upper Cretaceous to Lower Tertiary), São Luís Basin, northern Brazil. *Journal of Sedimentary Research* 68: 299-310.
- _____. (2001) Late Cenozoic sedimentary evolution in northeastern Pará, Brazil, within the context of sea level changes. *Journal of South American Earth Sciences* 14: 77-89.
- _____. (2004) Paleosurfaces from northeastern Amazonia as a key for reconstructing paleolandscapes and understanding weathering products. *Sedimentary Geology* 169: 151-174.
- _____. (2006) The Role of Tectonics on Preservation of Incised-Valley Estuaries in Areas with Low Accommodation Rates: Examples from Upper Cretaceous and Miocene Successions in Northern Brazil, p. 199-218. In: R. W. Dalrymple, D. A. Leckie and R. W. Tillman (eds.) *Incised Valleys in Time and Space*- SEPM Special Publication. 1st ed. Tulsa: SEPM Special Publication, v. 85.
- _____ and M. M. Valeriano (2006) Evolution of the lowest Amazon basin modeled from the integration of geological and SRTM topographic data. *Catena* 70: 253-265.
- _____, A. M. Góes, M. M. Valeriano and M. C. C. Miranda (In press a). Quaternary tectonics in a passive margin: Marajó Island, northern Brazil. *Journal of Quaternary Science*.
- _____, M. M. Valeriano, A. M. Góes and M. Thales (In press b). An Abandoned estuary within Marajó Island: implications for Late Quaternary paleogeography of northern Brazil. *Estuaries and Coasts*.
- _____ and Netto (2006) First Evidence of Marine Influence in the Cretaceous of the Amazonas Basin, Brazil. *Cretaceous Research*, 27 (in press).
- _____, A. M. Góes, W. Truckenbrodt and J. Anaisse Jr (2000) Tsunami-induced large-scale scour-and-fill structures in Albian to Cenomanian deposits of Grajaú Basin, Northern Brazil. *Sedimentology* 47: 309-323.
- _____, W. Truckenbrodt and A. M. Góes (1989) Estudo paleoambiental e estratigráfico dos Sedimentos Barreiras e Pós-Barreiras na região Bragantina, nordeste do Pará. *Boletim do Museu Paraense Emílio Goeldi, Série Ciências da Terra* 1: 25-74.
- _____ and W. Truckenbrodt (1997) Revisão estratigráfica para os depósitos do Albiano-Terciário na Bacia de São Luís, Maranhão. *Boletim do Museu Paraense Emílio Goeldi-Série Ciências da Terra* 9: 31-43.
- _____, P. M. Toledo, H. M. Moraes-Santos and A. E. A Santos Jr. (2004) Reconstructing habitats in Central Amazonia using megafauna, sedimentology, radiocarbon and isotope analysis. *Quaternary Research* 61: 289-300.
- _____, P. M. Toledo and A. M. Góes (2005a) New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. *Quaternary Research* 63: 78-89.
- _____ and P. M. Toledo (2005b) Biodiversity from a historical geology perspective: a case study from Marajó Island, lower Amazon. *Geobiology* 4: 215-223.
- Ruokolainen, K., H. Tuomisto and R. Kalliola (2005) Landscape heterogeneity and species diversity in Amazonia, p. 251-270. In: E. Bermingham, C. W. Dick and C. Moritz (eds.) *Tropical rainforests: past, present, and future*. Chicago: University of Chicago Press.
- Rüegg, W. and A. Rosenzweig (1949) Contribución a la geología de las formaciones modernas de Iquitos y de la Amazonia Superior. *Boletín de la Sociedad Geológica del Peru*, Volume Jubilar Parte II (3): 1-24.
- Sempere, T., R. F. Butler, D. R. Srichards, L. G. Marshall, W. Sharp and C. C. Fisher III (1997) Stratigraphy and chronology of Upper Cretaceous-Lower Paleogene strata in Bolivia and northwest Argentina. *Bulletin of Geological Society of America* 109: 709-727.

- Sifeddine A., L. Marint L., B. Turcq, C. Volkmer-Ribeiro, F. Soubiès, R. C. Cordeiro and K. Suguio (2001) Variations of the Amazonian rainforest environment: a sedimentological record covering 30,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 168: 221-235.
- Silva, C. (2005) *Análise da tectônica cenozóica da região de Manaus e adjacências*. Doctoral Thesis. Rio Claro: UNESP.
- Steppan, S. J., R. M. Adkins and J. Anderson (2004) Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Systematic Biology* 53: 533-553
- Souza Filho, J. P., J. C. Bocquentin and F. R. Negri (1993) Um crânio de *Hesperogavialis* sp. (Crocodylia, Alligatoridae) do Mioceno Superior-Plioceno do Estado do Acre, Acre-Brasil. *Ameghiniana* 30: 321-356.
- Souza Filho, J. P. and J. B. Villanueva (1989) Uma contribuição ao estudo da distribuição geográfica da família Gavaiidae (Crocodylia) da América do Sul. *Ameghiniana* 26: 237-252.
- Stehli, F. G. and S. D. Webb (1985) *The great American biotic interchange*. New York: Plenum.
- Suguio, K. and J. H. Barcelos (1983a) Paleoclimatic evidence from the Areado Formation, Cretaceous of the São Francisco Basin, State of Minas Gerais, Brazil. *Revista Brasileira de Geociências* 13: 229-231.
- _____ and _____ (1983b) Paleoclimatic evidence from the Bauru Group, Cretaceous of the Paraná Basin, Brazil. *Revista Brasileira de Geociências* 13: 229-231.
- Tuomisto, H. (2007) Amazon conservation: pushing the limits of biogeographical knowledge. *Journal of Biogeography* 34: 1291-1293.
- _____ and K. Ruokolainen (1997) The role of ecological knowledge in explaining biogeography and biodiversity in Amazônia. *Biodiversity and Conservation* 6: 347-357.
- _____, K. Ruokolainen and M. Yli-Halla (2003) Dispersal, environment, and floristic variation of western amazonian forests. *Science* 299: 241-244.
- Turcq, B., A. Sifeddine, L. Martin, M. L. Absy, F. Soubies, K. Suguio and C. Volkmer-Ribeiro (1998) Amazonian rainforest fires: a lacustrine record of 7000 years. *Ambio* 27: 139-142.
- Truckenbrodt, W., B. Kotschoubey and B. Hieronymus (1995) Aluminization: an important process in the evolution of Amazonian bauxites. *Tav. ICSOBA* 22: 27-42.
- Urdininea, J.A. (1977) *Aspectos Geoquímicos e ambientais dos calcários da Formação Pirabas*. Doctoral Thesis. Porto Alegre: Universidade Federal do Rio Grande do Sul.
- Valenton, I. (1999) Saprolite-bauxite facies of ferralitic duricrusts on palaeosurfaces of former Pangaea, p. 87-129. In: M. Thiry and R. Simon-Coinçon (ed.) *Palaeoweathering, palaeosurfaces and related continental deposits*. Special Publication of the International Association of Sedimentologists n° 27. Oxford: Blackwell Science.
- Van der Hammen, T. (2001) Paleocology of Amazonia, p. 19-44. In: I. C. Vieira, J. M. C. Silva, D. C. Oren and M. A. D'Incao (eds.) *Diversidade biológica e cultural da Amazônia*. Belém: Museu Paraense Emílio Goeldi.
- _____ and H. Hooghiemstra (2000) Neogene and Quaternary history of vegetation, climate and plant diversity in Amazonia. *Quaternary Science Reviews* 19, 725-742.
- _____, L. E. Urrego, N. Espejo, J. Duivenvoorden and J. M. Lips (1992) Late glacial and Holocene sedimentation and fluctuations of river water level in the Caquetá River area (Colombia Amazonia). *Journal of Quaternary Science*. 7: 57-68.
- Vieira, I. C., J. M. C. Silva, D. C. Oren and M. A. D' Incao (2001) *Diversidade biológica e cultural da Amazônia*. Belém: Museu Paraense Emílio Goeldi.
- Villanueva, J. B. and J. P. Souza Filho (1990) O crocodiliano sul-americano *Carandaisuchus* como sinonímia de *Mourasuchus* (Nettosuchidae). *Revista Brasileira de Geociências* 20: 230-233.
- Vivo, M. and A. P. Carmignotto (2004) Holocene vegetation change and the mammal faunas of South America and Africa. *Journal of Biogeography* 31: 943-957.
- Wallace, A. R. (1853) *A narrative of travels on the Amazon and Rio Negro*. London: Reeve.
- Webb, S. D. (1995) Biological implications of the Middle Miocene Amazon seaway. *Science* 269: 361-362.
- _____ and A. Rancy (1996) Late Cenozoic evolution of the neotropical mammal fauna, p. 335-357. In: J. Jackson, A. F. Budd and A. G. Coates (eds.) *Evolution and environment in tropical America*. Chicago: University of Chicago.
- Wijmstra, T. A. (1971) *The palynology of the Guiana coastal basin*. Ph.D. Thesis, The Netherlands: University of Amsterdam.