A Miocene perspective on the evolution of the Amazonian biota

F.P. Wesselingh & J.A. Salo

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F.P. Wesselingh, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands and Department of Biology, University of Turku, SF-20014 Turku, Finland (wesselingh@nnm.naturalis.nl); J.A. Salo, Department of Biology, University of Turku, SF-20014 Turku, Finland (jukka.salo@utu.fi).

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Between *c.* 23 and 8 Ma, western Amazonia was occupied by the vast Pebas long-lived lake/wetland system. The Pebas system had a variety of influences over the evolution of Miocene and modern Amazonian biota; it formed a barrier for the exchange of terrestrial biota, a pathway for the transition of marine biota into freshwater Amazonian environments, and formed the stage of remarkable radiations of endemic molluscs and ostracods. The lithological variation of the Pebas Formation has furthermore enhanced edaphic heterogeneity in western Amazonia, sustaining present-day high terrestrial diversity in the region.

Contents

Introduction

The Amazon lowland rainforests (Eva & Huber, 2005) are considered the most species-rich terrestrial ecoregion in the world (Morrison *et al.*, 2001; Cardoso *et al.*, 2005). The western part of Amazonia is particularly rich in species, though most of the known centres of endemism are located in the Andean-Amazonian uplands (Lamas, 1982; Balslev & Renner, 1989; Valencia *et al.*, 1994, 2004; Fjeldså, 1995; Clough & Summers, 2000; Rahbek & Graves, 2001). The history of the biodiversity in lowland Amazonia is incompletely known due to a poorly accessible geological record. The origin of high species numbers has in the past primarily been attributed to very young (Quaternary) diversifications (Haffer, 1969; but see Haffer, 1997; Haffer & Prance, 2001). With the advent of molecular phylogenetic research, a number of estimates of major diversifications in different animal groups became available (Clough & Summers, 2000; Lovejoy *et al.*, 1998, 2006; Zamudio & Green, 1997; Cheviron *et al.*, 2006). Major diversifications are consistently

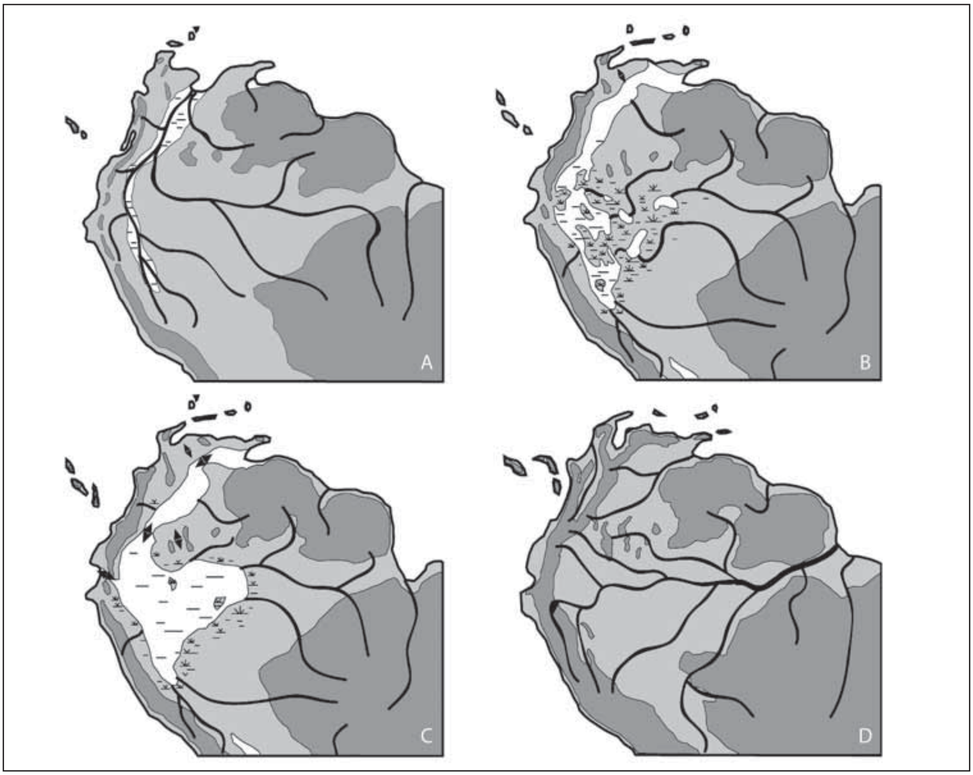

Fig. 1. Western Amazonia in the past 34 million years underwent three stages of development. At the Chambira stage (A. *c.* 34-23 Ma), the Andean foreland basins channelled rivers towards the Caribbean. Most of the Amazon system ran from east to west. Marginal marine conditions could occur in the foreland basin (including western Amazonia), but seasonally flooded wetlands and fluvial settings predominated. Mountain ranges, islands and river courses are conjectural.
During the first part of the Pebas lake/wetland system stage (B. *c.* 23-17 Ma), the foreland basin zone became submerged, and a mosaic of fluvial and lacustrine landscapes developed in western Amazonia.
Lacustrine settings at sealevel became to dominate western Amazonia during the latter part of the Pebas system (C. *c.* 17-9 Ma). Fluvial and marginal marine conditions were present as well. Connections with the Caribbean marine realm were through the Llanos basin and east Venezuela, and/or the Maracaibo/Falcon basins. Possibly episodic connection with the Pacific existed through the Cuenca basin and over the low western margins of the Guyana Shield (arrows).
At *c.* 8 Ma (D), the modern eastward Amazon River system had established, as well as the northward draining Orinoco system. Key: dark grey = uplands; intermediate grey = lowland.

placed in the pre-Pleistocene (see also Garcia Moreno *et al.*, 1988), rather then the Quaternary, and an overhaul of our models of diversification in lowland Amazonia is long overdue. The high diversity in western Amazonia is in part sustained by the regional diversity of the landscapes (Räsänen *et al.*, 1987, 1990; Salo & Räsänen, 1989). These include the Amazonian lowlands, Subandean and Andean zones, as well as the lower western margins of the Guyana Craton. However, landscape diversity in western Amazonia exists on far more subtle scales as well (Salo *et al.*, 1986; Räsänen *et al.*, 1998; Tuomisto *et al.*, 1995, 1998; Tuomisto & Poulsen, 1996; Linna *et al.,* 1998; Roddaz *et al.,* 2006). In the past decade, insight into the Neogene history of the western parts of Amazonia has drastically improved (Hoorn *et al*., 1995; Räsänen *et al*., 1996, 1998; Dobson *et al*., 1997, 2001; Harris & Mix, 2002; Wesselingh *et al*., 2002, 2006a, b, c; Gingras *et al*., 2002; Vonhof *et al*., 1998, 2003; Hermoza, 2005; Kaandorp *et al*., 2005; 2006; Hoviskoski *et al*., 2005). A major stage in the Miocene history of lowland western Amazonia was the Pebas system that initiated around 23 Ma ago in the foreland basins east of the tropical Andes (Wesselingh *et al*., 2006b). The Pebas system consisted of a series of lakes and wetlands that experienced fluvial and marine influence. The system expanded to cover large tracts of western Amazonia during especially the Middle Miocene (*c.* 16-9 Ma). In this paper we outline and discuss faunal developments in the Pebas system, and its relationships with faunas beyond Amazonia, and investigate the role that it played in the development of the modern Amazonian biota.

A history of a Miocene megalake-wetland system in western Amazonia

Before discussing the biotic development in Miocene Amazonia, it is necessary to outline the Neogene history of western Amazonia (Fig. 1). Before *c.* 23 Ma, major rivers in lowland Amazonia drained towards the west, and were captured by river/lake and marginal marine systems in the foreland basins of the Andes that had a Caribbean connection (Hoorn *et al*., 1995; Lundberg *et al*., 1998). The inverted Amazon system had its headwaters close to the present-day Xingu River that at the time was blocked from an Atlantic exit by the Marajo rift (Brandão & Feijó, 1994; Hoorn *et al.,* 1995; Lundberg *et al.,* 1998). The Andes at the time was a low, discontinuous, mountain range. During the Oligocene (Wesselingh *et al*., 2006b), western Amazonia was occupied by river belts, extensive seasonally inundated back swamps, lakes and some marginal marine environments that resulted in deposition of the Chambira Formation. The climate was characterised as seasonal with a distinct dry season, resulting in encrusted soil profiles (Wesselingh *et al*., 2006b), and the landscape may have resembled that of the present-day Llanos savannahs of northern Colombia and Venezuela.

At around the Oligocene-Miocene boundary (*c.* 23 Ma), although age control is problematic (Wesselingh *et al*., 2006b), the northern Andean foreland basins became under filled and drowned. The Pebas system and the Andean foreland basins were connected to marine conditions in present-day Venezuela (Wesselingh & Macsotay, 2006), forming an aquatic system that separated the northern Andes from the Guyana craton uplands. Amazonian rivers draining towards the west emptied into this predecessor of the Pebas system. The submergence of the foreland basins proceeded south- and eastwards during the Early Miocene (Aquitanian – Burdigalian, *c.* 23-17 Ma). The transition of fluvial to lacustrine settings is shown in well 1AS-4A-AM (Maia *et al.,* 1977; Hoorn, 1993), where Early Miocene deposits consist of an alternation of reddish fluvial sandstones and siltstones, and grey-blue lacustrine claystones and lignites. Based on pollen work, the existence of highly diverse rainforests during the Early to early Middle Miocene has been demonstrated (Hoorn, 1994b; 2006).

During the Middle Miocene (*c.* 17-11 Ma), the Pebas system became centred on present-day western Amazonia and covered the foreland basin zone, as well as pericratonic margins and intracratonic basins. At its maximum it occupied an area well over 1 million km^2 (Wesselingh *et al*., 2002). Connections with the marine realm existed through the Llanos basin and further north, and probably aquatic connections existed episodically through the Cuenca basin to the west towards the Pacific (Hoorn *et al.,* 1995; Vonhof *et al.,* 1998; Lundberg *et al.,* 1998; Steinmann *et al.,* 1999). Modern wet tropical monsoon types of climates were present during the late Early to early Middle Miocene (*c.* 16 Ma; Kaandorp *et al.*, 2005), but may have been present already since the Early Miocene (*c.* 23 Ma; Wesselingh *et al.*, 2006b). The Pebas system consisted of lakes and swamps, with fluvial as well as marginal marine influence (Wesselingh *et al.*, 2002, 2006d). Towards the west and southwest, the Pebas system graded into fluvial plains of Andean rivers (Hermoza, 2005; Hermoza *et al.,* 2005). In the east and northeast, blackwater rivers draining the craton areas entered the system (Hoorn, 1994a, 2006). Given the continuity of endemic mollusc and ostracod lineages, the Pebas system must have sustained large, permanent lakes between at least *c.* 17 and 9 Ma (Wesselingh, 2006a). At the same time, large areas could sustain lowland swamp forest, including *Mauritia* palm forests (Hoorn, 1994a, b, 2006), or lowland forests. During recurring base level high stands, aquatic conditions in the Pebas system became widespread and the region became effectively dominated by lakes (Wesselingh *et al.*, 2006b). Possibly, the Pebas system terminated with a major marine incursion, indicated, for example, by the presence of purported echinoid trace fossils in deposits south of Iquitos, Peru (Rebata *et al.,* 2006a, b). These latter deposits (confusingly indicated as uppermost Pebas Formation) yield no mollusc fossils and are assigned to the Late Miocene *Fenestrites* pollen zone, post-dating the Pebas Formation. It is quite possible that marine-derived Late Miocene intervals extended all the way to the Chaco basin in the south (Hoviskoski *et al*., 2005). Faunal indications discussed below strongly suggest that the marine conditions were not connected to coeval marine intervals in the Parana basin system further to the south.

In the early Late Miocene (8-9 Ma: Harris & Mix, 2002; Steinmann *et al*., 1999; Cooper *et al.,* 1995; Rousse *et al.,* 2003), the eastern Andean zones underwent strong uplift. Presumably as a result, the western lower margin of the Guyana Shield, that extends almost to the Andes in central Colombia, became emergent, blocking the northern aquatic corridor between the Pebas system and the Llanos through the foreland basin. The transformation of the lacustrine and marginal marine settings of the Leon Formation towards the fluvial settings of the Guayabo Formation in the Llanos basin is estimated at *c.* 10 Ma (Cooper *et al*., 1995) or even 8 Ma (Cazier *et al*., 1995; Rojas-Sarmiento, 2002). Possibly, aquatic connections persisted after the foreland basin corridor north of the Serrania de la Macarena became obstructed slightly longer through the lower western margin of the Guyana craton (Hoorn, 2006). At the same time, the western part of the continent must have experienced a slight tectonic tilt and erosion products of the emergent Andes quickly filled, and then bypassed western Amazonia. Significant widespread compressive deformation has been reported from the Peruvian Andes between 7 and 9 Ma (Rousse *et al*., 2003), coinciding with the onset of the Nazca Ridge collision to western South America and possibly a short period of increased Mid-Atlantic spreading rates (Sébrier & Soler, 1991). Major tectonic uplift is also reported from similar time intervals of the Ecuadorian Andes (Steinmann *et al*., 1999). The modern Amazon reached its present-day easterly course *c.* 8 Ma ago (Harris & Mix, 2002; Dobson *et al.,* 1997, 2001). During the Late Miocene and Pliocene, fluvial systems may have been poorly delimited and shifted drastically over lowland Amazonia. Regional uplift of lowland Amazonia, combined with strong glacio-eustatic sealevel variation in the Quaternary, finally entrenched the rivers into the more or less well-defined valleys of today.

Lake Pebas as a barrier for the exchange of terrestrial biota

Much of the species richness in Amazonian rainforests is found on *terra firme* (forests on elevated areas between river floodplains). Many animal and plant groups living there cannot survive or propagate in swampy conditions, and are unable to disperse over water surfaces. Hermoza (2005) has shown that aquatic settings were widespread in western Amazonia prior to the Miocene. The lowest part of the Chambira Formation and underlying Pozo Formation (Late Eocene to Early Oligocene, *c.* 45-34 Ma; Wesselingh *et al.,* 2006b) were deposited under marginal marine, lacustrine and floodplain settings. During deposition of the Chambira Formation (Oligocene), the predominant conditions were similar to those in the modern Colombian/Venezuelan Llanos (Wesselingh *et al.,* 2006b). Elevated channel belts amidst seasonally flooded savannahs should have provided biotopes and dispersal pathways for terrestrial biota. From the Late Eocene to Late Oligocene (*c.* 34-23 Ma), aquatic settings in western Amazonia were semi-continuous; during the Early to early Late Miocene (*c.* 23-8 Ma), these settings became widespread, permanent and formed the Pebas system. As a result of the sheer size, it may be assumed that terrestrial taxa with low dispersal capabilities were unable to move or be moved between the eastern and western margins of this Pebas system, that is, between the Guyana Shield and the northern Andes. Land connections existed at the southern rim of the Pebas system, permitting faunal and floral exchange between the central Andes and the Brazilian Shield. The size and long duration of the Pebas system as a barrier for dispersal between northern Andean and Guyana Craton biota has not been appreciated in biogeographic literature. For example, estimated divergence ages between two Guyana Craton and one Panamanian - western Colombian *Dendrobates* (poison dart frog) species (7.1-20.3 Ma; Clough & Summers, 2000) are concomitant with the age of the Pebas system (8-23 Ma). Divergence estimates of Central and South American *Lachesis* (bushmaster) species are between 6.4 and 17.9 Ma (Zamudio & Green, 1997), and estimated divergence ages between highland and lowland Mangoes (hummingbirds) at 12.6-13.9 Ma (Bleiweiss, 1998) are also within the same time span. These authors usually invoke uplift of the northern Andes to explain such divergences, but have so far overlooked the possibility that the aquatic barrier formed by the Pebas system also may have enhanced isolation and hence allopatric speciation. Furthermore, Lougheed *et al.* (1999) calculated divergence ages for frog populations within lowland Amazonian *Epidobates femoralis* of 5-15 Ma. These authors attributed divergence of populations in this area to the former presence of geological arches (a theory discarded below), and fail to consider either secondary contact of eastern and western Pebas margin populations or edaphic differentiation (for the latter, see below). In short, the aquatic nature, large size and long duration of the Pebas system, and its connections to the Caribbean, must have created a large aquatic barrier that debilitated exchange of terrestrial biota of the Guyanas and the northern Andean region during much of the Miocene. Kronauer *et al.* (2005) also indicated a possible role of the Pebas aquatic barrier in the divergence of terrestrial taxa (in their case geckos).

Marine-freshwater transitions in the Pebas system

The Pebas system was linked to marine conditions to the north (Llanos basin and eastern Venezuela and/or Maracaibo/Falcon basin; Fig. 1). Indications of such connections exist in the form of shared species between Miocene Amazonia and northern

Venezuela (molluscs, Nuttall, 1990; Wesselingh & Macsotay, 2006: flora, Hoorn *et al*., 1995: fish, Lundberg *et al*., 1998; Lovejoy *et al*., 1998, 2006; Albert *et al*., 2006). Indicators of marine influence are found throughout the stratigraphic range of the Pebas Formation, although body fossil and isotope geochemical evidence indicates that full marine conditions possibly never established in western Amazonia during that time interval (Vonhof *et al*., 2003; but see Gingras *et al*., 2002, for an alternative interpretation of salinity regimes).

A number of aquatic animal groups with a possible relatively recent marine ancestry occur within the Amazon region, such as stingrays, drums, anchovies, needlefish, iniid dolphins, manatees and various parasitic lineages (references in Lovejoy *et al*., 2006). For example, South America has its own family of freshwater stingrays, the Potamotrygonidae. Lovejoy *et al.* (1998) convincingly demonstrated through phylogenetic analyses and molecular divergence age calculations that these rays must have evolved from marine ancestors, and made the transition of the coastal Pacific-Caribbean realm to the freshwater Amazonian environments between 15 and 23 Ma. This estimate agrees with the presence of large transitional systems between the marine realm in northern Venezuela and the predominantly freshwater Pebas system in western Amazonia. Therefore, it is likely that the Pebas system provided a pathway for the establishment and adaptation of marine organisms into freshwater Amazonian environments. Furthermore, molecular age estimates for the origin of two of the three independently derived freshwater Amazonian needlefish (Belonidae) clades range from 14 to 17 Ma (Lovejoy *et al*., 2006). However, not all possible marine-derived Amazonian taxa have their origin through the Pebas system. A number of marine taxa occurring in the Amazon system, such as sharks and sawfishes, were and are able to cross the transition from the sea to the rivers repeatedly, so "Perhaps the Miocene upper Amazon wetlands could be considered a lineage pump that acted to 'inject' marine taxa into freshwater habitats over an extended period of time" (Lovejoy *et al*., 2006, p. 11).

Amazingly, the Pebas system seems to have played no role in the transition of marginal marine molluscs and ostracods towards modern South American freshwater environments. Marginal marine molluscs are known from the Pebas Formation (van Aartsen & Wesselingh, 2000, 2005; Vermeij & Wesselingh, 2002; Wesselingh, 2006a), but are rare and diminutive. According to Vermeij & Wesselingh (2002), the occurrence of relatively small and thin-shelled marine-derived gastropods may have been facilitated by a predation through in oligohaline environments, lacking the abundant highly specialized molluscivores of the Neotropical coastal and Amazonian freshwater biotopes. None of the marine mollusc taxa has made the successful transition towards the modern Amazonian freshwater biotopes that are dominated by representatives of cosmopolitan freshwater groups, such as pearly freshwater mussels, corbiculids, nut clams and planorbid snails (e.g., Irmler, 1975; Ituarte, 2004; Mansur & Valer, 1992; Haas, 1952 and references therein; own observations). In tropical Asia and Africa, a number of marine to freshwater molluscan transitions are known. The Pebas system was dominated by endemic mollusc and ostracod faunas (Wesselingh *et al*., 2002; Wesselingh, 2006a; see below). These faunas appeared to have been adapted to a range of ecological pressures, such as soupy bottoms, high predation pressure and foremost episodic widespread dysoxia (Wesselingh *et al*., 2006c; Wesselingh, 2006b). These pressures may have created an insurmountable barrier for the relatively immobile marine molluscs to overcome, even if some of these had the potential to adapt to freshwater systems. Mobile organisms, such as fish, would have been in great advantage to avoid episodic, possibly local, unfavourable settings. This might explain the co-occurrence of highly specialized, rather immobile and endemic invertebrate faunas next to non-endemic mobile vertebrate faunas in the Pebas system.

The Pebas system as a stage for mollusc and ostracod diversifications

The diversification of endemic mollusc (Wesselingh *et al.,* 2006a) and ostracod (Muñoz-Torres *et al*., 2006) faunas in the Pebas system is remarkable (Fig. 2). During the Early Miocene Mollusc Zone (MZ) 1, the presumable ancestor faunas were dominated by two species of *Pachydon* and one *Dyris* species. In a short period, covering the late Early to early Middle Miocene (*c.* 14-17 Ma), extensive radiations occurred. At the zenith of Pebasian diversity, during the late Middle to early Late Miocene (*c*. 13 Ma), nearly 70 co-occurring endemic species were present in the system (Fig. 2). During MZ9 (*c.* 11-12 Ma; Wesselingh *et al*., 2006a), diluted marine incursions were not rare in the Pebas system (Vonhof *et al.*, 1998, 2003). At this stage, a number of long-standing and common endemic species, such as *Neritina ortoni, Tryonia minuscula* and *Dyris tricarinatus,* went extinct and overall species numbers dropped. Furthermore, at MZ10, by far the commonest species, *Pachydon obliquus*, was suddenly replaced by *P. trigonalis*. During MZ10-MZ12, species numbers more or less remained constant. The Pebasian radiations probably abruptly ended with the onset of the modern Amazon system, between 8 and 9 Ma (Lundberg *et al.,* 1998; Wesselingh *et al.,* 2006d).

The mollusc and ostracod radiations are compatible with evolutionary longevity of the Pebas system. Similar radiations with high species numbers, endemicity rates and morphological disparity are well known from long-lived lakes (Martens, 1997; Wesselingh, in press). Ecological disturbance removed competitors and provided a stable set of biotopes on geological timescales, thus allowing members of usually competitively inferior groups to become established, specialise, radiate and dominate in long-lived lakes (Wesselingh, in press). In the case of the Pebas system, the diversity of substrate types, variable oxygenation, and high predation pressure as well as aquatic chemistry may all have added to the complexity of the ecosystem (Wesselingh *et al*., 2006c). The raw species data indicate that the cochliopid gastropods were more prone to radiation and extinction than the corbulid bivalves (Fig. 2). In almost any long-lived lake, gastropods are more prone to radiations and extinctions, and bivalve lineage survivorship is more stable. This can, in part, be explained by the rather immobile living position of bivalves after settling, promoting increased tolerance of environmental change on ecological scales. Such increased tolerances are of help during episodes of massive disturbance, which therefore hit the often more specialized snails harder (Wesselingh, in press). Furthermore, a higher specialization potential of gastropods may cause an average decrease of their ecological and geographic distribution range, increasing extinction risk during massive ecological disturbance. The continuity of the endemic lineages in the Pebas system reflects the geological continuity of the freshwater ecosystem between at least *c.* 17 and 9 Ma.

The Neotropical character of the Pebas mollusc fauna

Although most Pebasian mollusc taxa are endemic, a number of species, and most of the genera, are shared with areas outside western Amazonia and shed light as to the biogeographic affinity of the Pebas fauna. Table 1 lists six eco-biogeographic groups of

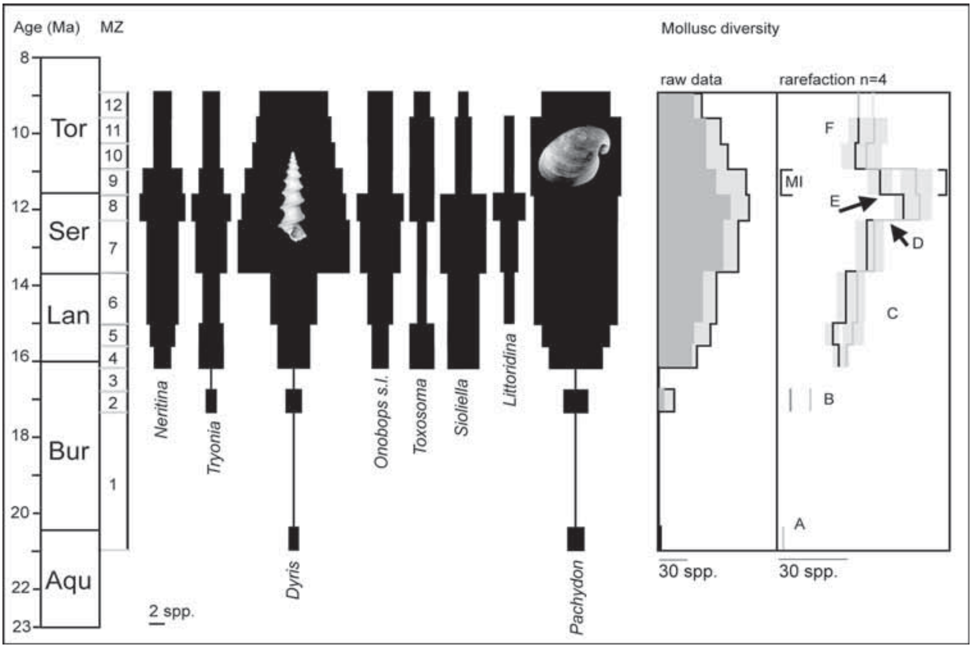

Fig. 2. Approximate diversity within a number of species-rich genera in the Pebas fauna. Species estimates are from Wesselingh (2006a). Light grey covers total species numbers and dark grey covers endemic component (under raw data). Under rarefaction, the dark line refers to the endemic fauna component and the light grey line to the total fauna; the light grey blocks refer to 1 standard deviation. MI = interval with increased (marginal) marine influence. At MZ 1, mollusc diversity is low and no Pebasian endemics occurred. From MZ2 (B) until MZ 7 a gradual increase in overall as well as endemic mollusc diversity occurred (C). A very steep increase in diversity occurred at MZ8 (D). The peak diversity is reached during MZ8, with some 95 species (78 of which are considered as endemics: Wesselingh, 2006a). During MZ9 (E), diversity remained high, but the diversity of endemic species dropped, possibly linked to increased marine influence (MI). Both overall and endemic diversity dropped further and stabilised in MZ10-MZ12 (F). Stratigraphic model from Wesselingh *et al.* (2006a). Note that age uncertainties for the MZ boundaries are typically one million years or so.

Miocene to modern mollusc taxa shared between the Pebas system and areas outside western Amazonia. These groups are envisaged in Figure 3.

Most taxa (15 out of 18; Table 1) are shared between the Pebas system and the Caribbean-Pacific region. The Panama isthmus is of a Pliocene age (Coates & Obando, 1996), and the western Pacific-Caribbean can be considered as a single marine biogeographic province before. The ancestry of the dominant groups (Cochliopidae, Corbulidae) is uncertain. Pebasian corbulids almost certainly relate to freshwater Paleocene corbulids of North America, but the origin of the Pebasian cochliopids is uncertain, due to a very poor pre-Miocene record.

There are a number of indications of a northern connection between Pebas and the marine realm (see, e.g., Lundberg *et al.*, 1998), but there is some evidence of short-lived lowland connections to the west through southern Ecuador during the Middle Miocene existed, as well. Neither can Neogene transcratonic connections through the Guyana

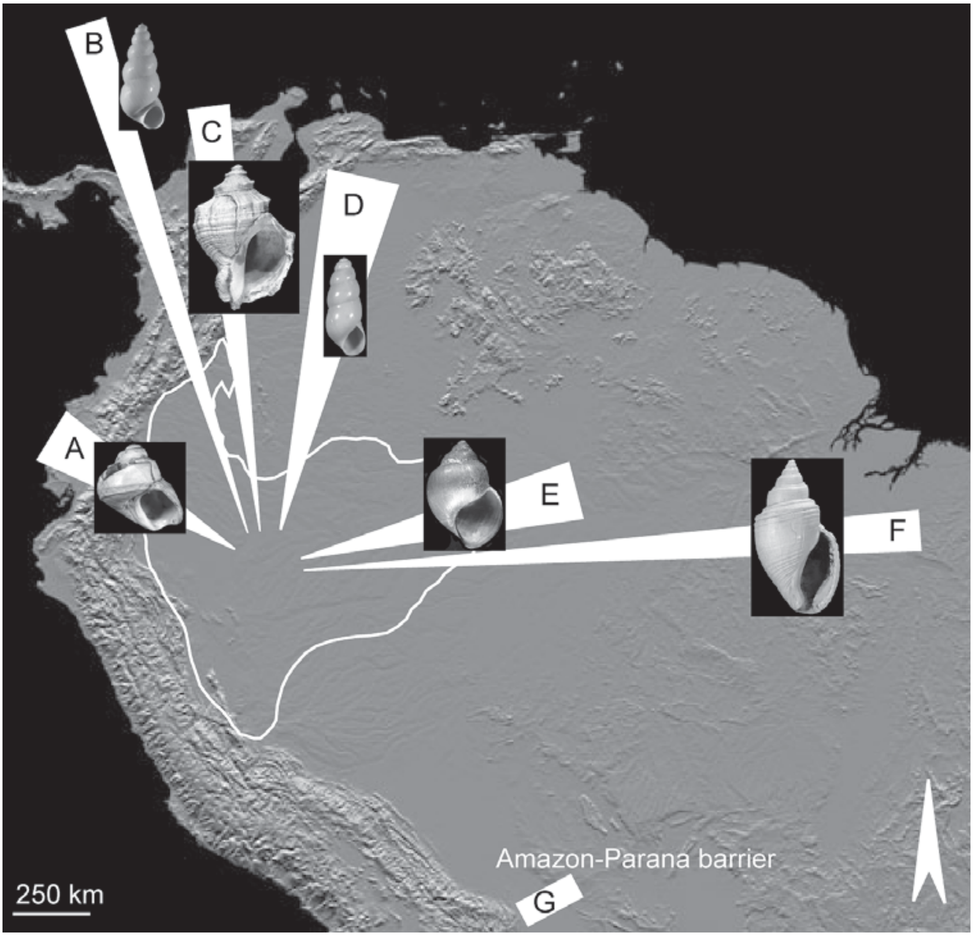

Fig. 3. Ecobiogeographic mollusc groups with a Pebasian affinity. The groups are explained in Table 1 and explored in the text. Key: A = *Lithococcus amazonicus*; B = *Onobops communis*; C = *Melongena woodwardi*; D = *Glabertryonia glabra*; E = *Sioliella effusa*; F = *Aylacostoma browni*. All specimens from the Miocene Pebas Formation (Wesselingh, 2006a), apart for *S. effusa* that is from the lower Tapajoz River, Brazil (Wesselingh, 2000). Background map (also in Figs. 4, 5) modified from www.photojournal.jpl.nasa.gov.

Shield be excluded, but there is very little evidence of direct faunal exchange between the Pebas system and eastern Brazilian Atlantic, and almost none for a close biogeographic connection with the Parana-Plate River system.

A shared distribution of Pebasian and northern Colombian/Venezuelan mollusc taxa was proposed by Nuttall (1990). However, these comprised merely shared species from the Early Miocene, preceding or only coeval with the earlier part of the Pebas system (Wesselingh & Macsotay, 2006). Indications of a northern connection of the Pebas system during the Middle-early Late Miocene also exist (Fig. 4).

Many of the shared taxa (8 out of 18; Table 1) have a Pebasian record and a Recent Caribbean-eastern Pacific distribution, but otherwise lack a Neogene record. This group

Table 1. Ecobiogeographic mollusc groups with a Pebasian affinity or lacking such an affinity. Capital characters refer to groups illustrated in Figure 3.

A. Pacific freshwater taxa	
Lithococcus spp.	Pebas system and Panamic-Pacific coastal fresh water biotopes
B. Circumcarribean freshwater and euryhaline taxa	
Littoridina spp.	Pebas system and Panamic-Pacific/Carribean coastal fresh- & brackish water biotopes
Pyrgophorus spp.	Pebas system and Circumcaribbean ~ fresh water biotopes
Onobops spp.	Pebas system and Gulf-Atlantic coastal brackish water biotopes
Littoridinops? spp.	Pebas system and northern Carribean-Atlantic coastal brackish water biotopes
Tryonia spp.	Pebas system and Miocene - Recent Circumcaribbean fresh- and inland brackish water biotopes
Cochliopina? spp.	Pebas system and fresh water biotopes of Central America and the Pacific lowlands of Ecuador and Colombia
Neritina ortoni s.l.	Pebas system and Miocene coastal deposits northern Venezuela (Nuttall, 1990)
Mytilopsis sallei	Pebas system and Circumcaribbean fresh- and coastal brackish water biotopes
C. Marine panamic taxa	
Melongena woodwardi	Marine incursions, Pebas system and Miocene marine deposits, Panama (Vermeij & Wesselingh, 2002)
Corbula cotuhensis	Marine incursions, Pebas system and Miocene marine deposits, northern Venezuela: close ally *C. gatunensis* in Miocene marine deposits of Panama
D. Guyana coastal plain marine taxa and freshwater associates	
Glabertryonia spp.	Freshwater species associated with marine incursions, Pebas system and Guyana Shield coastal plains
Anticorbula spp.	Freshwater species associated with marine incursions, Pebas system and Guyana Shield coastal plains; also known from non-marine fluvial Amazonian systems
Iolaea spp.	Brackish water inhabitant: marine incursions in the Pebas system and Guyana Shield coastal plains
E. Eastern Amazonian freshwater relic taxa	
Dyris amazonicus	Pebasian relic freshwater species in lower Tapajoz River (Wesselingh, 2000)
Sioliella effusa	Pebasian relic freshwater species in lower Tapajoz River (Wesselingh, 2000)
F. Eastern South American freshwater taxa	
Hemisinus kochi	Pebas system and Atlantic rivers eastern Brazil
Aylacostoma spp.	Pebas system and Atlantic rivers eastern Brazil south to Parana system southern Brazil-Argentina; Neogene southern Caribbean and NW South America
G. Amazon-Parana barrier	
Potamolithus spp.	Absent in Pebas system; common in modern Paranan fresh water biotopes
Heleobia spp.	Absent in Pebas system; dominant in southern South American Miocene-Recent fresh & brackish water biotopes
Erodona mactroides	Brackish water corbulid of southern South America and tropical Africa unrelated to Pebasian corbulids

is, however, the largest and clearly shows the Neotropical affinity of the Pebasian fauna. A Miocene Caribbean – Amazonian connection is also indicated by the presence of 'Amazonian' fish taxa in Miocene deposits of coastal northern Venezuela (Lundberg & Aguilera, 2003, and references therein).

The Pebas system may have had a lowland aquatic connection with the Pacific Ocean during the Middle Miocene. Steinmann *et al.* (1999) envisaged such a connection through a corridor including the present-day Gonzama, Vilcabamba and Loja basins (southern Ecuador). However, these southern basins were found to contain faunas dominated by *Heleobia* that are not compatible with the Pebas fauna (pers. obs.). In the Loja basin a single gastropod species, *Dyris* aff. *carinatus* (as *D. tricarinata* in Nuttall, 1990, figs. 76-78), indicates some potential affinity between the Pebas fauna and those of the southern basins. In a few of the south-central Ecuadorian basins, slightly to the north of the before mentioned basins, a number of species occur that are shared with the Pebas fauna. These include the freshwater cerithiodeans *Sheppardiconcha tuberculifera, S. bibliana* and *Charadreon eucosmius* (Wesselingh, 2006a; Wesselingh *et al.,* 2006b). Furthermore, faunas collected by M. Steinmann & D. Hungerbuehler in the Loyola Formation of the Cuenca basin (pers. obs.) were found to contain moulds of several poorly identifiable *Pachydon* species, indicating a direct faunal exchange between the Cuenca basin and lowland western Amazonia. Furthermore, one *Cyprideis* (ostracod) species in the nearby Giron-Santa Isabel basin is shared with the Pebas fauna (D. Peterson, pers. comm.). Steinmann *et al.* (1999) showed that the Cuenca basin was open to the west (Pacific Ocean). They did not show a connection from the Cuenca basin to the Amazonian lowlands, but, given the presence of the shared freshwater cerithiodean species and *Pachydon* species, such a connection should have existed. The Loyola Formation has been dated as Middle Miocene (10.7-15.3 Ma).

Up to four taxa are shared between the Pebas fauna and faunas from regions to the east (Table 1). *Sioliella effusa* and *Dyris amazonicus* live in the lower reaches of the central-eastern Amazonian Tapajos River of Brazil and are the sole extant representatives of genera that strongly diversified in the Pebas system (Wesselingh, 2000). These species may either have a relic vicariance occurrence or dispersed in eastern Amazonia with the establishment of the eastern course of the modern Amazon River (*c.* 8 Ma). The two other taxa, *Aylacostoma* spp. and *Hemisinus kochi*, are shared between the Pebas system and the eastern Brazilian Atlantic Rivers. The fossil record of both genera in northwestern South America and the Caribbean indicates that the modern distribution is a small relic of a former, widespread Neotropical range.

Mollusc indications of a possible connection between the Pebas and Parana systems through the interior of South America are lacking. The gastropod fauna of the southern South America is dominated by *Heleobia* and *Potamolithus* species (Nuttall, 1990). These genera were also dominant in Miocene times in northwestern Argentina (Alonso & Wayne, 1992; Herbst *et al.,* 2000; Morton & Herbst, 2003). The Pebas fauna is dominated by the gastropod genera *Dyris*, *Tryonia*, *Sioliella*, *Onobops* and *Toxosoma* that are lacking in the record of the Parana system. If lowland connections existed during the Miocene between western Amazonia and the Parana system, we would have expected more faunal interchanges between these regions then currently has been established. Similar low levels of fish taxon congruence between the Amazon and Parana system have been reported by Albert *et al.* (2006) and Lovejoy *et al.* (2006).

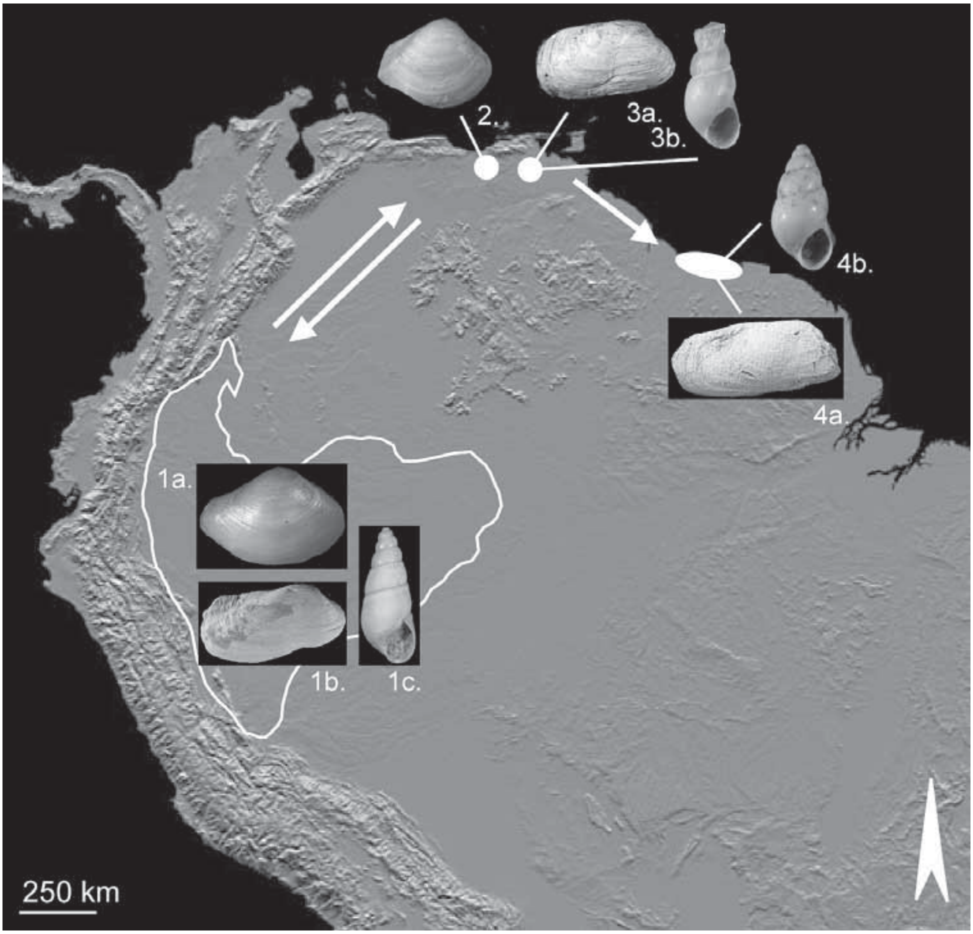

Fig. 4. During the Middle-late Early Miocene, a number of mollusc taxa occurred in the Pebas system that is shared with northern Venezuelan deposits. For example, the brackish water *Corbula cotuhensis* (1a) occurs in incursion levels in the Pebas system and also the Miocene Santa Ines Beds (2) of northern Venezuela (Hedberg, 1937). In the same stratigraphic intervals where marine species occur in the Pebas Formation, freshwater taxa, such as *Anticorbula* spp. (1b) and *Glabertryonia glabra* (1c), occur. The combination of *Glabertryonia* spp. and *Anticorbula* spp. is also known from the Pliocene Las Piedras Formation of eastern Venezuela, and the Holocene-modern coastal plains of Surinam and Guyana (Figs. 3b, a, and Figs. 4b, a, respectively).

The Pebas Formation and post-Miocene terrestrial biodiversity

The termination of the Pebas system, *c.* 8 Ma, made large tracts of western Amazonia available for the establishment of the terrestrial biota. In lowland Amazonia, the western part harbours the highest diversity levels (Fjeldså, 1995; Clough & Summers, 2000; Rahbek & Graves, 2001; Valencia *et al.,* 2004). Edaphic heterogeneity has been shown to correspond with high diversity in ferns and melastomatacean plants, as well as trees (Tuomisto *et al.,* 1995, 1998, 2003; Tuomisto & Poulsen, 1996; Ruokolainen *et al.,* 1997). In the study area (Peruvian Loreto, and adjacent border areas of Brazilian and Colombian Amazonia), a number of very different geological units crop out below the forest floor. A large part is formed by the Pebas Formation, itself a highly heterogeneous formation containing nutrient-rich smectite claystones, lithic arenites and lignites with large variations in carbon and sulphur content and permeability (Räsänen *et al.,* 1987, 1998; Linna *et al.,* 1998). In the region between the confluence of the Ucayali and Marañon (Peru) in the south and the Caqueta River (Colombia) in the north, the Pebas Formation is overlain by a thin cover of a variety of fluvial deposits. Along all rivers, Late Quaternary terrace deposits (made up of arenites and conglomerates) exist, but high on the watersheds, older fluvial deposits are found as well (Räsänen *et al.,* 1998). To the south of Iquitos, the Late Neogene White Sand Formation (made up of deeply weathered quartz arenites and younger arenite deposits still reflecting the original aggradation structures by a presumably earlier phase of the Nanay River) is present in patches over the Pebas Formation. In the same area and further south, yet unnamed Late Neogene deposits containing illite rich claystones and sandstones occur. River terraces are found along all larger rivers in the area. Some of these were erosive only, locally exposing Neogene strata; others were depositional. As a result, the region is a genuine edaphic mosaic that is enhanced by the variable lithologies of the Pebas Formation itself.

Several studies indicated that massive radiations in terrestrial biota occurred during the Late Miocene and Pliocene (*c*. 3-10 Ma; Fjeldså, 1994; Bleiweiss, 1998; Cheviron *et al*., 2006). Not only the establishment of large tracts of new forestine habitats may have accommodated increased species numbers, but also the deposition of a (nutrient-rich Andean to nutrient-poor cratonic) fluvial cover, and the subsequent uplift and dissection of these deposits (Räsänen *et al*., 1998), created a dynamic edaphic mosaic in the region that sustained high diversity.

Recent analyses have indicated that, in general, the floristic patterns of Melastomataceae and ferns, and to some extent also palms (Arecaceae), are reflecting the edaphic (soil) mosaicism of the western Amazon lowlands (Tuomisto *et al*., 1995; Ruokolainen *et al*., 1997, 2002; Tuomisto *et al*., 2003; Vormisto *et al*., 2004; but see Pitman *et al*., 1999; Pitman, 2000; Condit *et al*., 2002; Ruokolainen & Tuomisto, 2002; Ruokolainen & Vormisto, 2000). These results support the original hypothesis of Salo & Räsänen (1989) that the landscape dynamics driven by Andean foreland tectonics may have contributed to maintenance of spatial biodiversity patterns both in the flooded and in the non-flooded (*terra firme*) ecosystems through a shifting mosaic and metapopulation dynamics (Salo, 1986; Räsänen *et al*., 1990). Tectonics also may have forced biological differentiation through barriers created by the terrestrial/wetland shifts since the Miocene and the geochemical evolution of the forest bed (Salo & Räsänen, 1989; Schulman, 2003), creating an archipelago-like pattern in the lowland forest bed.

A well-known example of the latter are the white sands of Allpahayo-Mishana, a 500 km^2 site with well-documented bird endemism in the lowlands (Alvarez & Whitney, 2003; Whitney & Alvarez, 2005). Allpahuayo-Mishana is located within an area of neotectonic uplift (the Iquitos forebulge; Jacques, 2003; Roddaz *et al*., 2006). It is a mosaic of Quaternary fluvial sands on sites of abandoned floodplains of River Nanay and older, weathered, arenites.

Recently, two maps reflecting the actual habitat, ecosystem and vegetation heterogeneity in the Peruvian Amazon lowlands have become available (*Macrounidades Ambientales en la Amazonía peruana* and *Diversidad de vegetación de la Amazonía peruana*, BIODAMAZ, 2004a, b). These maps show that the Peruvian Amazon is not a homogenous closed-canopy forest, but a vegetation mosaic comprised of at least 24 vegetation units, including flooded and non-flooded forests on heterogenous forest beds, wetlands, and bamboo and palm-dominated monodominant forests. The distribution patterns of western Amazon terrestrial biota need to be checked against these actual vegetation types, which as such are mainly the outcomes of tectonic foreland dynamics and depositional/erosional patterns as external drivers. Many of the suggested western Amazon Pleistocene refugia are actually areas which reflect either high habitat heterogeneity and subsequent packing of habitat specialists (in the so-called 'Napo refugium') or special forest structure (*Gadua*-dominated bamboo forests of East Peru-Acre). If the maps reflecting the true heterogeneity of the western Amazon vegetation had been available in late 1960s, the Amazon Refugia Theory (Haffer, 1969) maybe never would have emerged in its original form, as it was based on the wrong assumption that the lowland rainforest forest was homogeneous and could not explain the variation in species diversity.

Gone with the arches

In the past, so-called 'geological arches' have been invoked as an explanation for landscape evolution (Roddaz *et al*., 2006) and phylogeographic structuring of populations in Amazonia (da Silva & Patton, 1998; Lougheed *et al.,* 1999; Patton *et al*., 2000). The concept of arches is fraught with difficulty. Arches include extinct forebulge remains (El Baul Arch, Venezuela; Pindell *et al.,* 1998), broadly uplifted pericratonic margins (Vaupes arch, Colombia) and distal doming thrust sheets (Contaya Arch, Peru-Brazil), as well as basin constrictions deep in the subsurface (Cararuari and Purus Arch, Brazil). Wesselingh *et al.* (2006a) showed that almost every author who dealt with the so-called Iquitos arch located this apparent structure in a different place (Fig. 5). On the other hand, these authors showed the presence of a broad regional anteclise that apparently shaped drainage patterns in the study area (Iquitos-Napo-Araracuara). We argue that the term arch should be abandoned. It covers a variety of geological and geomorphological features that should be indicated as such. Some of these, such as the doming distal Andean thrust sheets, the Serra de Moa and the Serra do Divisor ('the Contaya Arch' at the Peruvian-Brazilian border), provided rocky substrate, complex microclimates and soil conditions that facilitate ecological heterogeneity and packing of ecosystems and species. Others, such as the Iquitos-Araracuara anteclise, played a role in the structuring of catchment areas and drainage divides, that in turn influenced the continuity of aquatic habitats and communities. Yet for other, such as the Carauari and Purus Arches, that are basin thresholds at depths of hundreds of metres, any role in geographic structuring and distribution of modern biota is hard to imagine. Rodent phylogeographic discontinuities in the Juruá area reported by da Silva & Patton (1998) and Patton *et al.* (2000) may reflect the long-term edaphic/chronographic differentiation and mosaicism of the forest bed, rather that direct effect of an elusive arch as an uplifting structure.

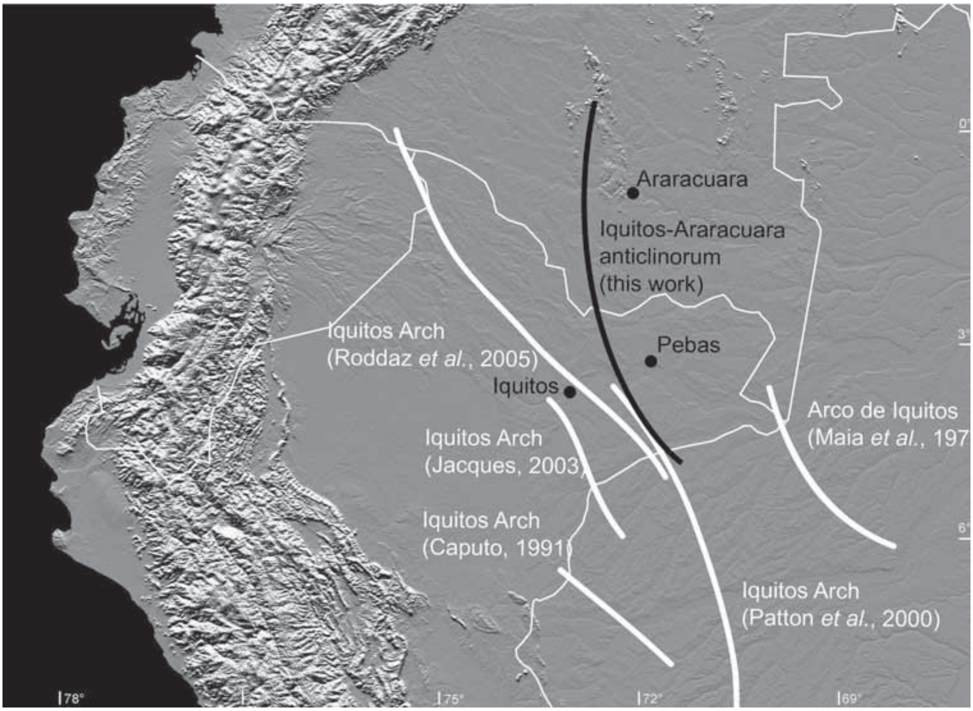

Fig. 5. The location of the 'Iquitos Arch', a supposed subsurface basin constriction according to literature (see text). The Iquitos-Araracuara anticlinorum refers to Wesselingh *et al*. (2006a).

Conclusions

The Pebas system provided a barrier to the dispersal of terrestrial biota between the Guyana Shield and the northern Andes during the Miocene, promoting separate biotic development on both sides. At the same time, it facilitated spectacular radiations of endemic molluscs and ostracods, and provided a pathway for the transition of marine biota to freshwater Amazonian settings. The demise of the Pebas system at the onset of the modern Amazon system, *c.* 8 Ma, provided large areas in western Amazonia for the colonization of terrestrial biota. The heterogeneous nature of the Pebas Formation, added to a subsequent Late Neogene history of fluvial deposition, denudation and erosion, resulted in a highly heterogeneous edaphic mosaic in western Amazonia that supports the highest species richness of lowland Amazonia. So-called (geological) 'arches', often invoked to explain landscape evolution and biotic development in lowland Amazonia, are unlikely to have played a major role as such. 'Arches' are a basket term for a variety of geological and geomorphological features, and we argue for its abandonment.

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