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New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution

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Abstract

Although many of the current hypotheses to explain the origin and distribution of the Amazon biodiversity has been based directly or indirectly on geological data, the reconstruction of the geological history of the Amazon region is still inadequate to analyze its relationship with the biodiversity. This work has the main goal to characterize the sedimentary successions formed in the Brazilian Amazon in the Neogene-Quaternary discussing the evolution of the depositional systems through time and analyzing their main controlling mechanisms in order to fill up this gap. Radar image interpretation, sedimentological studies, and radiocarbon dating allowed the mapping of Plio-Pleistocene to Holocene units along the Solimões-Amazonas River, Brazil. This integrated work led to the characterization of five sedimentary successions overlying Miocene deposits of the Solimões/Pebas Formation, which include the following: Içá Formation (Plio-Pleistocene), deposits Q1 (37,400–43,700 ^{14}C yr B.P.), deposits Q2 (27,200 ^{14}C yr B.P.), deposits Q3 (6730–2480 ^{14}C yr B.P.), and deposits Q4 (280–130 ^{14}C yr B.P.). These deposits occur mostly to the west of Manaus, forming NW–SE elongated belts that are progressively younger from SW to NE, indicating a subsiding basin with a depocenter that migrated to the NE. The reconstruction of the depositional history is consistent with significant changes in the landscapes. Hence, the closure of a large lake system at the end of the Miocene gave rise to the development of a Plio-Pleistocene fluvial system. This was yet very distinct from the modern drainage, with shallow, energetic, highly migrating, braided to anastomosed channels having an overall northeast outlet. This fluvial system formed probably under climatic conditions relatively drier than today's. During the early Pleistocene, there was pronounced erosion, followed by a renewed depositional phase ca. 40,000 ^{14}C yr B.P., with the development of prograding lobes and/or crevasse splays associated with a lake system (i.e., fan-delta) and/or fluvial flood plain areas. After a period of erosion, a fluvial system with eastward draining channels started to develop at around 27,000 ^{14}C yr B.P. The fluvial channels were overflooded in mid-Holocene time. This flooding is attributed to an increased period of humidity, with a peak between 5000 and 2500 ^{14}C yr B.P. The data presented herein support that, rather than being a monotonous area, the Amazonia was a place with frequent changes in landscape throughout the Neogene-Quaternary, probably as a result of climatic and tectonic factors. We hypothesize that these changes in the physical environment stressed the biota, resulting in speciation and thus had a great impact on modern biodiversity.

Keywords: Amazonia; Pleistocene; Sedimentology; Radiocarbon dating; Landscape evolution; Radar image; Biodiversity

Introduction

Amazonia is in urgent need of new geological data to provide models of landscape evolution that can serve as a foundation for discussing the origin, evolution, and the mechanisms controlling its modern biodiversity. This approach is of paramount interest to formulate strategies for conservation of this unique ecosystem, as species differentiation is motivated mostly by environmental stresses (Renaud and Dam, 2002; Sheldon, 1996) caused by the complex interplay of climate, sedimentary processes, tectonics, and sea level. The overall lack of geological data in the Amazonia is due to its immense size, dense vegetation cover, and difficult access. In particular, there have been few

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systematic sedimentologic and stratigraphic studies of the deposits formed from the late Tertiary to Holocene, the time span that witnessed the evolution of the modern biodiversity. As a result, many of the available discussions of species distribution and evolution based on geology are speculative (e.g., Bates, 2001; Patton and Silva, 2001; Patton et al., 2000; Räsänen et al., 1987, 1990, 1995; Rüegg and Rosenzweig, 1949; Van der Hammen and Hooghiemstra, 2000; Webb, 1995).

Resolving the problem with lack of geological data in Amazonia is a long-term commitment, but basic mapping and adequate characterization of the geological units are crucial to motivate this process. In the particular case of Western Brazilian Amazonia, there is a huge bias because the available geological maps oversimplifies the post-Miocene history with the inclusion of many sedimentary units (equivalent to 1,000,000 km^2) in the Içá Formation of Plio-Pleistocene age, with few areas of Holocene fluvial terraces.

To fill this gap, we mapped and characterized the sedimentary units overlying the Miocene deposits of the Solimões and Barreiras formations with basis on an integrated study combining analysis of radar images, field and laboratory sedimentologic data, and C^{14} dating. The area emphasized in this work includes a 300-m-wide belt on both sides of the Amazon-Solimões River that extends from the vicinity of Tabatinga, near the Colombia border, to Gurupá, in the State of Pará (Fig. 1). The results of this approach provide new elements for the reconstruction of the Amazon geological history, and so for discussion of the validity of the currently accepted hypothesis concerning to biome evolution and species distribution (Ayres and Clutton-Brock, 1992; Patton and Silva, 2001; Patton et al., 2000; Peres et al., 1996; Räsänen et al., 1990; Van der Hammen and Hooghiemstra, 2000).

Methods

The morphological and topographic characterizations of the study area were made with basis on SRTM-1 and SRTM-3 radar images provided by National Aeronautics and Space Administration (NASA), National Imagery and Mapping Agency (NIMA), DLR (German Space Agency), and ASIA (Italian Space Agency).

The fieldwork included facies and stratigraphic descriptions of exposures along riverbanks. This study was combined with sedimentologic characterization of the deposits based on the analysis of heavy, light, and clay minerals, which helped to distinguish the stratigraphic units and allowed discussions on the climate dominant during deposition, respectively. Sands and disaggregated sandstone samples were wet sieved to obtain the 63- to 125-μm size fraction. The heavy minerals (specific gravity 2.9 or more) were separated from light minerals by means of gravity settling using bromoform and mounted on glass slides for microscopic studies. The proportion of heavy minerals were determined from a count of at least 100 grains per slide, excluding opaques and micas to avoid dubious interpretation. The light minerals were studied under a binocular, with qualitative estimations of proportions to help classify the lithologies better. The unstable/stable ratio was calculated using the sum of amphibole, pyroxene, and epidote divided by the sum of zircon, tourmaline, and rutile. The ZTR indicates the sum of zircon, tourmaline, and rutile.

For clay mineral analysis, grain <63 μm in diameter from 24 samples were treated with H_2O_2 for removal of organic matter and mounted in glass slides, forming oriented films that were analyzed in the X-ray diffractometer. Three analyses were run for each sample using normal-oriented, ethylene glycol-solvated and -heated (550°C) modes.

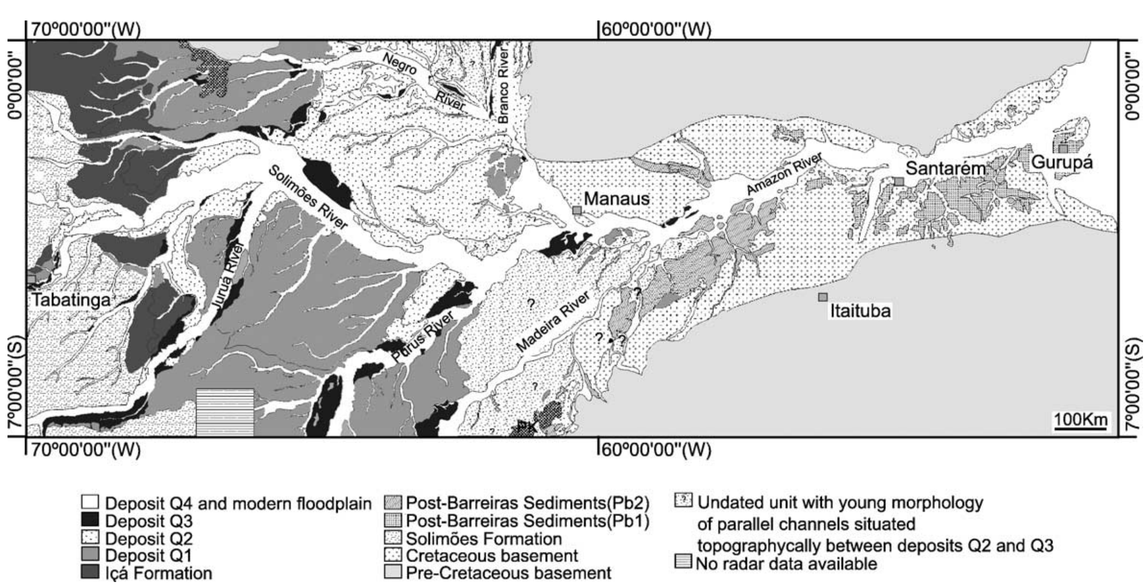

Figure 1. New geological map for Western and Central Amazonia along the Solimões-Amazon River. Discrimination among Plio-Pleistocene to Holocene sedimentary units was possible with basis on the integration of radar images, sedimentological data, and radiocarbon dating.

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Relative proportions of clay minerals were estimated with basis on the measurement of peak intensity.

A total of 14 samples were dated at the Beta Analytic Radiocarbon Dating Laboratory, using accelerator mass spectrometer (AMS) for small size samples. The samples were pretreated with acid to remove carbonates and weaken organic bonds, washed with alkali to remove secondary organic acids, and then combined with acid again to provide more accurate dating. Conventional ^{14}C ages were calibrated to calendar years using the Pretoria Calibration Procedure program, based on tree-ring data as calibration curves (Talma and Vogel, 1993).

Characterization of the depositional units

The Brazilian Amazonia to the east of Manaus is mostly floored by Cretaceous rocks of the Alter do Chão Formation, which forms a W–E-oriented belt overlying Paleozoic rocks of the Amazon Basin, and a variety of igneous and metamorphic Precambrian rocks of the Guianas and Central Brazilian shields (Fig. 1). After the late Cretaceous, this area showed scarce deposition, represented by spotty occurrences of fluvial Miocene deposits known as the Barreiras Formation (Albuquerque, 1922; Oliveira and Leonardos, 1943), as well as a few unnamed late Pleistocene–Holocene alluvial deposits formed along river banks. A comparison between the Miocene deposits from this area and the Cenozoic units exposed in Northeastern Amazonia (Góes et al., 1990; Rossetti, 2000, 2001; Rossetti et al., 1989, 1990) suggests that the Barreiras Formation is actually restricted to few occurrences of poor-sorted, medium- to coarse-grained, usually iron-cemented, quartz sandstones formed mostly in fluvial channels. The remaining deposits are lithologically similar to the post-Barreiras sediments formed during the Pliocene/Pleistocene, as described below.

In contrast, the area located to the west of Manaus remained as a depositional site throughout the late Cenozoic, as revealed by a variety of sedimentary units that overlies the lacustrine to transitional marine Miocene Solimões/Pebas Formation (e.g., Hoorn, 1994; Hoorn et al., 1995; Monsh, 1998; Nuttall, 1990; Räsänen et al., 1995; Vonhof et al., 1998; Wesselingh et al., 2001). Our mapping (Fig. 1) shows that the post-Miocene deposits, represented by the Içá Formation, are much more restricted than previously thought (e.g., Maia et al., 1977), with an exposure of only 300,000 km^2. In contrast, 700,000 km^2 of Pleistocene–Holocene deposits are exposed. These are referred to herein as deposits Q1 (base) to Q4 (top). Table 1 summarizes the main characteristics of these deposits and Table 2 shows a list with the corresponding C^{14} ages.

Sedimentology

Içá formation

This unit (Fig. 2) lies unconformably on the early to middle Miocene Solimões Formation (Latrubesse et al.,

Table 1
Characteristics of the sedimentary units formed from Plio-Pleistocene to Holocene in Western Amazonia

Sedimentary unit	Altitude (m)	Morphology/drainage pattern	Sedimentological characteristics	Age ^{14}C yr B.P.
Deposits Q4 (3–7 m thick)	35–45	Planar with abundant meandering channels	Coarsening and fining-upward successions consisting of dark gray to black, very fine to fine-grained, mostly cross-laminated sands interbedded with dark gray to black, parallel laminated muds.	240–130
Deposits Q3 (7 m thick)	55	Planar with very low density of meandering channels and abandoned loops; planar areas without channels.	Fining-upward successions 0.2–1.8 m thick, formed by light gray to brownish massive muds that grade-upward to light gray to brownish, siltic- to fine-grained sands.	6730–2480
Deposits Q2 (6 m thick)	70	Planar with low density, subdendritic channels	Coarsening-upward successions 0.3–1 m thick, formed by dark gray, parallel laminated muds that grade-upward into light-gray to brown, fine- to medium-grained, parallel or climbing ripple cross laminated, sands. Fining-upward cycles are locally present, with sandy components displaying medium- to small-scale trough cross stratification.	27,200
Deposits Q1 (10 m thick)	85–100	Planar with moderate density, trellised to rectangular channels	Either isolated or amalgamated lobate bodies of yellowish, fine- to medium-grained, sands 1.5 m thick and 15–20 m long. Medium-size cross stratification and climbing ripple cross lamination. Coarsening/thickening-upward successions and minor fining-upward successions bounded at the base by erosive surfaces with a lag of mud intraclasts.	43,700–37,400
Içá Fm. (25 m thick)	100–140	Smooth hills with dense, dendritic to subdendritic channels	A fossiliferous, white to light reddish feldspathic, fine- to coarse-grained, incipiently cross-stratified feldpathic sandstones and sub-arkoses and argillites. Fining/thinning-upward successions with planar erosional surfaces mantled by intraformational conglomerates.	Plio-Pleistocene

Table 2
List of ^{14}C dating of samples collected from deposits Q1 to Q4

Laboratory sample no.	Deposit unit	Type of material	^{14}C yr B.P.
Beta-168589	Q1	wood	37,700 (±540)
Beta-184364		wood	37,410
Beta-184365		wood	39,650
Beta-184366		wood	40,010
Beta-184377		wood	43,730
Beta-184362	Q2	wood	27,130 ± 200
Beta-184361	Q3	wood	5030 ± 70
Beta-184359		wood	2480 ± 40
Beta-168590		wood	4620 (±60)
Beta-184376		shell	6730 ± 100
Beta-184360	Q4	wood	140 ± 50
Beta-184371		wood	240 ± 80
Beta-184369		wood	130 ± 40
Beta-184370		wood	220 ± 40

1994; Maia et al., 1977), cropping out in an N/NW–SE elongated belt in the west of the study area. It occurs at altitudes between 100 and 140 m and forms a land surface displaying smooth hills and dense dendritic to subdendritic drainage patterns. Exposures of this unit along riverbanks are up to 25 m thick, but total thickness may be as much as 80 m (Maia et al., 1977). The Içá Formation is characterized by a fossiliferous, white to light reddish feldspathic, fine- to coarse-grained, poorly cross-bedded sandstones and sub-arkoses (73% monocrystalline quartz; 25% feldspar; 2% muscovite), and secondarily argillites. The sand grains are, in general, angular to very angular and moderately sorted. The heavy mineral assemblage is very altered, being constituted by dominantly stable minerals, with a ΣZTR = 55 and the unstable/stable ratio = 0.31 (Table 3; Figs. 3A and B).

The deposits are arranged into fining/thinning-upward successions with planar erosional surfaces mantled by intraformational conglomerates. Given the absence of fossils, the Içá Formation could not be dated, but its position overlying an upper Miocene unconformity and underlying deposits dated to the late Pleistocene provides an estimated Plio-Pleistocene age.

Post-Barreiras sediments

These deposits occur at two topographic levels, each with distinctive morphological and topographic characteristics. One stands ca. 200 m above the modern sea level and is located between the Xingu and Tapajós rivers and on the left margin of the latter, and along the right margin of the Madeiras River, close to the confluence with the Amazon River; these deposits are deeply incised by V-shaped river valleys arranged into a trellised pattern. The other deposits are located near the town of Óbidos and occur at altitudes between 45 and 60 m. They are characterized by a dense drainage with dendritic and less commonly subparallel channel patterns.

At the outcrop scale, two corresponding sedimentary successions were also recognized: a lower one (post-Barreiras 1), consisting of light red, fine- to coarse-grained, massive sands; and an upper one (post-Barreiras 2), represented by typically yellow, fine-grained sands. Both sands consist of mostly monocrystalline, subangular to subrounded quartz grains. The base of these deposits is an unconformity with erosional relief of up to 6 m at the outcrop scale, which is mantled by a lag of reworked laterite concretions, as well as by quartz and ferruginous sandstone pebbles. These deposits present distinctive assemblages of heavy minerals (Table 3; Figs. 3A–C) Hence, the post-Barreiras 1 is characterized by highly stable species, as indicated by the ΣZTR = 80, and unstable/stable ratio = 0.12. In contrast, the post-Barreiras 2 shows ΣZTR = 55, but the unstable/stable ratio = 0.05 still points to a very stable mineral assemblage. In this case, the lower ΣZTR relative to the post-Barreiras 1 is due to the high andaluzite content (31%).

Deposits Q1

These deposits (Fig. 2) are only 10 m thick at the outcrop scale, occurring along a wide belt paralleling the Içá Formation, as well as in a few isolated areas southeast of Manaus and on the right margin of Negro River. Between 85 and 100 m above present sea level, this succession forms a plateau that is distinguished from the Içá Formation by the planar morphology with less dense drainage arranged in a trellised to rectangular pattern. Deposits Q1 consist of yellowish–white, fine- to medium-grained, moderately sorted and mostly angular sands (70% monocrystalline and polycrystalline quartz; 30% muscovite, biotite, and chlorite). These deposits occur as lobes averaging 1.5 m in thickness and 15–20 m in length. The sand lobes are either amalgamated or separated by thin mud layers and internally display medium-sized (thickness averaging 0.4 cm) tabular and cross stratification and abundant climbing-ripple cross lamination. The strata are organized into coarsening/thickening-upward successions; locally, there are fining-upward deposits bounded at the base by erosive surfaces and a lag of mud intraclasts. Organic plant debris preserved in the mud layers provided ages between 37,400 and 43,700 ^{14}C yr B.P. (Table 1).

The Q1 heavy mineral assemblage is composed of very altered but predominantly unstable minerals (mostly epidote, amphibole, and augite), as indicated by the ΣZTR = 5 and the unstable/stable = 14 (Table 3; Figs. 3A–C).

Deposits Q2

These deposits (Fig. 2) are volumetrically best represented in a large area (i.e., nearly 12,000 km^2) between the Solimões and Negro rivers, with minor occurrences forming narrow belts along the Solimões River near Colombia and in the confluences of the Içá, Jutaí, Japurá, and Juruá rivers. This sedimentary unit stands at a mean altitude of 70 m and forms a planar area characterized by a low-density drainage system with incipient subdendritic channels. One interesting characteristic of these deposits is the ragged, “half-moon”

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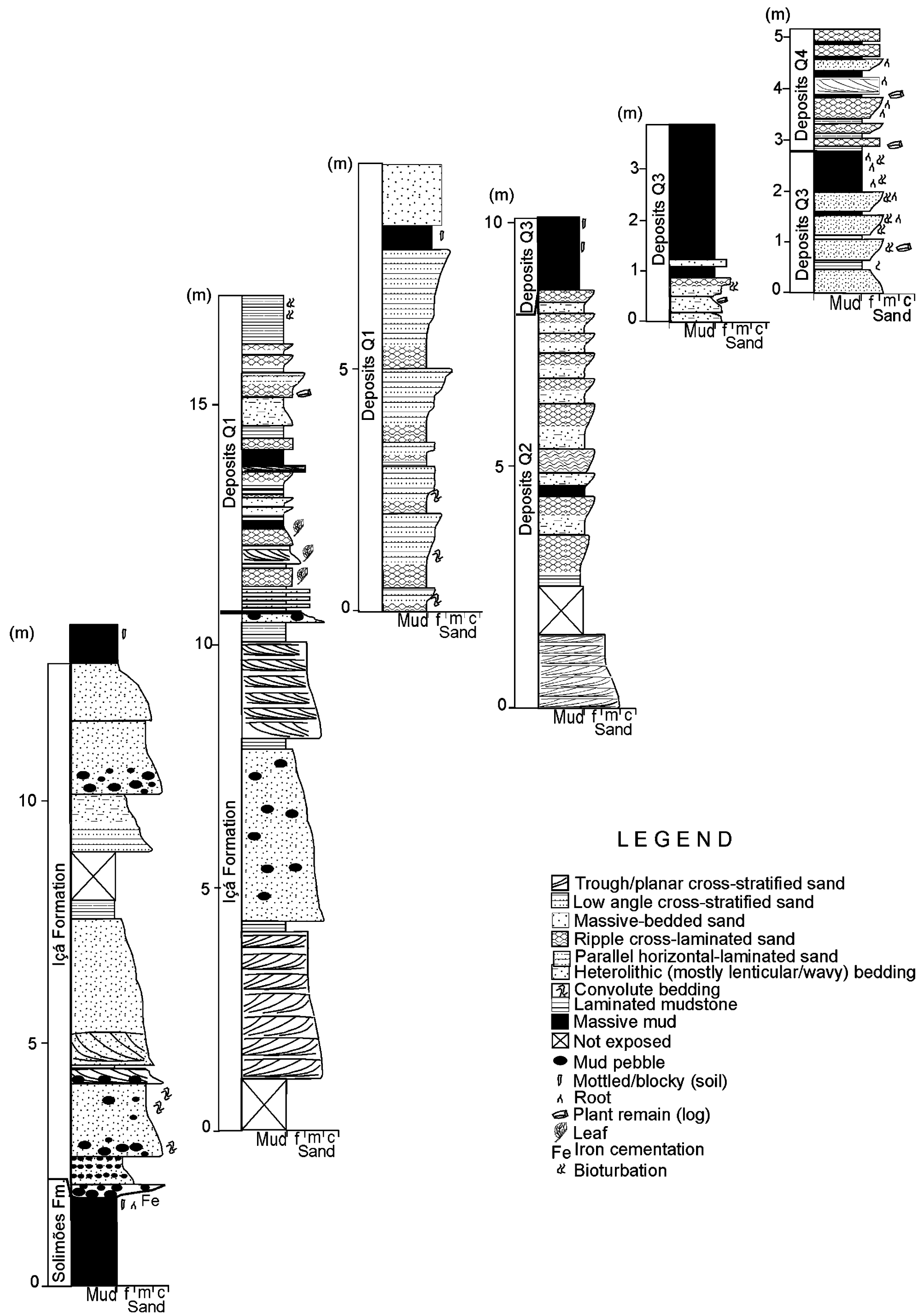

Figure 2. Lithostratigraphic profiles representative of the Plio-Pleistocene to Holocene deposits in the study area.

morphology of their margins, denoting strong erosion by younger channel migration.

The facies of Q2 are distinct from Q1, consisting of coarsening-upward successions 0.3–1 m thick. They consist of dark gray, parallel-laminated muds that grade upward into light gray to brown, fine- to medium-grained, moderately to poorly sorted, angular to subangular, sands (85–90% polycrystalline, monocrystalline quartz, and chert; 5% feldspar; 5–10% muscovite, biotite, and chlorite). Internally, they display parallel or climbing-ripple cross lamination. Fining-upward sequences are locally present, and the sandy component displays medium- to small-scale sets (<0.4 cm thick) of trough cross stratification. Plant remains dispersed in the muds were dated at 27,160 ^{14}C yr B.P.

The assemblage of heavy mineral in deposits Q2 is relatively more unstable than in Q1, as shown by the unstable/stable ratio = 20 and the ΣZTR = 4.4 (Table 3; Figs. 3A–C). The minerals are well preserved and repre-

Table 3
Distribution (%) of heavy mineral assemblages in the studied sedimentary units

Stratigraphic unit	Afb	Hip	Aug	Epi	And	Cian	Est	Gra	Tur	Zir	Rut	Ats	Olv	Sil	Apa	Sep	ΣZTR	Un/S
Içá	8.7	0.6	2.3	5.2	11	4.9	4.7	0.1	13	43	2.9	–	0.2	–	–	0.9	55	0.3
Post-Barreiras 1	2	1.3	1.8	4.8	1	0.8	6.5	0.3	11	66	3	1.5	–	–	–	–	80	0.13
Post-Barreiras 2	0.3	–	0.7	1.7	31	9.7	–	0.3	11	38	5.7	1.7	–	0.3	–	–	55	0.05
Q1	34	4.4	14	34	2	1	0.8	2.2	1.4	3.2	0.4	0.6	–	–	0.2	0.2	5	17.3
Q2	29	9.4	20	31	1.2	2.4	0.4	1.4	0.8	3	0.6	–	–	0.6	–	–	4.4	20
Q3	45	14	16	15	3.3	1.7	–	1.3	0.7	1.3	–	0.3	–	1	–	1.3	2	44.5
Q4	27	14	27	21	4	2.8	1	2.5	0.5	1	–	–	–	–	–	–	1.5	59

The ΣZTR (%zircon + %tourmaline + %rutile) and unstable/stable ratios (Un/S) are also included in the two last columns to the right (Afb = amphibole; Hip = hypersthene; Aug = augite; Epi = epidote; And = andalusite; Cian = kyanite; Est = staurolite; Gra = garnet; Tur = tourmaline; Zir = zircon; Rut = rutile; Ats = anatase; Olv = olivine; Sil = sillimanite; Apa = apatite; Sep = serpentine).

sented, in order of importance, by epidote, amphibole, augite, and hypersthene.

Deposits Q3

These deposits (Fig. 2) are really much more restricted than Q1 and Q2, occurring discontinuously around the riverbanks throughout the study area, reaching as far east as the locality of Santarém, from where they become spottier. These deposits form a flat area at mean altitude of 55 m, with a very low density of meandering channels that cut into flood-plain areas having abundant abandoned loops. As with deposits Q2, these deposits display ragged margins with "half-moon" morphology. Planar areas without any channels are common.

Deposits Q3 are up to 7 m thick at the outcrop scale and consist of fining- and coarsening-upward successions 0.2–1.8 m thick. They are formed by light gray to brownish massive muds that grade into light gray to brownish, moderately sorted, mostly angular, siltic- to fine-grained, sands (60% muscovite, chlorite, and biotite; 40% polycrystalline quartz). The clay layers frequently display plant remains, which locally form peats that are up to 0.6 m thick dated at 6700 to 2480 ^{14}C yr B.P.

The heavy mineral assemblage in deposits Q3 is relatively more unstable than in Q2, as indicated by lower ΣZTR of 1.9 and much higher unstable/stable ratio = 47 (Table 3; Figs. 3A–C). The main minerals are the same than in Q2 but are ranked in order of importance as follows: amphibole, augite, epidote, and hypersthene.

Deposits Q4

These deposits (Fig. 2) are distributed throughout Western Brazilian Amazonia, corresponding to fluvial terraces that stand only at 3 m higher than the dry-season water level. These deposits are included together with the modern flood plain and river complex in the geological map (Fig. 1) because they occur discontinuously at the of the map. In the field, deposits Q4 cut deposits Q3, forming a listric contact at a slightly lower topographic level. They consist of dark gray to black, moderately to well sorted, angular to subangular, very fine to fine-grained sands (50% polycrystalline and monocrystalline quartz; 45% muscovite, biotite, and chlorite; and 5% of feldspar grains). As opposed to deposits Q3, these sands are very well structured, being represented by ripple cross lamination and, secondarily, medium-scale trough cross stratification. The sands are interbedded with dark gray to back, parallel-laminated muds. The volume of plant remains is high in these deposits, which display ages between 280 and 130 ^{14}C yr B.P.

The heavy mineral assemblage is composed by unstable species, mostly represented by amphibole, augite, epidote, and hypersthene (Fig. 3A). The unstable/stable ratio is 59 and the ΣZTR is 1.5 (Figs. 3B and C).

Clay mineral analysis

X-ray analyses of the studied deposits revealed a mixture of clay minerals consisting of smectite, kaolinite, chlorite, and illite. While these minerals occur in most of the analyzed samples, their relative proportion may change significantly, allowing inferences on the main climatic regimes that prevailed during deposition. The Içá formation was not considered for this analysis because this unit shows a high degree of alteration, indicated by the red to white color. In addition, these deposits contain a high volume of feldspar grains, whose alteration led to an increase in the volume of kaolinite.

In particular, the smectite/kaolinite ratio varies significantly among the deposits, corresponding to 2.7, 1.54, 0.42, and 0.52 in deposits Q1, Q2, Q3, and Q4, respectively (Fig. 3D). In order to compare the climate during the formation of these deposits with the modern climate, X-ray analyses were also run for modern muds, which indicated smectite/kaolinite ratio of 0.31.

Reconstruction of the geological evolution

The morphological and sedimentological characteristics of the stratigraphic units described above suggest that the study area experienced several environmental changes during the Neogene-Quaternary. The heavy mineral assemblage, in particular the unstable/stable ratios and the ΣZTR, differentiated the sedimentary units, indicating a progressive increase in unstable minerals in younger deposits. The

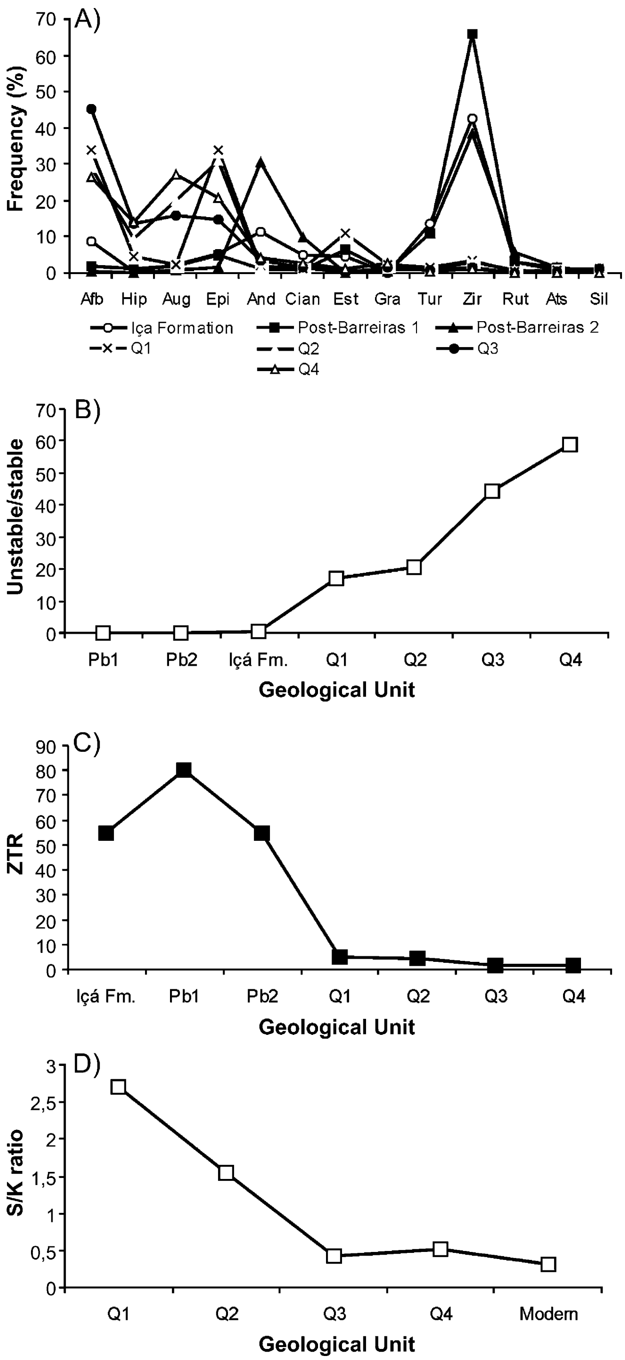

Figure 3. Heavy mineral assemblages in the Plio-Pleistocene to Holocene deposits exposed along the Solimões-Amazonas River. (A) Comparative distribution among main heavy minerals (Afb = amphibole; Aug = augite; Epi = epidote; And = andaluzite; Cian = kyanite; Est = staurolite; Gra = garnet; Zi = zircon; Tur = tourmaline; Rut = rutile; Ats = anatase; Sil = sillimanite). (B) Curve with the relative proportion among unstable/stable heavy minerals (unstable = amphibole + pyroxene + epidote; stable = zircon + tourmaline + rutile). (C) Curve with the ΣZTR (zircon + tourmaline + rutile). (D) Smectite/kaolinite ratio obtained from X-ray diffractograms of the stratigraphic units formed during the Pleistocene to Holocene in Western and Central Amazonia (Q1 = deposits Q1; Q2 = deposits Q2; Q3 = deposits Q3; Q4 = deposits Q4).

increase in the frequency of unstable minerals can be attributed to a lower degree of alteration in younger deposits. The accompanying decrease in ΣZTR suggests differences in source rocks between the Plio-Pleistocene and the late Pleistocene to Holocene deposits Q1–Q4. In addition, the Içá Formation displays a mixture of heavy minerals derived both from basic igneous Andean rocks, indicated by the presence of amphibole, augite and hypersthene, and acid igneous and metamorphic rocks derived from the Amazonian Craton, indicated by the presence of zircon, tourmaline, staurolite, kyanite, and andaluzite. In as much, the post-Barreiras sediments display an assemblage with dominance of sedimentary rocks from the Cretaceous Alter do Chão Formation, and secondarily, igneous and metamorphic rocks from the craton. Considering that these deposits are probably correlatable, we take this as an indication for the absence of eastward flowing drainage to the Atlantic during the Plio-Pleistocene, which is also supported by other sedimentological evidence, as discussed in the following.

The distribution of the sedimentary units as belts progressively younger from southwest to northeast suggests that Western Amazonia behaved as a subsiding basin, with the depocenter migrating to the northeast in the late Tertiary–Holocene. This basin is bounded to the east by Cretaceous rocks of the Alter do Chão Formation, as well as older Paleozoic and Precambrian rocks. In addition, our sedimentological record indicates a huge area located to the west of Manaus that underwent to several phases of subsidence and stability since the early/middle Miocene (Fig. 4A). The initial deposits in this basin, represented by the Solimões Formation, record a huge lake system that might have been punctuated by marine transgressions (Wesselingh et al., 2001). Marine transgressions also affected sedimentation to the east of Gurupa (Góes et al., 1990; Rossetti, 2000, 2001; Rossetti et al., 1989, 1990, 2004), but the data presented herein do not support a W–E marine connection through central Amazonia, where Miocene strata (i.e., Barreiras Formation) was alluvial in nature. Tectonic studies suggest that the area between Manaus and Santarém was under compression (Costa et al., 1996), favoring the development of an eastward-flowing fluvial system (Fig. 4A).

The unconformity at the top of the Solimões Formation records a time of erosion and/or nondeposition. This unconformity is correlatable with the unconformity at the top of the chronologically equivalent Barreiras Formation exposed in the Eastern Amazonia, where it is associated with widespread lateritic paleosol formed during tectonic stability combined with a fall in sea level (Rossetti, 2000; Rossetti and Góes, 2001; Rossetti et al., 2004). During the Plio-Pleistocene, fault reactivation, probably associated with transgression (Bezerra, 2003), caused subsidence of the area west of Manaus, where the northwest-flowing river system reached the Atlantic Ocean through the Essequibo River in the Demerara plain. As a consequence, widespread fluvial deposits were formed, as recorded by the Içá Formation

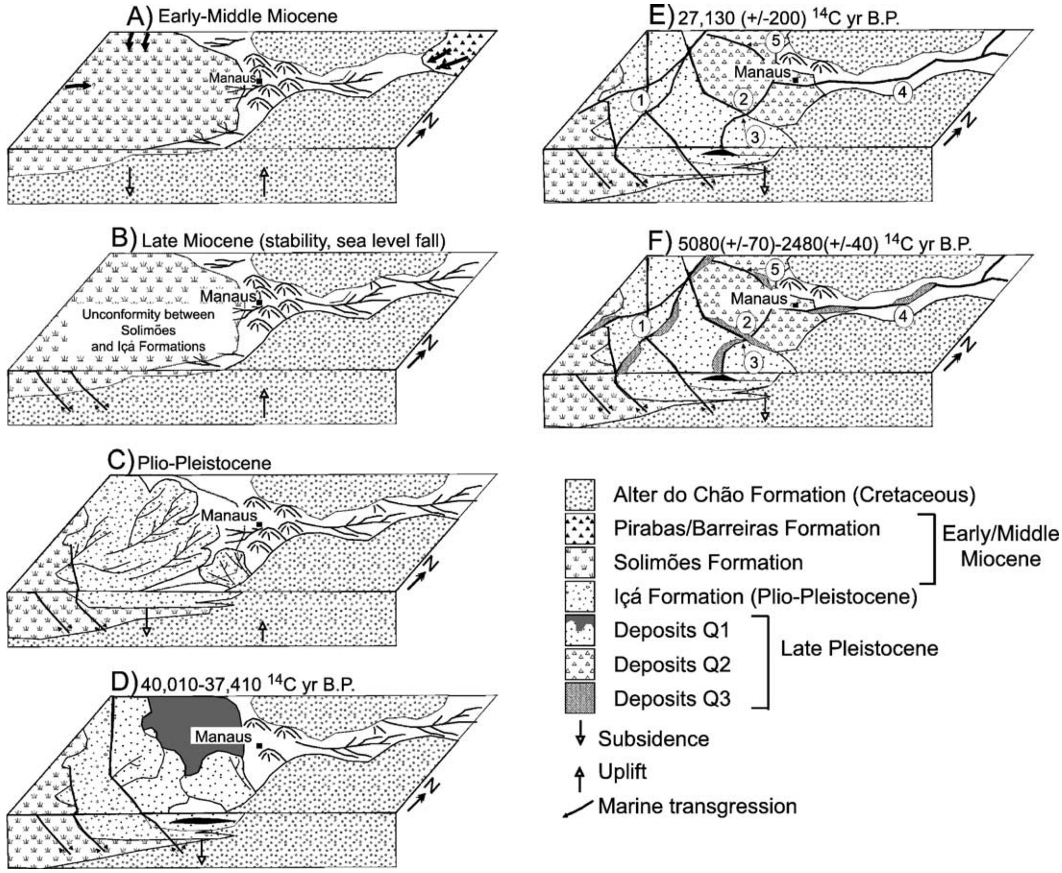

Figure 4. Schematic diagrams with the simplified landscape evolution proposed for Western Amazonia since the Miocene. As the basin depocenter migrated northeastward due to tectonics, the area located to the west of Manaus developed a lake system in the early/middle Miocene (A) that dried out during the late Miocene low eustatic level (B). Plio-Pleistocene tectonics, combined with a dry climate resulted, in renewed subsidence and establishment of a main northeastward anastomosed to braided fluvial system (C). Following a period of stability and nondeposition (not represented), the area experienced new episodes of subsidence, creating space to accommodate deposits of a large delta-fan (D) and/or a fluvial system with floodplains and widespread lakes (E). Simultaneously to the later phase, the northeastward flowing drainage was then captured by southeast–northwest faults, allowing the amplification of the Amazon system as we see today (F). See text for further explanation (1 = Juruá River; 2 = Solimões River; 3 = Purus River; 4 = Amazon River; 5 = Negro River).

(Fig. 4C). An area near Manaus was still topographically high, preventing the rivers from reaching much farther eastward, as demonstrated by the thinning and disappearance of the Içá Formation near Manaus. The abundance of fining-upward, cross-stratified sandstones with basal erosive surfaces mantled by conglomerates are consistent with channelized flows. The small thickness of the successions, the planar basal surfaces, and the dominance of fine- to coarse-grained sands all suggest a fluvial system different from the modern Amazon River. These characteristics support shallow, energetic, migrating, braided to anastomosed channels. The abundance of feldspars is attributed to a drier climate than today. The abundance of feldspar also suggests a granitic source area, as proposed previously on the basis of heavy mineral assemblage.

After deposition of the Içá Formation, the Western Amazonia was again stable. Sediment supply was reduced and erosion prevailed, producing an unconformity at the top of this unit. This situation remained until the late Pleistocene, but between 43,730 and 37,400 ^{14}C yr B.P. resumed (deposits Q1; Fig. 4D). It is possible that Q1 includes older Pleistocene deposits, considering that some of the C^{14} dates (Table 3) are close to the limit of the method. The dominance of sand lobes displaying climbing cross lamination suggests rapid deposition with high suspension flows, as occurs in deltaic or fluvial crevasse splay environments. Within this context, the fining-upward sandstones with basal surface of intraformational lags are attributed to either interdistributary or fluvial channels. Considering the first interpretation, a standing water body must be considered to have existed northeast between Solimões and Branco Rivers. This area might have acted as a basin where lobes prograded, forming either a fan-delta setting or a type of fluvial system with high-density crevasse splay deposition. Accommodation space was then reduced, culminating with the basin infill by prograding lobes, and ultimately returning to deposition by northeast-oriented channels.

After 27,160 ^{14}C yr B.P., there was a renewed phase of deposition, which resulted in formation of deposits Q2 further northeastward, between Solimões and Negro Rivers (Fig. 4E). We argue that this time correlates with the formation of a rhombic basin caused by W–E strike-slip motion and NW–SE extension, as suggested by Bezerra (2003), a process that might have caused the reorientation of the drainage to the east, forming the modern Amazon River. Subsidence promoted flooding of large areas, with a renewed phase of lobe/fluvial crevasse splay progradation as recorded by the coarsening-upward successions of Q2. However, flow energy was lower than during the formation of Q1, producing smaller finer-grained sand bodies that prograded either into a wide, shallow lake, or several lakes within extensive fluvial floodplains. In both hypotheses, areas with associated either lacustrine or channel deposits remains to be recorded. There is no surface record of deposits correlatable to Q1 east of Manaus. Exceptions are deposits with ages between 15,290 and 11,340 ^{14}C yr B.P. near Itaituba, where they contain a megafauna of *Haplomastodon waringi* and *Eremotherium laurilardi*, attributed to arboreal-like savannas (Rossetti et al., 2004).

A flooding event between 6700 and 2480 ^{14}C yr B.P. resulted in widespread development of fluvial terraces along all the extension of the Amazon drainage basin, a phase recorded by deposits Q3 (Fig. 4F). The abundance of peat is consistent with this flooding. This mid-Holocene Amazon flooding, also suggested by many other authors (e.g., Baker et al., 2001; Behling and Costa, 2000; Behling and Hooghiemstra, 1998, 1999, 2000; Turcq et al., 1998), coincides with an increased period of humidity as recorded in several other places, as well as with an eustatic rise associated with orbital forces (Martin et al., 1997; Mörner, 1996). This phenomenon would have interfered in the position of the Intertropical Convergence Zone, promoting increased humidity in Amazonia (Mayle et al., 2000), with the consequent amplification of the rainforest. In fact, the relative decrease in the proportion between smectite and kaolinite in the studied deposits is consistent with increased humidity since the late Pleistocene. Noteworthy is a subtle increase in kaolinite to values closer to modern muds (smectite/kaolinite = 0.31) in deposits Q3, consistent with increased humidity between 6730 and 2480 ^{14}C yr B.P.

Implication of geological factors in the evolution of the Amazon biodiversity

Analysis of the factors controlling the distribution of a group of organisms depends largely on the knowledge of its geographic range, population structure, and prevailing environmental controlling conditions, as climate, soil, and physiographic setting. Attributing the high modern biodiversity of the modern Amazonia to a single mechanism is impossible, as the alpha and beta diversities vary at different rates (Patton and Silva, 2001; Tuomisto et al., 2003). Researchers working with speciation events in Amazonia support the idea of sympatric speciation (e.g., Endler, 1977). Therefore, diversification in tropical environments seems to be a rather very complex process, with the main factors varying among different taxonomic groups. Regardless, we believe that geological processes may have played an important role in species diversification. This is because, in general, stable geological periods may favor generalist species with gradual evolution, whereas periods characterized by constant changes motivate speciation, increasing the interspecific competition. This creates conditions that are favorable for morphological differentiation due to the adaptation of the organisms to the new environmental conditions (Renaud and Dam, 2002; Sheldon, 1996).

Many theories attempting to explain the distribution of the Amazon biodiversity have been based directly or indirectly on geological information (e.g., Bates, 2001; Patton and Silva, 2001; Patton et al., 2000; Räsänen et al., 1987, 1990, 1995; Rüegg and Rosenzweig, 1949; Webb, 1995). Testing these models depends on the presentation of new geological information including paleontology, sedimentology, stratigraphy, paleoecology, and tectonics, which can serve as a solid basis for definition of those factors that may have had the greatest potential in controlling the origin and evolution of species. In addition to the spotty nature, the available geological information used to formulate hypothesis of evolution and distribution of the Amazon biodiversity represents, in most cases, indirect interpretations rather than primary geological data.

A good example of extrapolation and/or improper utilization of secondary geological data to understand species distribution is the assumption that tectonic arches constitute main geographic barriers (Räsänen et al., 1987; 1990). Although still accepted by many authors (e.g., Patton and Silva, 2001; Patton et al., 2000), the application of structural arches as vicariant limits for biodiversity distribution and speciation (e.g., Patton and Silva, 2001; Patton et al., 2000; Räsänen et al., 1987; 1990) should not be further considered, because most of these are Paleozoic or Mesozoic structures buried under a mantle of Cretaceous and Cenozoic deposits (e.g., Caputo, 1991), thus no longer representing elevated elements of the terrain. For instance, the Purus Arch located to the west of Manaus, considered to be an important vicariance feature, is a geologic structure that occurs >1000 m of depth under Cretaceous rocks of the Alter do Chão Formation (Wanderley Filho, 1991).

The concept that marine transgression formed islands that could motivate speciation is another theory that overinterprets geological data (e.g., Bates, 2001; Frailey et al., 1988; Rüegg and Rosenzweig, 1949; Webb, 1995). Several authors support marine transgression in Amazonia (e.g., Campbell, 1990; Frailey et al., 1988; Hoorn, 1994; Hoorn et al., 1995; Irion, 1984; Irion et al., 1995). This hypothesis became particularly attractive after publications that recorded marine transgression in Western Amazonia during the late Miocene, with the establishment of an interior seaway derived from the Pacific and/or Caribean sea (Räsänen et al., 1995). Despite episodic marine incursions in the early/middle Miocene, there is no further support of transgressive events affecting Western Amazonia thereafter (Hoorn, 1993, 1994; Lundbergh et al., 1998; Monsh, 1998; Nuttall, 1990; Vonhof et al., 1998). In particular, the sedimentological data provided herein are more consistent with the dominance of continental processes in Western Amazonia since at least the Pliocene.

Despite the dominance of continental conditions, tectonics are revealed to be an important factor controlling sedimentation patterns, and consequently landscape evolution, during the Neogene-Quaternary, when seismological zones were still active in several places throughout Amazonia (Costa and Hasui, 1997). Therefore, tectonics may have also affected the modern ecosystem, via the development of drainage, relief, soil, and the distribution of the depositional environments.

Molecular studies focusing on some vertebrate groups have led to the inference that many modern species might have had their origin during the Pliocene (Patton and Silva, 2001). This period of the geologic history was marked by significant worldwide changes in environmental conditions (e.g., Crowley and North, 1991), with the uplift of the Panama Isthmus playing an important role on biotic exchange between the Americas (Webb and Rancy, 1996). This process was accompanied by a worldwide tendency for aridity, reflected by expansion of savannas in replacement of forests (Hooghiemstra and Van der Hammen, 1998; Van der Hammen, 2001; Van der Hammen and Hooghiemstra, 2000), with the reorganization of several terrestrial fauna elements, including a trend for large-sized mammalian groups typical of open habitats, as recorded in Western Amazonia (e.g., Rancy, 2000; Rossetti et al., 2004). In addition to cooling, we hypothesize that the drastic environmental change from a large lake (early middle Miocene) to an anastomosed or braided fluvial system (Plio-Pleistocene) might have had a profound impact in community patterns in this region, expanding the distribution of terrestrial species while limiting the aquatic ones to restricted fluvial areas. Such rearrangements possibly enabled a series of synchronous speciation events, setting up the molecular clock of many modern vertebrate groups 3–4 myr ago (Bates, 2001; Patton and Silva, 2001). Therefore, a complex interplay of climatic, tectonic, and paleoenvironmental changes may have acted together as main abiotic driver mechanisms, enhancing environmental stresses and possibly promoting successive species adaptations (Vrba, 1992).

The model with a progressive northeast shift in deposition due to tectonics, as proposed herein, might provide the basis to test possible effects on community structures by analyzing the distribution of the modern species. The areas between Solimões and Negro Rivers and along the Branco and Madeira rivers are particularly interesting in this context, as they show evidence for tectono-environmental changes even in the last few thousand years. This type of investigation might provide new elements to review the hypothesis that major river systems represent important biogeographic barriers. This hypothesis, widely applied to explain the distribution of several vertebrate groups (e.g., Ayres, 1986; Ayres and Clutton-Brock, 1992; Bates, 1863; Capparella, 1988; Wallace, 1853), has been questioned because a river is insufficient to cause isolation to the point of motivating speciation (Haffer, 2001; Haffer and Prance, 2001). Major Amazon river systems commonly bound tectonic compartments with distinctive sedimentary units. Therefore, although rivers may appear to be important biogeographic boundaries, the cause of vicariance could actually be directly related to differences in landscape evolution of individual large-scale tectonic compartments. Areas experiencing more active tectonism and sedimentation are more prone to develop environmental stresses and thus induce the appearance of endemic groups of plants and animals. This pattern has been recently confirmed by phylogenetic studies of bird communities (Aleixo, 2004). Under this viewpoint, species differentiation would not be controlled by river location, but by geomorphological, sedimentological, pedological characteristics inherent to individual tectonic compartments (see also Tuomisto et al., 1993, 2003). Together with other proposed speciation mechanisms (e.g., sympatric speciation), this geological model should be considered in future studies of the Amazonian diversity.

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