

Environmental changes in Amazonia as evidenced by geological and paleontological data

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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 both their controlling mechanisms and the succession of the associated biota through geological times. For 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 oscillations 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 and 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 Amazonian 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 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 the 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

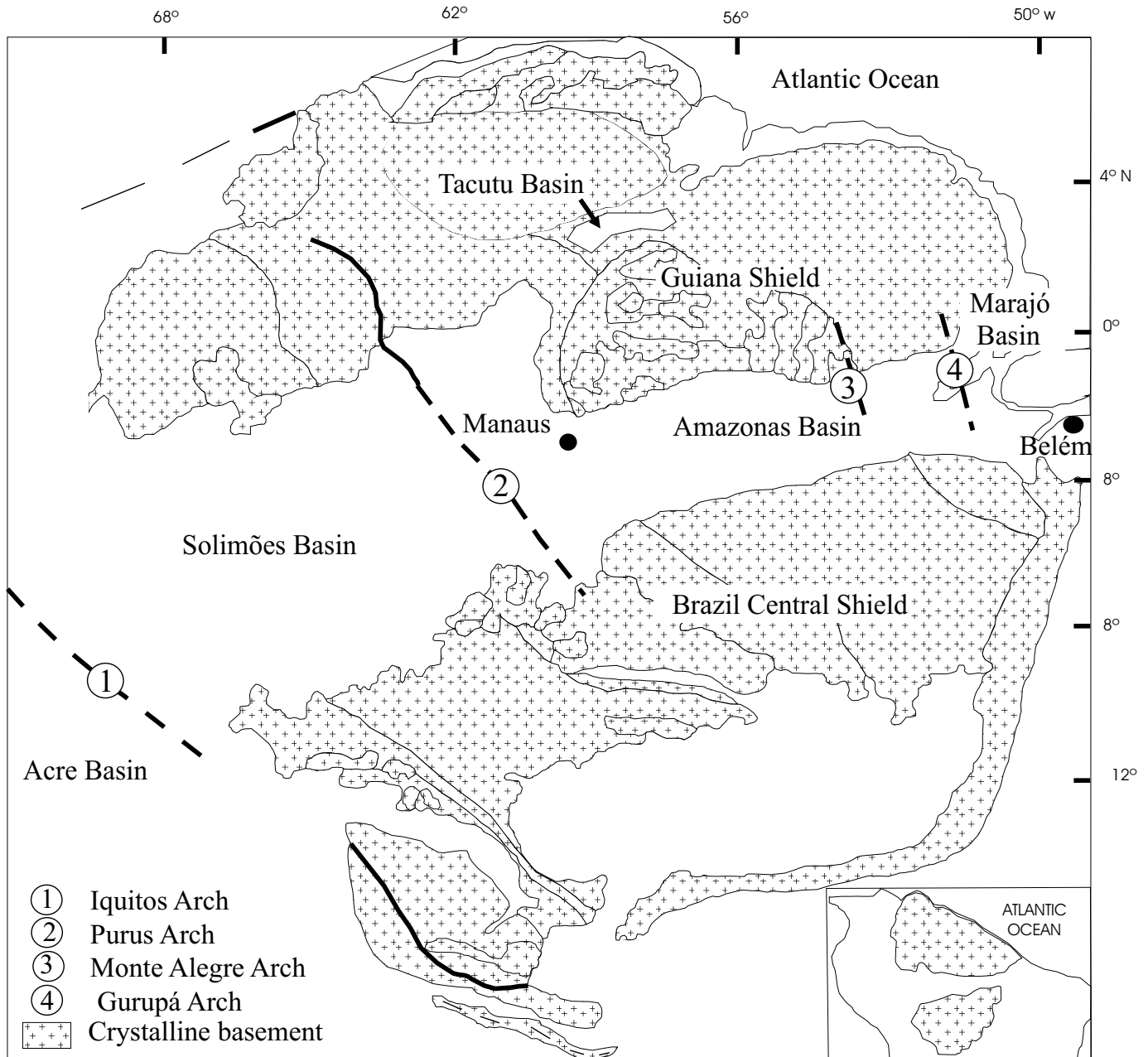
Amazonian Craton, represented by the Guiana and Brazil Central Shields (Fig. 1), whose ages range from 2.6 to 0.5 billion years. These areas are cut by depressions that served as sites for sediment deposition since approximately 500 million years ago. These depressions are represented by the Amazonas, Solimões and Acre sedimentary basins, which are defined by structural arches formed by ancient folding or faulting. 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 the State of Maranhão and northeastern of the State of 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 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 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 northeast-

ern 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 the 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 the 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 the Oligocene, humid forests became amplified again in South America (Behrensmeyer *et al.* 1992). Pollen record indicates tropical forests in Amazonia during the 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 the Pirabas Formation, northeastern Amazonia, demonstrate that many plant species similar to modern ones might have been established even in the 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 the Içá Formation to the west and the 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 ver-

tebrate 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 the Pleistocene, with periods cooler/drier than today's in the 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 *Ereotherium 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). This 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 the 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 the Pleistocene (e.g., Moritz *et al.* 2000, Glor *et al.* 2001), being probably related to the Miocene (Aleixo 2004, Patton and Silva 2004) or even the 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 the 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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