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**MOLLUSCAN RADIATIONS AND
LANDSCAPE EVOLUTION IN MIOCENE
AMAZONIA**

by

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TURUN YLIOPISTO
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- III. Wesselingh, F.P., Guerrero, J., Räsänen, M.E., Romero Pitmann, L. & Vonhof, H.B. 2006. Landscape evolution and depositional processes in the Miocene Pebas lake/wetland system: evidence from exploratory boreholes in northeastern Peru. *Scripta Geologica* 133: 323-361.
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- IV. Wesselingh, F.P., Kaandorp, R.J.G., Vonhof, H.B., Räsänen M.E., & Renema, W. 2006. The nature of aquatic landscapes in the Miocene of western Amazonia: an integrated palaeontological and geochemical approach. *Scripta Geologica* 133: 363-393. <http://www.repository.naturalis.nl/document/41350>
- V. Wesselingh, F.P. 2006. Evolutionary ecology of the Pachydontinae (Bivalvia, Corbulidae) in the Pebas lake/wetland system (Miocene, western Amazonia). *Scripta Geologica* 133: 395-417.
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- VI. Wesselingh, F.P., Ranzi, A. & Räsänen, M.E. 2006. Miocene freshwater Mollusca from western Brazilian Amazonia. *Scripta Geologica* 133: 419-437.
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- VII. Wesselingh, F.P. & Salo, J. 2006. A Miocene perspective on the evolution of Amazonian biota. *Scripta Geologica* 133: 439-458.
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1. INTRODUCTION

1.1 The quest to the origin of Amazonian biodiversity

Lowland Amazonian rainforests are among the most species rich ecosystems in the world. The origin of this diversity has intrigued many researchers over the past one and a half century. Insights into the age and context of diversification of Amazonian floras and faunas should ideally be preserved in the geological record. However, due to the poor accessibility of this vast region as well as the apparent lack of outcrops, its geological history is comparatively poorly understood. The lack of geological data has led to the emergence of many grand theories about the origin of the present-day Amazon system and its high diversity, often based on dubious interpretations of the little data available. For the Quaternary alone, it has been proposed that lowland Amazonia was covered by glaciers (Agassiz & Coutinho, 1868), savannah with forest patches (Haffer, 1969), deserts (Ab'Saber, 1982), megalakes (Campbell & Frailey, 1984), seaways (Nores, 1999) or just by the Amazon river system in a mostly lowland tropical rainforest setting (Colinvaux *et al.*, 1996; Irion *et al.*, 2005). With the advent of the refuge hypothesis (Haffer, 1969), the predominant paradigm in the history of Amazonian diversifications was one of speciation during the Quaternary. Molecular phylogenetic evidence of Quaternary speciation does exist (e.g., Rull, 2006; Quijada *et al.*, 2007). However, various molecular phylogenetic studies locate major faunal and floral diversifications in the Neogene (e.g., Givnish *et al.*, 2004; Willis & Niklas, 2004; Cheviron *et al.*, 2005; Ribas *et al.*, 2005; Elmer *et al.*, 2007). Improved understanding of the Neogene history of Amazonia is therefore key to understanding the origin of the modern Amazonian biota.

An excellent Miocene geological record, and in particular fossil record, is available in many areas in western Amazonia. The deposits, mainly of the Pebas Formation that commonly crop out in erosive riverbanks in Peruvian and Colombian Amazonia, form an exceptionally well-preserved, rich archive that should facilitate the reconstruction of the Neogene history of western Amazonia. Within these Miocene deposits very abundant and well-preserved mollusc faunas occur. This fossil mollusc record and its geological context are explored in this thesis to investigate the geological history of lowland Amazonia and to elucidate historical-geological aspects of the modern Amazonian diversity hotspot.

1.2 Insights from the Amazonian geological record by the mid 1990's

The assumed presence of glacial moraines and the proposal of Quaternary glaciations in lowland Amazonia by Agassiz in Washington D.C. in 1866 (see Agassiz & Coutinho, 1868) marks one of the first widely published geological accounts of the region. The first scientific signals about the dynamic Amazonian past from fossils were published by Gabb (1869), who reported a small, alleged brackish-marine mollusc fauna from the vicinity of Pebas along the Peruvian Amazon. In the following decade various publications about the molluscs from the Pebas Beds emerged (Conrad, 1871, 1874a, 1874b; Woodward, 1871; Dall, 1872; Boettger, 1878; Etheridge, 1879). The ecological signature (terrestrial to fully marine) as well as the age (Paleocene to subrecent) of these faunas were very differently interpreted (see de Greve, 1938, for a review). Most authors agreed that the Pebas faunas contained some indication of

marine influence. Only more than a century later, the age of the Pebas Beds (referred below to as Pebas Formation) became undisputedly established as Miocene (Nuttall, 1990; Hoorn, 1993).

The notion of seas in the history of lowland Amazonia has been elaborated further since the early 20th century (e.g., Kätzer, 1903; von Ihering, 1927; Domning, 1982; Nuttall, 1990) in order to explain, e.g., the occurrence of marine-like groups such as dolphins, manatees and a variety of marine-like fish groups in freshwater Amazonian biota. However, documentation of the Amazonian geology and palaeontology was sketchy at best. Since the 1920's, oil exploration missions carried out mapping exercises resulting in some regional geological works in the foreland basins and Subandean zones (see e.g., Kummel, 1948; Tschopp, 1953). Palaeontological studies had often a local scope and focussed entirely on the faunas and did not include the depositional context of these faunas (e.g., Roxo, 1924, 1937; de Greve, 1938; Willard, 1966; Santos & Castro, 1967).

Geological investigations in Brazilian Amazonia increased in the 1970's as a result of two large programmes. The search for economically exploitable lignite in Miocene deposits resulted in a huge borehole programme, the *Projecto de Carvao no Alto Solimões*, which has led to broad insights into the architecture of the Brazilian Amazonian subsurface (Maia *et al.*, 1977). At the same time geological surface mapping combined with radar mapping produced broad insights into the surface distribution of geological units (Radambrasil, 1977). Some palaeontological studies were carried out alongside these programmes (e.g., Costa, 1980, 1981), but these too provided fragmentary insights into the dynamic depositional history of the region.

A new era of geological investigations into the Neogene history of lowland western Amazonia emerged in the beginning of the 1990's. Three independent workers investigated very different aspects. Patrick Nuttall (BMNH, London, UK) concluded his decade long work on western Amazonian fossil molluscs with a lengthy systematic review (Nuttall, 1990). He concluded that fossiliferous sediments widespread in lowland western Amazonia, known as the Pebas Formation, were of a mostly Middle Miocene age. Actualistic comparison of Pebasian taxa led Nuttall to interpret the Pebas as a system of lakes, swamps and streams of varying salinities, with a connection to the Caribbean marine realm. Carina Hoorn (University of Amsterdam, the Netherlands), who worked on the palynology and sedimentary geology of Neogene successions in Colombia, Peru and Brazil as part of her PhD thesis, published a number of papers on the subject (Hoorn, 1993; 1994a, 1994b; Hoorn *et al.*, 1995). She established a palynostratigraphic framework. By correlation with dated Venezuelan marine units she corroborated and refined the age estimates of Nuttall (1990). Furthermore, she reconstructed the Pebas system as marine influenced floodplain to fluviolacustrine system based on pollen and the nature of the sediments. In her 1995 paper (Hoorn *et al.*, 1995), a model for the depositional history of the Amazonian region was presented that, with some modifications (Lundberg *et al.*, 1998), still holds today. Finally, Matti Räsänen (University of Turku, Finland) and his co-workers started to publish on the depositional context of Neogene sediments of Peruvian and Brazilian Amazonia, with special emphasis on the occurrence of tidal deposits (Räsänen *et al.*, 1996). Many insights into depositional environments of Neogene Amazonia were gathered. His emphasis on widespread marine influence sparked a lengthy discussion about the landscape development of western Amazonia during the Neogene (see Hoorn, 1996; Paxton & Crampton, 1996; Marshall & Lundberg, 1996). This

discussion has not yet been concluded (see Westaway, 2006 and chapter **IV** and references therein). In the 1990's more papers started to emerge on Amazonian Miocene vertebrate faunas from the Magdalena Basin in Colombia (Kay *et al.*, 1997) and the Acre region in Brazil improving insights into Miocene biogeographic provinciality. Finally, in the early 1990's the indirect role of geology in explaining present day biodiversity through edaphic heterogeneity became apparent for lowland Amazonia (Ruokolainen & Tuomisto, 1993; Tuomisto, 1993; Tuomisto & Ruokolainen, 1994; Tuomisto *et al.*, 1995).

Thus, at the beginning of the present research project, the results of which are presented in this thesis, the approximate age of Neogene deposits in western Amazonia was known and general agreement existed over the presence of predominantly aquatic settings in the region during the Miocene. At the same time, fierce debates developed as to the size and duration of the wetland system and the type and amount of marine influence and marine connections. Large uncertainties existed over climate regimes, landscape structuring and development, and the relationship between the Miocene history and the development of the present-day Amazonian biota. Even the age of the establishment of the modern Amazon was poorly constrained by the mid nineteen nineties.

1.3 Aims of this thesis

This PhD study aims to exploit the archive provided by the Miocene mollusc fauna of the Pebas Formation and other inland Miocene Amazonian formations to reconstruct landscape evolution and biotic development in lowland Amazonia during the Neogene.

In order to do so, the mollusc species were documented (**I, VI**). By documenting the stratigraphic distribution of mollusc species it was aimed to improve and refine the temporal control of the deposits and faunas in order to pinpoint ages of major landscape reorganisations and biotic developments (**II, III, VII**). The architecture and size of the Miocene wetlands as well as the type of depositional processes and their forcing mechanisms were explored from outcrop (**IV**) to basin (**III**) scales and temporal scales ranging from thousands (**IV**) to millions of years (**III, VII**). In order to facilitate research and discussion, stratigraphic and lateral boundaries of the Pebas Formation had to be investigated (**III**). A major objective of this study was to document the anatomy of molluscan diversifications (**VII**) but also to understand the (evolutionary-ecological) context of these diversifications and extinctions (**VI, VII**). Finally, this thesis aims to shed light on the various roles that the Pebas system played in shaping modern Amazonian landscapes and biodiversity (**VII**).

2. MATERIAL AND METHODS

2.1 Why use fossil molluscs?

Molluscs are very useful in geological investigations. Their shells have a good fossilisation potential and are common in the fossil record. The carbonate of the shells is formed by accretionary growth recording events happening during life (e.g., Kaandorp *et al.*, 2005). Individual species are very often highly informative as to ecological preferences. Within molluscs, taxa with widely varying habits and habitats occur. Feeding strategies include carnivorous, chemoautotrophic and herbivorous habits, to name but a few. Some molluscs are active swimmers, others are parasites or live a cemented life, and many more are burrowers. Molluscs live on alpine peaks, on tropical rainforest trees as well as in the oceanic abyss; they occur almost anywhere. Although shifts in behaviour and ecological distribution within lineages and groups have occurred over evolutionary time intervals, for the majority of taxa ecological/behavioural preferences can be deduced using actualistic approaches (V; Wesselingh, 2007). Mollusc assemblages are very robust (palaeo-) environmental indicators. The ecological signature of the assemblage components provides insight into the ecological frame in which assemblages occurred. Furthermore, such assemblages often show high correspondence to specific sedimentary facies (e.g., Dominici, 2001; Hendy & Kamp, 2007). Finally, by using taphonomic analyses, it is possible to look at fossil molluscs as sediment particles (Davies *et al.*, 1990; Kidwell, 1991; Martin, 1999). The robuste shells can easily be reworked without total destruction. Processes of reworking and time averaging can thus be recognised by studying patterns of wear and dissolution, strongly adding to understanding depositional processes in past environments.

Their excellent utility in reconstructing past environments and depositional processes is mirrored by a fairly poor utility in detailed stratigraphy. Individual mollusc species may persist millions of years. Mollusc faunas from ecologically isolated ecosystems, such as oceanic islands, cave systems and long-lived lakes form an exception. In such systems rapid evolution in unrelated lineages may drastically improve the utility of molluscs for detailed biozonation, if they become preserved (Magyar *et al.*, 1999). This is the case for the Pebas system that is considered a long-lived lake wetland system (I, IV)

The occurrence of very different reproductive modes, habitat preferences and locomotory types makes molluscs very well suited for comparison between regions (biogeography). There are mollusc groups whose shells do not allow discrimination of species, but these are typically parasitic molluscs or groups with cryptic habitat preferences, both of which are lacking or are very rare in the studied material.

Finally, molluscs are a practical object for study because they are easily collected and recognised and easily handled. For most analyses a set of standardised sieves, binocular and callipers is enough to perform basic analyses. They are easily collected by non-specialist and specialist alike. As a result it is possible to collect and process relative large numbers of specimens in a limited period of time, allowing all kind of analyses, including statistical approaches. Because of the abundance and easy handling, living molluscs have been widely observed and been used in controlled laboratory experiments. This has added to a vast knowledge of the ecological preferences of groups of molluscs.

In summary, molluscs are abundant, contain a variety of environmental signals, preserve well in the fossil record and easy to handle, and therefore form an ideally suited study group.

2.2 Localities and samples

The focus area of this study is north-eastern Peruvian Amazonia and the border zone of adjacent south-eastern Colombia. Over 160 samples from more than 70 Pebas Formation outcrops mostly collected by the author were processed for this study (**I, II, IV, V**) (Figure 1). Most samples contain of about 1-1.5 kg of fossiliferous sediments that have been washed, sieved and sorted at the facilities of Naturalis, Leiden.

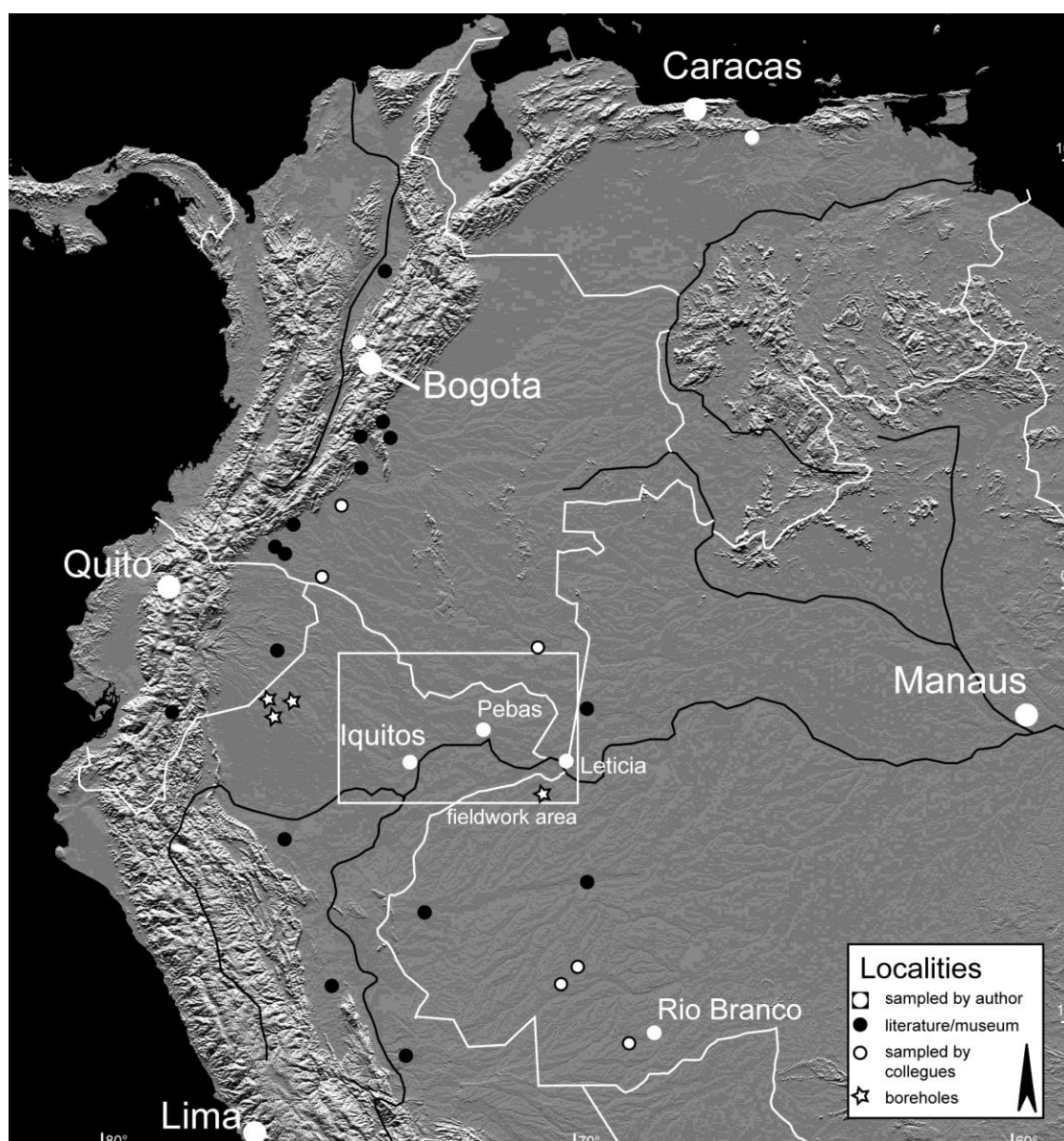


Figure 1. Localities, material of which has been treated in this thesis. Most samples are from the region indicated as fieldwork area. For detailed locality information in the fieldwork area the reader is referred to chapters **I** and **II**.

Lithological descriptions were made for the outcrops, and for about a third of the sections detailed sedimentological data were recorded by Matti Räsänen (University of Turku). The sample set covers slightly less than half the total amount of samples collected: samples were chosen to cover the various Miocene intervals (based on pollen age indications: Hoorn, 1994a and pers. comm.) as well as different depositional environments (Wesselingh *et al.*, 2002). Additional samples from 28 Pebas Formation localities held in museum collections were also included in this study. Mollusc samples from the Miocene Solimões Formation of western Brazilian Amazonia from three localities were made available for study by Matti Räsänen and Alceu Ranzi (UFAC, Rio Branco). The fauna of a fourth locality was studied in the Museu Nacional in Rio de Janeiro (VI). Borehole data and Pebas Formation samples made available by Occidental Peru from three wells (Capahuari, Huayuri and Jibaro) in the Marañón Basin in Peru (III) were also investigated. Finally, some Neogene mollusc faunas from the Andean regions of Peru, Ecuador, Colombia and Venezuela were studied from literature, museum collections and two additional Andean localities were newly collected by the author during this study.

2.3 An integrated approach

Despite their wide application, fossil molluscs alone cannot “tell” an entire geological history. It is the context in which mollusc faunas waxed and waned that enables to assess landscape evolution and biotic development in general. In the papers underlying the current thesis various analytical disciplines have been combined in order to frame the temporal and spatial depositional context of the fossil molluscs (Table 1).

Table 1. Disciplines involved in the current thesis. Investigators: CH Carina Hoorn; FW Frank Wesselingh; HV Hubert Vonhof; JG Javier Guerrero; MG Murray Gingras; MR Matti Räsänen; Ron Kaandorp; WR Willem Renema.

Disciplines	Investigators	Objectives
Ichnological analyses (IV)	MG	Reconstructing depositional regimes and salinity through ichnofacies
Molluscan community analyses (IV)	FW, WR	Documenting molluscan communities
Pollen analyses (II)	CH	Documenting palynoflora for palaeoenvironmental reconstruction and age estimates
Sedimentological analyses (IV)	MR, MG, HV	Reconstructing depositional environments and processes
Sequence stratigraphy (III, IV)	JG, MR, FW	Reconstructing size, shape and duration of depositional environments and processes
Sr isotope geochemistry (IV)	HV	Reconstructing water chemistry and water sources
C/O isotope geochemistry (IV)	FW, RK, HV	Reconstructing water chemistry, seasonal climate variation and investigating reworking
Taphonomic analyses (IV)	FW	Reconstructing depositional processes from fossilization signatures
Trace element analyses (IV)	HV	Reconstructing depositional and ecological processes
Well-log analyses (III)	FW, JG	Defining and characterizing geological units and depositional processes

Ideally, indications from different analyses are complementary. For example, the preservation of organic matter, the presence of pollen of rainforest taxa, the lack of red soils with carbonate concretions and the negative oxygen isotope signature of molluscs in the Pebas Formation all point to wet climate conditions. However, different data sets led to very different

interpretations of paleosalinity regimes in the same outcrops and beds (IV). In the latter case the common occurrence of sedimentary structures such as inclined heterolithic stratification indicates the presence of tides and the presence of *Glossifungites* ichnofacies mesohaline conditions. In the same layers, negative mollusc Oxygen isotope signatures, the rare in-situ presence of strict fresh water mollusc taxa such as pearly fresh water mussels and an Andean strontium isotope signature of the faunas all are indicative of strict fresh water settings. These conflicting datasets are further treated below, but the example shows the importance of assessing palaeoenvironmental interpretations using independent methods and proxies.

3. RESULTS

3.1 Composition of the Miocene mollusc faunas

The number of mollusc species attributed to the Pebas fauna has improved from slightly over 50 (Nuttall, 1990) to 156 (I, Table 2). During this study four genera and 74 species have been described and a further 13 species have been introduced in open nomenclature. Several taxa remain to be described, thus the species numbers are expected to rise somewhat further. Some 85 species co-occurred in the Middle Miocene time intervals with maximum mollusc diversity (VII, Table 2). The Pebas fauna is dominated by two families (Figure 2), viz. the Cochliopidae (86 snail species; 54%) and Corbulidae (24 bivalve species; 15%: I). Numerically, the corbulid bivalves dominate the Pebas fauna, with the Cochliopidae being second. The two families are almost entirely composed of Pebasian endemics and harbour a profuse range of morphological oddities. The Pebas fauna can be characterised as aquatic, endemic (Figure 2, Table 2) and extinct.

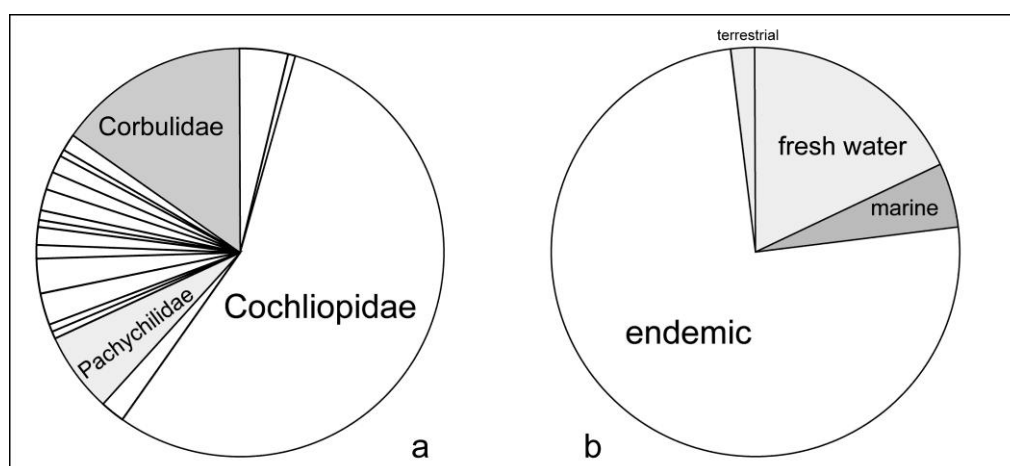


Figure 2. Composition of the Pebas mollusc fauna. Data from (I). (a) Species richness per family. The three most diverse families are indicated. (b). Nature of Pebasian mollusc species. The Pebas fauna is dominated by endemic aquatic species.

Table 2. Mollusc species from the Pebas Formation. For extensive synonymy and author references see (I). ¹endemic species, ²fresh water species, ³(marginal) marine species, ⁴terrestrial species. Asterix denotes species occurring in Mollusc Zone (=MZ) 8 intervals which was the time of maximum species richness in the Pebas system. Slightly different species numbers between Table 1 and (I) stem from the exclusion of La Cira taxa from the Pebas fauna.

Gastropoda

Neritidae

- Neritina roxoi* de Greve, 1938*²
- Neritina puncta* Etheridge, 1879*¹
- Neritina elephantina* Wesselingh, 2003*²
- Neritina patricknuttalli* Wesselingh, 2003*¹
- Neritina etheridgei* Roxo, 1924*¹
- Neritina orton* Conrad, 1871*¹

Ampullariidae

Ampullariidae sp.*²

Cochliopidae

- Tryonia minuscula* (Gabb, 1869)*¹
- Tryonia acicularis* (Nuttall, 1990)*¹
- Tryonia s. scalarioides* (Etheridge, 1879)*¹
- Tryonia s. tuberculata* (de Greve, 1938)*¹
- Tryonia semituberculata* (Nuttall, 1990)¹
- Tryonia nuttalli* Wesselingh, 2006*¹

- Feliconcha feliconcha* Wesselingh, 2006^{*1}
Feliconcha reticulata Wesselingh, 2006^{*1}
Glabertryonia glabra Wesselingh, 2006^{*2}
Dyris ortonii (Gabb, 1869)^{*1}
Dyris pebasensis Wesselingh, 2006¹
Dyris tricarinatus (Boettger, 1878)^{*1}
Dyris lataguensis Wesselingh, 2006¹
Dyris lineata (Conrad, 1871)^{*1}
Dyris hershleri Wesselingh, 2006¹
Dyris gracilis Conrad, 1871¹
Dyris microbispiralis Wesselingh, 2006¹
Dyris renemai Wesselingh, 2006^{*1}
Dyris microturritella Wesselingh, 2006^{*1}
Dyris regularis Wesselingh, 2006^{*1}
Dyris elongatus Wesselingh, 2006¹
Dyris romeroi Wesselingh, 2006^{*1}
Dyris lanceolatus Wesselingh, 2006^{*1}
Dyris acicularis Wesselingh, 2006^{*1}
Dyris hauxwelli Nuttall, 1990¹
Dyris mattii Wesselingh, 2006^{*1}
Dyris huberti Wesselingh, 2006^{*1}
Dyris guerreroi Wesselingh, 2006^{*1}
Dyris bicarinatus bicarinatus (Etheridge, 1879)¹
Dyris bicarinatus sofiaensis Wesselingh, 2006¹
Dyris hoornae Wesselingh, 2006^{*1}
Dyris ariei Wesselingh, 2006¹
Dyris carinatus Wesselingh, 2006^{*1}
Dyris megacarinatus Wesselingh, 2006¹
Dyris denticulatus Wesselingh, 2006¹
Onobops communis Wesselingh, 2006^{*1}
Onobops minissimus Wesselingh, 2006^{*1}
Onobops ventricosus Wesselingh, 2006^{*1}
Onobops bispiralis Wesselingh, 2006^{*1}
Onobops elongoides Wesselingh, 2006¹
Onobops microconvexus Wesselingh, 2006^{*1}
Onobops iquitensis Wesselingh, 2006¹
Onobops bisulcatus Wesselingh, 2006¹
Onobops erectus Wesselingh, 2006^{*1}
Pyrgophorus sp.^{*1}
Pyrgophorus thompsoni Wesselingh, 2006¹
Littoridinops? amazonicus Wesselingh, 2006¹
Toxosoma eboreum Conrad, 1874^{*1}
Toxosoma denticulatum Wesselingh, 2006^{*1}
Toxosoma contortum Wesselingh, 2006^{*1}
Toxosoma grande Wesselingh, 2006¹
Toxosoma ovatum Wesselingh, 2006¹
Toxosoma globosum Wesselingh, 2006¹
Toxosoma carinatum Wesselingh, 2006¹
Toxosoma multicarinatum Wesselingh, 2006¹
Longosoma curtum (Conrad, 1874)^{*1}
Longosoma glabrum Wesselingh & Kadolsky, 2006¹
Longosoma fusiforme Wesselingh & Kadolsky, 2006¹
Sioliella crassilabra (Conrad, 1871)¹
Sioliella woodwardi (Kadolsky, 1980)¹
Sioliella ovata Wesselingh, 2000^{*1}
Sioliella grevei (Kadolsky, 1980)¹
Sioliella bella (Conrad in Woodward, 1871)^{*1}
Sioliella sp.¹
Sioliella kadolskyi Wesselingh, 2006¹
Sioliella bisiphonata Wesselingh, 2006¹
Sioliella umbilicata Wesselingh, 2006^{*1}
Sioliella fusiformis Wesselingh, 2006^{*1}
Sioliella carinata Wesselingh, 2006¹
Sioliella littoridinaeformis Wesselingh, 2006¹
Sioliella saloi Wesselingh, 2006^{*1}
Tropidebora tertiana (Conrad, 1874)^{*1}
Tropidebora sp.¹
Tropidebora simplex Wesselingh, 2006¹
Tropidebora? conica Wesselingh, 2006^{*1}
Lithococcus carinatus Wesselingh, 2006¹
Lithococcus amazonicus Wesselingh, 2006²
Littoridina pebasana (Conrad, 1874)^{*1}
Littoridina crassa (Etheridge, 1879)^{*1}
Littoridina elongata Wesselingh, 2006^{*1}
Littoridina conica Wesselingh, 2006^{*1}
Cochliopina? colombiana (Nuttall, 1990)¹
Cochliopina? bourguyi (Roxo, 1924)^{*1}
Cochliopina? hauxwelli (Nuttall, 1990)^{*1}
Cochliopina? convexa Wesselingh, 2006¹
*Cochliopina? sp.*²
Thiaridae
Hemisinus kochi (Bernardi, 1856)^{*2}
Aylacostoma lataguensis (Nuttall, 1990)¹
Aylacostoma browni (Etheridge, 1879)¹
Pachychilidae
Charadreon eucosmius (Pilsbry & Olsson, 1935)²
Charadreon intermedius Wesselingh, 2006^{*1}
Charadreon glabrum Wesselingh, 2006¹
Sheppardiconcha tuberculifera (Conrad, 1874)²
Sheppardiconcha coronata (Etheridge, 1879)^{*1}
Sheppardiconcha septencincta (Roxo, 1937)²
Sheppardiconcha lataguensis Nuttall, 1990¹
Sheppardiconcha colombiana (Nuttall, 1990)²
Sheppardiconcha solida Wesselingh, 2006¹
Sheppardiconcha? clavata Wesselingh, 2006¹
Melongenidae
Melongena woodwardi (Roxo, 1924)³
Nassariidae
Nassarius? reductus Vermeij & Wesselingh, 2002³
Pyramidellidae
Odostomia nuttalli van Aartsen & Wesselingh, 2000³
Odostomia cotuhensis van Aartsen & Wesselingh, 2000³
Odostomia s.l. sp.³
Iolaea amazonica van Aartsen & Wesselingh, 2005³
Planorbidae
Helisoma sp.1^{*2}
Helisoma sp.2^{*2}

<i>Tropicorbis</i> sp. ^{1,2}	<i>Pisidium</i> sp. ²
<i>Tropicorbis</i> sp. ²	Corbulidae
Acroloxidae	<i>Corbula cotuhensis</i> Wesselingh & Anderson, 2006 ^{*3}
<i>Gundlachia radiata</i> ? Guilding, 1928 ^{*2}	<i>Pachydon obliquus</i> Gabb, 1869 ^{*1}
<i>Gundlachia</i> sp. ²	<i>Pachydon carinatus</i> Conrad, 1871 ^{*1}
Orthalicidae	<i>Pachydon tenuis</i> Gabb, 1869 ^{*1}
<i>Orthalicus</i> sp. ⁴	<i>Pachydon amazonensis</i> (Gabb, 1869) ^{*1}
<i>Orthalicus linteus</i> (Conrad, 1871) ⁴	<i>Pachydon ellipticus</i> Wesselingh, 2006 ^{*1}
Acavidae	<i>Pachydon andersonae</i> Wesselingh, 2006 ¹
<i>Pebasiconcha immanis</i> Wesselingh & Gittenberger, 1999 ⁴	<i>Pachydon cuneatus</i> Conrad, 1871 ^{*1}
<u>Bivalvia</u>	<i>Pachydon trigonalis</i> Nuttall, 1990 ¹
Tellinidae	<i>Pachydon hettneri</i> (Anderson, 1928) ¹
<i>Macoma</i> sp. ³	<i>Pachydon cebada</i> (Anderson, 1928) ¹
Hyriidae	<i>Pachydon maaikae</i> Wesselingh, 2006 ¹
<i>Diplodon longulus</i> (Conrad, 1874) ^{*2}	<i>Pachydon erectus</i> Conrad, 1871 ^{*1}
<i>Diplodon amygdalaeformis</i> Wesselingh, 2006 ^{*2}	<i>Pachydon iquitensis</i> (de Greve, 1938) ^{*1}
<i>Diplodon indianensis</i> Wesselingh, 2006 ^{1/2}	<i>Pachydon ledaeformis</i> (Dall, 1872) ^{*1}
Mycetopodidae	<i>Pachydon telliniformis</i> Wesselingh, 2006 ^{*1}
<i>Anodontites batesi</i> (Woodward, 1871) ^{1/2}	<i>Exalloecorbula dispar</i> (Conrad, 1874) ^{*1}
<i>Anodontites capax</i> (Conrad, 1874) ^{*2}	<i>Ostomya papyria</i> Conrad, 1874 ^{*1}
Dreissenidae	<i>Ostomya carinata</i> Wesselingh, 2006 ^{*1}
<i>Mytilopsis scripta</i> (Conrad, 1874) ^{*2}	<i>Ostomya myiformis</i> Wesselingh, 2006 ^{*1}
<i>Mytilopsis sallei</i> (Recluz, 1849) ^{*2}	<i>Anticorbula mencheri</i> (Palmer, 1945) ²
Corbiculidae	<i>Anticorbula miocaenica</i> Wesselingh, 2006 ^{*2}
<i>Cyanocyclus</i> cf. <i>cojambitoensis</i> Palmer, 1941 ^{*2}	<i>Pachyrotunda rotundata</i> Wesselingh, 2006 ^{*1}
Sphaeriidae	<i>Concentricavalva concentrica</i> Wesselingh, 2006 ^{*1}
<i>Eupera</i> sp. ²	

During this study, a mollusc fauna of only thirteen species from the Solimões Formation of two regions within western Brazilian Amazonia (VI), was also described. After publication it turned out that the Solimões faunas from the Jurua region are of a Middle Miocene age and that of the Acre region of a Late Miocene age (see below). The Middle Miocene Jurua fauna was numerically dominated by the freshwater snail *Sheppardiconcha septencincta* and contained other freshwater indicators such as an unidentified *Eupera* species (Table 3). The Late Miocene Solimões fauna from Acre was entirely dominated by in-situ preserved pearly freshwater mussels. The latter fauna can be considered as a typical modern fluvial - fluviolacustrine fauna. It lacks both indicators of marginal marine settings as well as species considered as Pebasian endemics. Recent age estimates show that the Acre part of the Solimões fauna lived in the Late Miocene, circa 9 Ma ago, when already some sort of transcontinental river system was established (Figuereido *et al.*, 2008). By that time the endemic Pebas mollusc fauna had vanished.

Table 3. Middle versus Late Miocene faunas from the Solimões Formation in Brazil

Middle Miocene taxa	Late Miocene taxa
Ampullariidae	Ampullariidae
Ampullariidae sp. 1	Ampullariidae sp. 1
Ampullariidae sp. 2	Pachychilidae
Cochliopidae	<i>Sheppardiconcha septencincta</i>
<i>Pyrrophorus</i> ? sp.	Hyriidae

<i>Littoridina?</i> sp.	<i>Castalia</i> cf. <i>ambigua</i>
Pachychilidae	<i>Castalia</i> sp. 1
<i>Sheppardiconcha septencincta</i>	<i>Castalia</i> sp. 2
Sphaeriidae	<i>Callonaia</i> sp.
<i>Eupera</i> sp.	<i>Diplodon</i> cf. <i>longulus</i>
	Mycetopodidae
	<i>Mycetopoda</i> ? <i>pittieri</i>
	<i>Anodontites</i> cf. <i>trapesialis</i>

3.2 Temporal framework of Miocene deposits

Despite several efforts, not a single radiometric age estimate could be obtained for the Pebas Formation during this study (II). Failed attempts of obtaining age estimates through strontium analyses did, however, provide fruitful new venues for the study of aquatic geochemical regimes (see Vonhof *et al.*, 1998; 2003; Wesselingh *et al.*, 2002, chapter IV and Kaandorp *et al.*, 2006). Nevertheless, considerable progress was made with the stratigraphic subdivision of the Pebas Formation. Twelve mollusc zones (indicated with MZ) were introduced (II), all of which based on a combination of occurrence data from different taxa and lineages. The upper eleven zones cover a time interval of approximately seven million years that were covered previously by only three pollen zones.

A simplified version of the mollusc biozonation scheme was applied to borehole material from the Mara on Basin (III). This allowed for the erection of an age calculation model for the Pebas Formation and underlying formations. The assumption-laden model provided crude age estimates for the Pebas Formation and the underlying Chambira Formation that are in agreement with the few radiometric dates that have been published from foreland basin deposits since then (see Discussion below). The age calculation model suggested a mostly Oligocene age (circa 35-23 Ma) for the Chambira Formation and an Early to early Late Miocene age (circa 23-9 Ma) for the Pebas Formation. New well data from the Amazon fan (Figuereido *et al.*, 2008) indicate, however, that the transcontinental Amazon drainage did not establish between 8 and 9 Ma ago as previously thought, but at around 11 Ma ago. As a result the calculated formation ages in the model are slightly adjusted (see below: the age of the Pebas Formation is now estimated between 24 and 11 Ma).

Also some insights into the possible duration of the regularly recurring sequences in the Pebas Formation have been gathered (III, IV). Dividing the thickness of apparent sequences, as identified from logs in some borehole intervals, by the general calculated sedimentation rates, two sequence durations were found: 24 Ka and 42 Ka respectively (adjusted for the new model ages they are 23 and 42 Ma). These estimates are very close to known durations of precession (23 Ka) and obliquity (41 Ka) cycles. If confirmed, it would provide a very strong additional possibility to improve age estimates within the Pebas Formation outcrops. For example, in the Peruvian outcrop Santa Rosa de Pichana (IV) there are five larger sequences exposed that if the sequence duration estimate is correct and no sequences are missing, would represent slightly over 200 Ka of history.

3.3 Size, scale and nature of depositional processes and environments in the Pebas wetlands

The mollusc fauna of the Pebas Formation is dominated by endemic taxa (**I**, Table 2). Many of the families represented by a few species in the Pebas fauna include important ecological indicator groups (Figure 2) such as indicators of marine influence (rare), terrestrial settings (very rare) and stagnant or slightly agitated freshwaters (rare). About one fifth of the fauna consists of undisputed freshwater taxa. For most of the endemics the salinity tolerances are not known a priori (but have been established as fresh water otherwise, see below). The Pebas system experienced profuse radiations of molluscs that led to an overwhelmingly endemic fauna, typical of a long-lived lake environment. The stratigraphic continuity of species and lineages, at least for the late Early-early Late Miocene interval (circa 18-11 Ma), indicates that lakes continuously occupied the system and never were entirely replaced by rivers or the sea (**IV**). The rare occurrence of marginal marine taxa indicates that the system was at sea level and experienced occasionally diluted marine incursions.

The Pebas system formed a temporal continuum with the fluvial dominated Oligocene Chambira „system“ before, and the modern Amazon system afterwards (**III**). The Oligocene Chambira system was deposited under more pronounced seasonal conditions than today. Around the Oligocene-Miocene boundary (some 23-25 Ma ago), climate shifted towards the modern wet tropical conditions. Western Amazonia became a mosaic of lakes, swamps and meander belts, but tidal regimes were present as well. During apparently regularly recurring base level high stands, open aquatic settings (lakes at sea level) were widespread, permitting aquatic taxa to exchange widely within the Pebas system. The depositional system was driven by tectonic subsidence in the area, uplift and erosion in the Andean hinterland and the western rim of the Pebas system (the developing Subandean zone), delta lobe switching and river belt avulsions, as well as presumable Mylankhovitch scale of precipitation/erosion cycles and eustatic sea level variation. The onset of the Pebas system is located within the foreland basin zone (Wesselingh *et al.*, 2002), but wetlands extended eastwards into pericratonic and intracratonic basins already during the Early Miocene. By the Middle Miocene, the Pebas system reached its maximum extension (Figure 3). By the early Late Miocene (the authors estimated that at 9 Ma, but it has been shown since then it is about 11 Ma ago: Figueredo *et al.*, 2008, see below), fluvial activity increased, as a result of increased Andean tectonic activity, and the modern Amazon system became established. From outcrops in the Nauta area (Peru), indications of a simultaneous increasing marine influence are found that may have enhanced the termination of the Pebas system (Rebata *et al.*, 2006).

The Pebas Formation is characterised by the common occurrence of well-defined sequences (**IV**). Three such sequences containing a succession of transgressive, highstand and regressive/prograding facies were studied in detail in the section Santa Rosa de Pichana (Loreto, Peru). The sequences possibly represent obliquity or precession cyclicity (c. 23-41 kA). Ichnofossil data in these intervals indicate episodic lower-mesohaline salinities, especially at flooding surfaces. These have not been corroborated by body-fossil or isotopic evidence that instead point to freshwater settings. Molluscs are most common in the transgressive/highstand intervals and are almost entirely absent in regressive/prograding intervals. The fauna is dominated by endemic Pebasian species, such as *Pachydon* and *Dyris* spp. The nature of the sediments as well as the availability of oxygen varied in a predictable way within each of the sequences, and determined the nature of the faunas. Highest diversity

was reached in the late transgressive phase before the development of dysoxia that was widespread during the late highstand and early regressive/prograding phase. Fluvial influence was limited. The salinity discrepancies between ichnofossil and mollusc/isotope data has not been resolved and interpreted to result either from a subtle temporal separation of the ichnofossils and the mollusc fossils or from supralimital evolution of taxa (see Wesselingh, 2007) that produced these ichnofossils into freshwater settings.

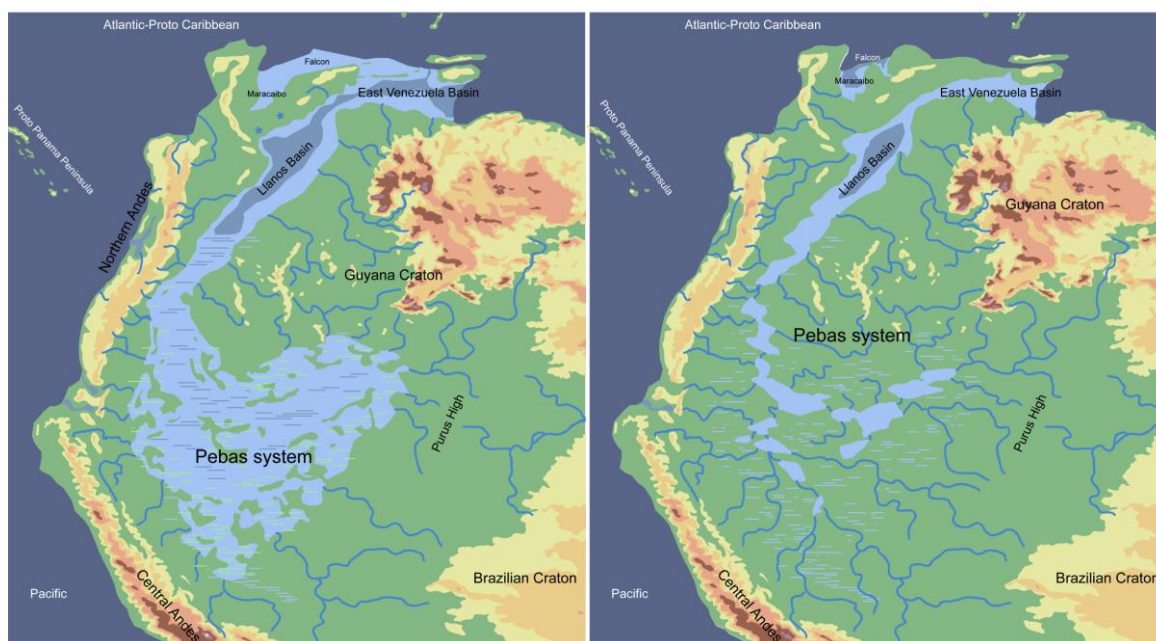


Figure 3. Palaeogeographical model of northwestern South America during the Middle Miocene (some 14 Ma ago). Mountain ranges, shorelines and river courses are conjectural. Left panel represents episodes of base level highstand with maximum marine influence into the Llanos Basin. Right panel represents the system during eustatic lowstands.

3.4 Lake Pebas as stage of molluscan radiations

The Pebas system was the stage for remarkable mollusc and ostracod radiations (VII; Muñoz Torres *et al.*, 1998, 2006). Mollusc radiations started in the Early Miocene and intensified during the Middle Miocene. The intensification was possibly linked to the eastward extension of the Pebas system to include large intracratonic areas in the eastern part of the Solimões Basin (VII). However, diversification was halted, and species levels dropped somewhat during the late Middle - early Late Miocene, in times of increased marine influence in the Pebas system, but nevertheless remained substantial in the final parts of the Pebas system. The endemic Pebas fauna disappeared with the termination of the Pebas system (VI).

Within the Pebas fauna, the pachydontine corbulid bivalves are the most successful in terms of abundance (V). With their relative high syntopic species numbers, relative large number of endemic species and profuse disparity, they are representative for long-lived lake faunas. Although the zenith of pachydontine diversification was in the Pebas system, the origin of three of its genera (*Pachydon*, *Ostomya* and *Anticorbula*) has been tracked back to at least the Paleocene of North America (Anderson *et al.*, 2006). The Pebasian corbulid fauna is

composed of seven genera yielding 24 species (I). One species, *Corbula cotuhensis*, occurs only in rare marine incursion levels, and is not considered to be a typical Pebasian endemic. Two species of *Anticorbula*, that are also rare in the studied samples, also (may have) had a riverine and estuarine distribution beyond the Pebas system. Two *Pachydon* species were already widespread in northwestern South America at the onset of the Pebas system (Wesselingh & Macsotay, 2006). Nevertheless, 19 species (belonging to five genera) are considered as Pebasian endemic corbulids (I). The endemic Pebasian corbulids harbour a spectacular array of morphologies (V). Some morphological characters, such as thick, convex shells in some species, may have deterred incidence of cracking type of predation (by fish and birds). Relative high predation levels are apparent from common reparation scars on the shells, as well as fossils of typical molluscivorous fish, such as sciaenids. However, the shells are often thickened at the anterior margin, away from potential predators. Such selectively thickening may have enhanced an anchoring mode of living in soft substrate. Several species developed flat and thin shells, possibly also in response to the common presence of soft bottoms in the Pebas system. Finally, a variety of morphological modifications were interpreted in terms of adaptation to recurring lowered oxygen levels in the Pebas system (IV). The combination of these factors explains the numerical dominance of the Pebasian corbulids over other freshwater or marginal marine bivalve groups. Of the Pebasian corbulid group, only *Anticorbula* has an extant representative species, which happens to be the single freshwater species in the cosmopolitan Corbulidae, whose members inhabit otherwise marine and brackish biotopes.

3.5 Miocene biogeography of northern South America

The predominant endemic status of Pebasian mollusc taxa indicate a strong ecological isolation of the Pebas wetland system (I). The isolation was not total, as fluvial and marginal marine mollusc taxa also occurred in the system, albeit in low numbers (Figure 2). Furthermore, endemism in mobile organisms, such as fish, was distinctly lower (cf. Monsch, 1998). Amazonian fish groups already occurred over larger parts of northern South America at the time (Aguilera & Aguilera, 2004; Albert *et al.*, 2006; Dahdul, 2004; Lundberg, 1997; Lundberg & Aguilera, 2003).

Nowadays, two South American molluscan provinces occur: the Neotropical and the Austral South American biogeographic province (VII). Several taxa in the Pebas Formation, such as the gastropod genera *Tryonia*, *Dyrus*, *Onobops*, *Sioliella*, *Lithococcus* and *Hemisinus* and the bivalve genus *Anticorbula* show the Neotropical character of the Pebas fauna (I). This also applies to the marginal marine snail *Melongena woodwardi* (Vermeij & Wesselingh, 2002) that is known from the Pebas Formation and from Miocene coastal deposits of Panama. Typical Austral South American genera such as *Heleobia* and *Potamolithus*, that were common in southern South America during the Miocene, are lacking in the Pebas and Solimões Formations. All mollusc evidence therefore indicates the Pebas system was connected to tropical marine and lowland areas (VII). No faunal support is found for direct biogeographic connections with the Parana Basin in the south during the Miocene as suggested, e.g., by Webb (1996).

4. DISCUSSION

4.1 Estimating ages of Amazonian history turning points: stratigraphic advances in the past decade

The timing of the break-through of the modern Amazon became apparent through the documentation and dating of Andean derived sediments in deep-sea cores at the Amazon mouth and Ceara Rise. The event was initially dated at slightly before 8 Ma (Dobson *et al.*, 1997; 2001; Harris & Mix, 2002). However, extensive new surveys in the Amazon fan by the Brazilian oil company Petrobras (Figuereido *et al.*, 2008) has shown that an initial onset of Andean derived mineral assemblages goes as far back as 10.7-11.1 Ma. The details of the lowered age estimate are in the process of publication by these authors (J. Figuerido, pers. comm.). This new age estimate has made some modification of the age model proposed in (III) necessary (Table 4). The age of the establishment of the Amazon has given us a reference date for the termination of the Pebas system, whose age is otherwise very poorly constrained.

Very few, but nevertheless important radiometric ages have been established for Miocene lowland Amazonian deposits in the past decade (Campbell *et al.*, 2001; Hermoza, 2005; Roddaz *et al.*, 2005; Burgos, 2005; Burgos *et al.*, 2006). Many more radiometric ages have become available for geological units in intramontane basins, such as the Cuenca Basin (Ecuador), that can partially be correlated to the lowland Amazonian strata (Steinmann *et al.*, 1999; Hermoza *et al.*, 2005). These newly obtained ages improved insight into the timing of major Andean uplift and the transition towards modern Amazonian fluvial settings that ended the Pebas Formation during the early Late Miocene. Together with new radiometric ages for Paleogene units (Hermoza, 2005), they formed the input of an age calculation model in (III) that indicate the Pebas system to have existed between c. 23 and 9 Ma ago (now recalculated as c. 24 and 11 Ma, Table 4).

Table 4. Recalculated ages for late Paleogene and Neogene horizons in the Marañón Basin, based on the model of (III) with adjusted upper boundary of the Pebas Formation at around 11 Ma following Figuerido *et al.* (2008). Model assumptions are extensively discussed in (III). In bold the estimated age for the upper and lower boundary of the Pebas Formation. Depth in feet, age in Ma.

	Capahuari		Huayuri		Jibaro	
	depth	age	depth	age	depth	age
Base Marañón Formation	2335	11.5	n.a.	n.a.	1170	11.0
Base upper part Pebas Formation	4190	18.0	3310	18.4	3100	18.5
Base lower part Pebas Formation	5710	23.3	4915	24.1	4695	24.7
Base Chambira Formation, subunit 3	6765	27.0	6315	29.1	5960	29.6
Base Chambira Formation, Subunit 2	8850	34.4	7788	34.3	7200	34.4
Base Chambira Formation, Subunit 1	8974	34.8	7880	34.6	7230	34.6
Depth CZ3-CZ4 boundary	3050	14.0	2050	14.0	1950	14.0
Depth middle part Lower Pozo Formation	9402	36.3	8368	36.3	7675	36.3

Another major improvement in Amazonian age estimates comes from the combination of a few newly obtained radiometric age estimates together with improved mammalian and pollen stratigraphic insights into depositional units referred to as Nauta Formation (northern Peru), upper Solimões Formation in Brazil and Madre de Dios Formation (southern Peru: Campbell *et al.*, 2001; Hermoza, 2005; Rebata *et al.*, 2006; Cozzuol, 2006). These deposits are assigned a Huayquerian mammal zone and the *Fenestrites* pollen zone that both indicate a Late Miocene (Tortonian) age. Three radiometric ages of about 9 Ma (Campbell *et al.*, 2001; Hermoza, 2005) confirm these age estimates. This implies that the Miocene vertebrate faunas of Acre and associated tidal deposits lacking endemic invertebrate faunas from these units are younger than the Pebas Formation. This also implies that a precursor of the Amazon was already in place while tides still were present in lowland Amazonia.

4.2 Driving forces of Miocene wetland development in Amazonia

The various roles of tectonics and climate in the development of the Miocene Amazonian wetlands are starting to emerge. The role of regional tectonic processes included both Andean uplift providing sediment sources for lowland Amazonia and foreland/intracratonic basin subsidence providing accommodation space enabling wetland development. Furthermore, the complex uplift history of the northern (Venezuelan) Andes affected the architecture of marine Caribbean portals. Study of the Neogene tectonic history of the central-eastern Andes and the foreland basin zones accelerated in the past decade (e.g., Cooper *et al.*, 1995; Pindell *et al.*, 1998; Steinmann *et al.*, 1999; Villamil, 1999; Rojas, 2002; Rousse *et al.*, 2003; Roddaz *et al.*, 2005; Burgos *et al.*, 2007; Bayona *et al.*, 2007). However, large discrepancies still exist in the interpretation of depositional environments in the Llanos Basins and other northern Andean areas. Also, the location and timing of possible basin thresholds is completely uncertain. At around 10.5 Ma, a surge in tectonic uplift in the emergent Colombian eastern Cordillera apparently shut down any northern Amazonian connection and the shape of the present day Amazon drainage basin came into existence. At the moment no causal relationship with the onset of the transcontinental Amazon system (Figuereido *et al.*, 2008) has been demonstrated, but both may be linked. Further compartmentalisation of drainage areas in western Amazonia is partially of a later age. Espurt *et al.* (2007) showed that uplift of the Fitzcarrald Arch in southern Peru and adjacent Brazil occurred approximately 4 Ma ago, forced Amazonian rivers in the area into radial drainage patterns. River patterns in north eastern Peru also appear to have resulted from broad regional uplift that postdates the Middle Miocene (II).

Climate variation has affected Miocene wetland development in two ways: directly through increased and decreased erosion of Andean hinterland and indirectly through eustatic base level changes that affected the Pebas system (IV). Already through the palynological work of Hoorn (1993, 1994a,b) it became apparent that the Pebas system experienced essentially modern tropical wet climates. Isotope data from mollusc growth bands corroborated and refined these insights, indicating that monsoonal settings alike those of today's, existed in western Amazonia c. 16 Ma ago (Kaandorp *et al.*, 2003, 2005). The transition of deposits formed under strongly seasonal climates towards ever-wet depositional conditions took place around 24 Ma ago in the region (III, see Table 4). During the Middle Miocene, climates towards the north (the Magdalena Basin that at the time was part of the lowland Amazon-Llanos system) were subhumid to humid tropical with a marked seasonality (Guerrero, 1997), very comparable to that in the present-day Llanos region. This indicates that during the

Middle Miocene the present-day tropical rainforest belt and savannah belt to the north were in effect in place. Cyclical base level changes, possibly caused by orbital cycles (III) triggered the formation of the very characteristic fining-up to coarsening up sequences in the Pebas Formation (IV). The lacustrine Pebas system persisted over a major global cooling event at the end of the Mid Miocene climate optimum (Zachos *et al.*, 2008). Increased ice coverage of Antarctica caused sealevel lowering at the time (14 Ma ago). The continuation of wetland settings must therefore have relied on increased rates of subsidence in the Amazonian basins.

4.3 Miocene seaways?

The Miocene Amazonian salinity debate has intensified and diversified in the past decade. On the one hand, faunal and geochemical evidence has consistently concluded that most of western Amazonia during the Miocene was dominated by freshwater settings (Vanhof *et al.*, 1998; 2003; Wesselingh *et al.*, 2002; IV; Kaandorp *et al.*, 2006). On the other hand various studies in the past years based on ichnofossils and tidal depositional features have been consistently arguing for the common presence of mesohaline and higher salinities (Räsänen *et al.*, 1996; Gingras *et al.*, 2002a, 2002b; Hoviskoski *et al.*, 2005; Rebata *et al.*, 2006). Indications exist that many of the deposits that yield the most abundant brackish and marine ichnofossil assemblages are slightly younger than the Pebas Formation as defined in this work (Rebata *et al.*, 2006; Latubresse *et al.*, 1997; IV). However, Murray Gingras and colleagues also uncovered large amounts of brackish trace fossil assemblages and tidal depositional facies within outcrops in the Pebas Formation from where molluscan and geochemical evidence points to exclusive freshwater settings (see e.g. Räsänen *et al.*, 1998; Gingras *et al.*, 2002a; IV). Tidal deposits are not indications of brackish water per se, but the succession of ichnofossil assemblages should be a pervasive argument in favour of common brackish settings in the Miocene Pebas system. Based on the molluscan palaeontological and geochemical lines of evidence presented in this volume and in earlier works (Vanhof *et al.*, 1998; 2003; Wesselingh *et al.*, 2002; IV; Kaandorp *et al.*, 2006), I believe that the depositional system was mostly a freshwater system. The presence of marine ichnofossils in the Pebas Formation (in the strict sense) might be explained by the evolution of ecological tolerances beyond the usual limit for the burrowing organisms (mostly shrimps). This supralimital evolution has also been demonstrated for several of the Pebasian mollusc groups (chapters I and V) and is a common phenomenon in long-lived lake faunas (Wesselingh, 2007). However, subtle temporal separation of mollusc communities and brackish ichnofossil communities within the Pebas Formation cannot be entirely ruled out at the moment.

The Pebas system was located at sealevel and experienced episodic marine influence (IV). The origin of marine influence has been elucidated by taxonomic/biogeographic work on molluscs (van Aartsen & Wesselingh, 2000, 2005; Vermeij & Wesselingh, 2002; I, VII). Additional work by Wesselingh & Macsotay (2006) has also improved insight into the biogeographic connection between the Pebas fauna and the La Cira fauna of the Colombian Magdalena Basin. Nuttall (1990) proposed a biogeographic continuity between both faunas and therefore envisaged a lowland marine connection of Amazonia through the Magdalena valley towards the Caribbean. Refined age estimates of both faunas (II) show that continuous wetland settings existed in the very early stage (Early Miocene) of the Pebas system, but that these were severed by the Middle Miocene. Also, the character of the La Cira fauna is not marine, but predominantly fresh water with some Pebasian species. As a result, the

Magdalena valley did not play a role as a marine portal into lowland Amazonia during the main part of the Pebas system. Finally, indications of potential short-lived lowland connections between western Amazonia and the Pacific through Ecuador (Steinmann *et al.*, 1999) are still to be investigated using faunal distributions.

In summary, there is no evidence for transcontinental seaways in South America during the Miocene. There is plenty of evidence for marine influence of varying intensity in lowland Amazonia. Connections between lowland Amazonia and marine settings during the Early-Middle Miocene almost certainly were through the Llanos Basin towards the Caribbean although additional short-lived Pacific connections cannot be ruled out.

4.4 The role of the Pebas system in shaping and understanding modern Amazonian biodiversity

Molluscan diversifications in the Pebas system played almost no role in shaping the modern Amazonian mollusc faunas with the exception of a few possible relic taxa living in Brazilian Amazonia such as *Sioliella effusa* and *Dyris amazonicus* (Wesselingh, 2000). However, the Pebas system and its deposits did play a role in shaping modern Amazonian faunas and floras in other ways (VII). The Pebas wetland system formed a barrier for the exchange of terrestrial biota between the emergent tropical Andean zone and the Guyana craton areas for approximately 13 Ma. At the same time it provided an interface for the evolution and establishment of marine biota into the Amazon freshwater biotopes. Where mobile aquatic organisms, such as stingrays and needlefish, successfully entered into freshwater Amazonian habitats through the Pebasian interface (Lovejoy *et al.*, 1998), marginal marine mollusc failed to do so (Vermeij & Wesselingh, 2002). The latter was explained in terms of ecological stresses (salinity, predation, seasonal water level variation) in the Pebas system as well as in modern Amazonian fresh water systems. The role of oxygen stress in preventing successful establishment of marginal marine mollusc clades in Amazonian freshwater biotopes (V) should also be added.

Despite large molluscan diversifications, only the gastropod genus *Onobops* that nowadays lives in brackish habitats in the Caribbean and American Atlantic coast may have originated in the Pebas system. The termination of the Pebas system about 11 Ma ago (and of widespread wetlands in western Amazonia some 7 Ma ago) made an area of more than one million square kilometres available for colonization of terrestrial biota. These ages coincide with major diversification events of Amazonian taxa as reconstructed from DNA phylogenies, although a causal relationship is speculative at the moment.

The aerial distribution of mollusc zones in the study area (north eastern Peru, south eastern Colombia and adjacent Brazil) revealed a regional structuring of geological strata around the broad Iquitos-Araracuara antecline (II). The structure of the subsurface appears to have been a major factor in the determination of present-day second and lower order river courses in the study area, and provided insights into a hidden edaphic mosaic in western Amazonia. In the past decade, the role of edaphic heterogeneity in sustaining high biodiversity has become established (Tuomisto *et al.*, 1995; Ruokolainen *et al.*, 2007 and references therein). Mapping the biostratigraphic zones of the Pebas Formation in north-eastern Loreto has shown that the so-called Iquitos Arch that has featured prominently in a variety of geological and

biogeographical works appears to be non-existent. It also shed doubts as to the application of geological arches in general in explaining present-day Amazonian biodiversity (e.g., Patton *et al.*, 2000). The notion of shifting uplift axes through time as proposed by Pindell *et al.* (1998) for e.g. the Venezuelan El Baul Arch, also might be applied to lowland Amazonian thresholds termed arches.

4.5 Comparison with other long-lived lakes

Based on the endemic signature and disparity of the mollusc (and ostracod) fauna as well as the stratigraphic continuity of these lineages, the Pebas lake system is considered a long-lived lake system (**I, V, VII**). Long-lived lakes occur throughout the world and throughout geological history (Figure 4). Their ecological isolation from ordinary freshwater or coastal biotopes enables the derivation of endemic species from non-endemic founder species. On top of these derivations long-lived lakes often sustain spectacular intralacustrine radiations (Martens, 1997).



Figure 4. Examples of fossil and extant long-lived lakes. D = Dinariid lake system; Oh = Lake Ohrid; K = Lake Kosovo. Data in Wesselingh (2007) and Harzhauser & Mandic (2008).

The huge size of Lake Pebas (>1.1 million km^2 at its maximum: Wesselingh *et al.*, 2002) is almost unrivalled. Only the Permian Parana Lake system of South America with an estimated size of about 1.5 million km^2 (references in Wesselingh, 2007) has been larger. The Caspian Sea with its surface of 374.000 km^2 is the largest existing long-lived lake.

The Pebas Lake system spans a time interval of approximately 13 Ma (**III**). Currently, the oldest long-lived lake is Lake Baikal. The Baikal Basin came into existence about 60 Ma ago and permanent lake conditions established 28 Ma ago (Sherbakov, 1999). Lake Tanganyika, with an age of 9-12 Ma is the second oldest modern long-lived lake. The duration cannot be

estimated for all fossil long-lived lakes, but typically it is in the order of hundreds of thousands to several millions of years (e.g., Wesselingh, 2007). The 13 Ma duration of the Pebas lake system makes it among the longest-lived of long-lived lakes.

Although we have no direct evidence for maximum depths in the Pebas Lake system, it appears to have been a shallow system. Maximum depths probably were in the order of at most some tens of metres. The common presence of charophytic algae in lacustrine ramp facies where the highly diverse small *Dyris* associations occurred (Wesselingh *et al.*, 2002) indicates that clear waters were common in the Pebas system and that much of the fauna lived in the photic zone. Charophytic meadows are known to sustain the most diverse endemic mollusc associations within long-lived lake Ohrid (Albania/Macedonia).

The Pebas lakes system was episodically connected to marine settings. This is not uncommon in fossil long-lived lakes. Episodic marine connections are known from Permian Lake Parana and several of the Neogene and Quaternary Paratethyan Lakes of eastern Europe (Sarmatian Lakes; Caspian Sea and its precursor Lake Akchagyl, etc.). Long-lived lakes with episodic marine connections have in common that their endemic bivalve fauna includes groups with clear marine ancestry (cardiid and mactroid bivalves in Paratethyan lakes, corbulid bivalves in Lake Pebas and megadesmiid and veneroid bivalves in Lake Parana). In long-lived lakes lacking marine connections only typical freshwater bivalve clades occur such as pearly freshwater mussels in the modern East African lakes and sphaeriids in Lake Baikal (Wesselingh, 2007).

In long-lived lakes, no correlation exists between species richness and lake area (Harzhauser & Mandic, 2008), nor is there a correlation between species richness and lake longevity. In general, endemism in long-lived lakes is high (e.g., Figure 5), as is the number of co-occurring (syntopic) species.

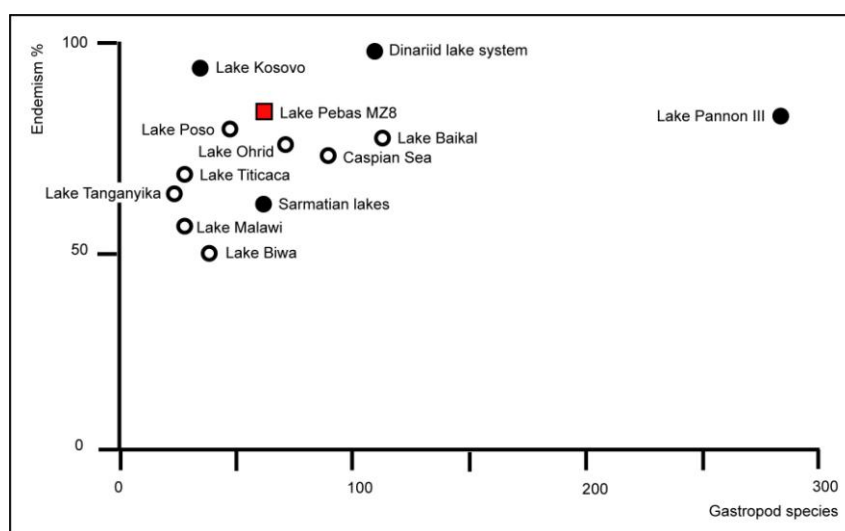


Figure 5. Gastropod species numbers and percentage endemics in selected fossil (black dots) and modern (circles) long-lived lakes, modified from Harzhauser & Mandic (2008). Caspian sea data from Kantor & Sysoev (2006) with addition of two endemic *Gyraulus* species (Zhadin, 1965). Gastropod numbers for mollusc zone (MZ) 8 (the interval with highest species numbers) of Lake Pebas based on data from (I).

The high diversity in long-lived lakes is attributed to three processes: (1) the persistence of relic species, (2) speciation from non-endemic sister taxa living in adjacent biotopes and (3) intralacustrine speciation. Compared to modern long-lived lakes, endemism in lake Pebas is high (Figure 4). The number of gastropod species is among those of the better-known and larger extant long-lived lakes. The high species numbers in Lake Pebas can be mostly attributed to intralacustrine diversification.

4.6 A model of biotic development and landscape evolution in the Neogene of Amazonia

In Figure 6, a model for landscape evolution and biotic development of aquatic mollusc faunas in western Amazonia is presented. The model is adapted from (III). It summarizes insights from the present PhD thesis (the interval between 10 and 30 Ma ago: II, III, VI).

During the Late Eocene (Figure 6A: c. 45-34 Ma) the area to the west of the Iquitos region was occupied by a shallow marine embayment, the Pozo embayment. Fossil faunas from this interval are scarce, poorly allocated, and appear to contain marine molluscs, such as a mitriform gastropod (*Mitricaulus incarum* Pilsbry, 1944). Coeval deposits containing planktonic foraminifera indicative of open marine settings have been reported from adjacent Oriente Basin in Ecuador (Tschopp, 1953; Burgos, 2005; Burgos *et al.*, 2006).

During the Oligocene (Figure 6B: c. 34-24 Ma) the region was occupied by a trunk river system that flowed northwards towards the Caribbean (the Chambira system: Hermoza, 2005; III). From the low-lying Andes in the west, river belts in otherwise seasonally flooded back swamps emptied into this river. From the east side, rivers joined draining lowlands and craton areas to the east. The trunk river system was located at low elevations and may have experienced at times some tidal influence. The climate was more seasonal, including more pronounced dry seasons (III). Mollusc faunas from this interval are scarce, but include poorly identified cerithoid gastropods, corbiculid clams and pearly fresh water mussels.

In the Early Miocene (Figure 6C: c. 24-18 Ma) the region became mostly submerged and transformed into a continually shifting mosaic of lakes, wetlands and river belts, the Pebas system (III). In the early phase of this system (C), faunas were dominated by fluviolacustrine taxa, and few endemic corbulid and cochliopid species occurred. Possibly the area experienced episodic widespread fluvial or marginal marine settings that restrained faunal diversifications.

During the Middle Miocene (Figure 6D: c. 18-11 Ma), the endemic fauna Pebas fauna diversified to reach maximum diversity levels at around 13 Ma ago (VII). Mollusc diversity dropped somewhat during an episode with increased marine influence in the Pebas wetland system but remained high. The region experienced a wet tropical monsoon climate (Kaandorp *et al.*, 2005), and rainforests were present within and alongside the Pebasian wetlands (Hoorn, 1993; Antoine *et al.*, 2006; Pons & de Franceschi, 2007).

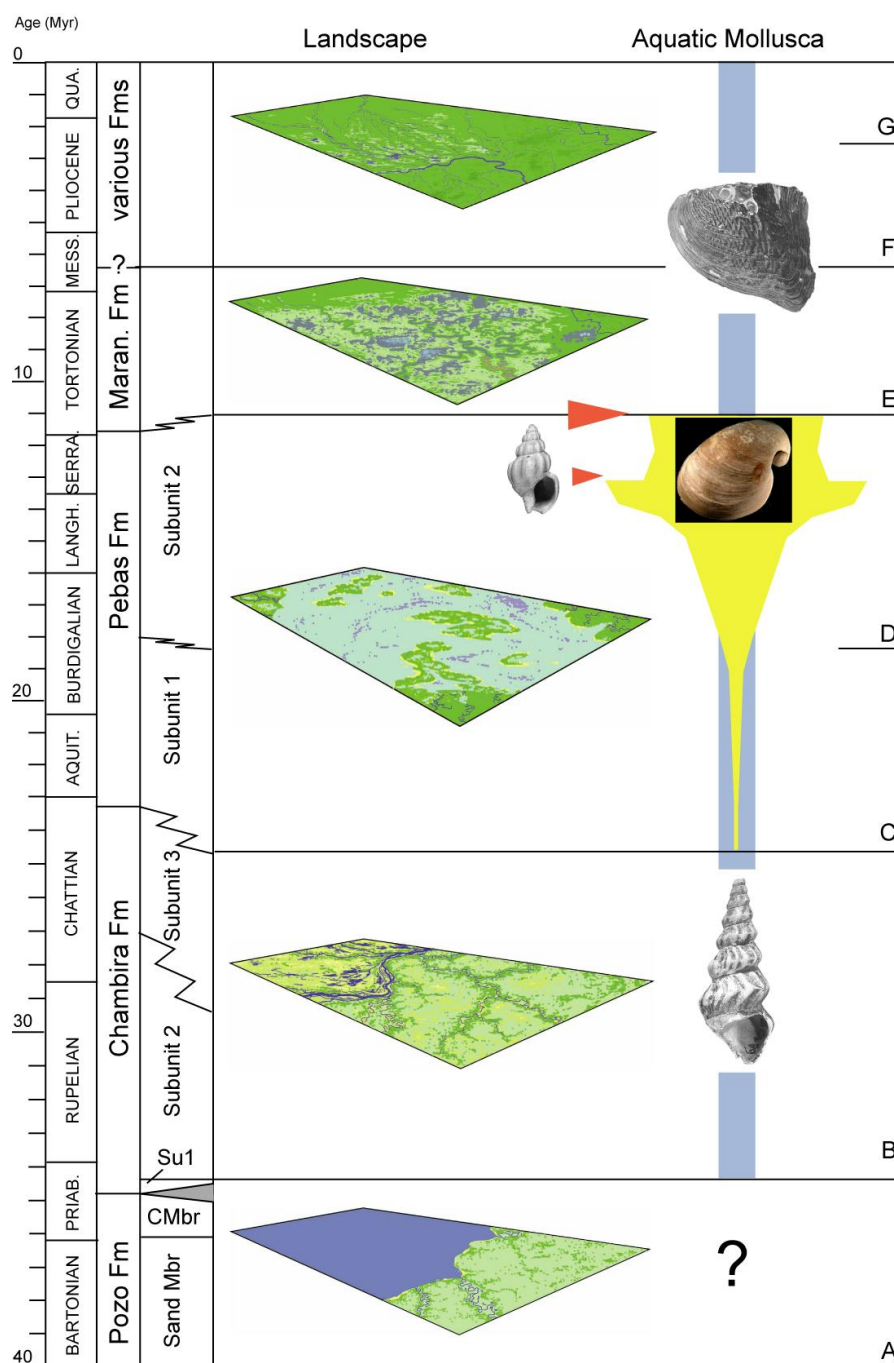


Figure 6. A model of landscape evolution and biotic development in western Amazonia. Stratigraphic model from (III) with termination of the Pebas system/onset of the proto Amazon system at 11 Ma from *Figuereido et al.*, 2008. Block diagrams cover an area in the northern Peruvian Amazon approximately between the Corrientes River in the west and Pebas in the east. River courses, shorelines and landscapes are conjectural. The grey triangle indicates a regional hiatus, many more of which must exist in the time interval after deposition of the Pebas Formation. The red triangles indicate increased marine influence, although some influence may have been possible throughout the history of this area, with the exception of the last 7 Ma. The blue line represents rather low-diverse fluvial faunas, the yellow spindle represents schematically endemic pebasian diversification.

Chronostratigraphic intervals from old to young: B = Bartonian, P = Priabonian, R = Rupelian, C = Chattian, A = Aquitanian, B = Burdigalian, L = Langhian, S = Serravallian, T = Tortonian, M = Messinian, P = Pliocene, Q = Quaternary. Lithostratigraphy: CM = Clay Member; Su1 = Subunit 1, Marañon Fm = Marañon Formation. At (B) *Sheppardiconcha colombiana* (from I, fig. 255). This fresh water cerithioidean is from younger intervals, but resembles poorly identified fresh water cerithioideans reported in literature as well as seen in borehole samples (pers. obs.). The bivalve at (D) is *Pachydon obliquus*, the most common endemic Pebasian species. Specimen data in I. The gastropod representing elevated salinities is *Nassarius reductus* (data in I). The pearly fresh water mussel at (E/F) is *Diplodon* sp. from the Nanay River near Iquitos (data in Kaandorp *et al.*, 2006).

A drastic reorganization of the landscapes occurred in the early Late Miocene, around 11 Ma ago (Figure 6E: Figuerido *et al.*, 2008). In short time, fluvio-tidal dominated wetlands fed by the uplifting Andean hinterland to the west replaced part of the former Pebasian wetlands, and the modern easterly course of the Amazon became established. At this turnaround, a short period with widespread marine settings may have been present in the area, as judged from the presence of echinoid trace fossils in deposits in the Nauta region (Rebata *et al.*, 2006). Such a marine incursion would have enhanced the decline of the endemic Pebas fauna by the change towards strongly tidally influenced fluviolacustrine settings. Unfortunately, no mollusc faunas have been preserved in these possible marine settings. Tidal depositional settings with possible slightly elevated salinities may have been present in western Amazonia up to about 7 Ma ago. The few mollusc faunas from this Late Miocene interval are very comparable to present-day Amazonian river and floodplain lake faunas (VI).

The latest Miocene and Pliocene Amazon system is not treated in this study. The period (Figure 6F: c. 7-2.5 Ma) is poorly understood due to the scarcity of well-exposed sediments and fossils. The landscape probably was dominated by river systems, possibly in mobile channel belts and megafan systems that made large lateral shifts. Some entrenchment of rivers into valleys only occurred at neotectonic uplift zones. Climate regimes remained probably wet, and rainforest occupied most of the area. Increased glacioeustasy as well as broad uplift of the area almost certainly forced rivers into increasingly entrenched valleys in the last 2.5 Ma (Quaternary, Figure 6G), with the exception of the foreland basin zone, where aggrading megafans could persist. During these Quaternary times, edaphic heterogeneity increased through uplift and denudation, and the landscapes, as we know them today developed.

4.7 Research perspectives

The reconstruction of the Neogene history of lowland Amazonia and its biota currently is a very dynamic field of research. New data and knowledge is added in high tempo. Molluscan palaeontological investigations, as presented in this thesis, should add into understanding the subject. Various issues of Amazonian history remain poorly understood and have great scientific potential.

In the western part of Amazonia, the fossiliferous Miocene deposits will continue to bring new data, insights and debates as to the history of lowland Amazonia. Paramount to improved insights will be better absolute age determinations, as well as better definition of, and

improved insight into the internal architecture and type and scales of depositional processes of the geological units.

The geological history of the area during the latest Miocene, Pliocene and Quaternary is, counter intuitively, even poorer understood than that of the Miocene. From the Late Neogene – Quaternary period few deposits are available for study and these are typically fluvial and lack almost entirely fossils. Not even a start has been made with a concerted, multidisciplinary attempt to deal with major questions in the Late Neogene-Quaternary landscape development of lowland Amazonia. How would lowland Amazonia have looked like before the massive glacioeustatic sea levels drops facilitated entrenchment of the river into valleys? How stable were climate regimes? On what scales did drainage reorganizations occur in lowland Amazonia? How and when did edaphic heterogeneity develop? Improved definition of geological units, the (subsurface) mapping of their distribution and understanding of the internal facies architecture, as well as improved age estimates are badly needed in order to unravel the landscape evolution in the last 11 million years and assess the possibilities for the development of the modern Amazonian biota. From radar images of the highest interfluvial parts in Brazilian Amazonia (for example between the Iça and Rio Negro) we can see very large extinct river courses, hinting at a very dynamic fluvial past that awaits further documentation and age corroboration.

The Pebas Formation itself has plenty of scope for more precise documentation of evolutionary patterns within ostracods, bivalves and gastropods. Possibly palaeomagnetic analyses might constrain ages for (parts of the) Pebas Formation and associated deposits. Crude ecological and stratigraphic frameworks exist and much of the fossil mollusc species (and possibly also the majority of ostracod species) have been named and described, enabling more precise documentation of and insight into the biotic evolution in the Pebas system. Not only ancestor-descendant relationships can be reconstructed, but also the occupation and vacation of biotopes by successive members of lineages and the structure of mollusc communities over successive stratigraphic intervals. For example, a number of shifts from lacustrine to marginal lacustrine biotopes are apparent in successive *Dyris* species within supposed lineages during the younger intervals of the Pebas Formation. Documentation of such patterns will help us to gain insight into the driving mechanisms of such biotope-shifts, and hence to evolution in more general. Study of the Early Miocene parts of the Pebas system (mollusc zone MZ1-MZ4 intervals), for which outcrops exist in the Colombian Putumayo Basin and the Ecuadorean Oriente Basin, should shed light as to the origin of many of the genera in the Pebas system. Such documentation will have to await an improvement of the security situation, especially in the Colombian Putumayo Basin. Macrofloral fossils, common but almost unstudied in the Pebas Formation (with the exception of Pons & de Franceschi, 2007), should give insights into the timing and development of the modern Amazonian flora, additional to insights from pollen studies. Increased study of the vertebrate faunas, remains of which are not uncommon in e.g. lignites of the Pebas Formation, also should add insight into the biotic and landscape history of the Amazon area. Finally, the Pebasian salinity debate deserves further interdisciplinary attention.

The outline of the palaeogeographic history of adjacent areas, and especially the Llanos Basin in the north (Colombia-Venezuela) are emerging (Bayona *et al.*, 2007). From some poorly documented samples in several old museum collections, possibly originating from the Leon Formation of the Colombian Llanos foothills, a close faunal affinity with the Miocene Pebas

mollusc fauna of western Amazonia is shown. During deposition of the Middle Miocene Leon Formation, the Llanos Basin experienced widespread freshwater settings but widespread marine incursions occurred repeatedly (Cooper *et al.*, 1995; Rojas, 2002; Bayona *et al.*, 2007). The organisation of the Pebas and the Llanos system during the Miocene resembles that of the Caspian and the Black Sea during the Quaternary. For most of the Quaternary the saline Caspian Sea has been a centre of radiation that occasionally spilled over into the Black Sea Basin. The so-called Ponto-Caspian mollusc taxa could persist in the Black Sea when the latter was a brackish lake or as remnant populations in brackish estuaries. Episodically the Black Sea became entirely fresh and the Ponto-Caspian taxa mostly vanished. Opposite accounts of marine incursions through the Black Sea into the Caspian Sea region also exist, but the latter was never occupied by fully marine settings and faunas. The possible analogue with the Pebas system (alike the Caspian Sea a centre of origin) and the Llanos Basin (as the Black Sea) is striking. For the Llanos Basin very few outcrops are available, and no coordinated study as to the macro palaeontology from borehole data has been undertaken to date. The architecture and tectonic history of thresholds between the marine realm and the Llanos Basin, as well as between the Llanos Basin and western Amazonia deserve further attention. Other areas that almost certainly were connected to lowland Amazonia during the Miocene, such as some of the Ecuadorian Andean Basins may have provided short-lived corridors for the exchange of Pebasian and Pacific fauna also await further study. The lower western margin of the Guyana shield may hide Miocene lowland aquatic corridors that shaped the aquatic history of the region, as for example shown by Hoorn (2006).

Although considerable progress is being made in the insight of the origin of Amazonian biodiversity, many and large uncertainties on the history of this vast and wonderful region remain to be addressed.

5. CONCLUSIONS

The main conclusions of this thesis are:

- During the Early and Middle Miocene (c. 11-24 Ma) a long-lived lake system, the Pebas system, occupied much of western Amazonia. At its maximum the system measured over one million km².
- Lake Pebas was located at sea level and was open to marine settings through a northern portal running through the Llanos Basin and East Venezuela Basin towards the Caribbean. Additional episodic connections with the Pacific realm through the western Andean portal during the Middle Miocene cannot be ruled out.
- Depositional environments in the Pebas system were controlled by (a) subsidence, (b) sediment input mostly deriving from the emergent Andes and (c) baselevel change that probably (partially) was driven by eustatic sealevels.
- The composition of the Pebasian mollusc fauna that is dominated by endemic species as well as occasional in-situ obligate fresh water taxa implies that the Pebas system was mostly a fresh water system. Such an interpretation is matched by strontium isotope ratios as well as very negative $\delta^{18}\text{O}$ ratios found in the shells, but is at odds with oligohaline and mesohaline ichnofacies found in the same strata.
- The stratigraphically uninterrupted occurrence of several endemic mollusc lineages from the late Early to early Late Miocene shows that the lakes in the Pebas system could not have been entirely replaced by (marginal) marine or fluvial settings between c. 17 and 11 Ma.
- Spectacular diversifications of molluscs and ostracods occurred in the Pebas system. Increased diversity concerns Pebasian endemic species, implying in-situ cladogenesis to be the principal process behind Pebasian diversification.
- Maximum diversity was reached at the base of the late Middle to early Late Miocene *Grimsdalea* pollen zone, possibly some 13 Ma. At the time some 85 species co-occurred, 67 of which are considered as Pebasian endemics.
- A diversity drop occurred in the Late Middle Miocene coinciding with evidence of increased marine influence. A causal relationship between the two is still to be confirmed.
- The dominance of pachydontine bivalves in the Pebas system is attributed to their successful simultaneous adaptation to fresh water, dysoxia, soupy substrates as well as high predation pressure.
- The Pebasian mollusc fauna probably went extinct with the termination of the Pebas system 11 Ma ago. Apart from two possible relic species, Pebasian molluscs have not contributed to the modern Amazonian fauna.
- The limited fossil mollusc record from the Late Miocene part of the Solimões Formation in western Amazonia closely resembles present-day pearly fresh water dominated faunas that live in rivers and floodplains of Amazonia. No Pebasian endemics have been found in the Late Miocene parts of the Solimões Formation.
- The mapping of newly established mollusc biozones has revealed the architecture of the geological units below the forest floor in northern Peruvian Loreto and adjacent areas. Post Pebasian uplift has resulted in a broad dome termed here the Iquitos-Araracuara antecline. It appears that river courses in the study area are determined by the architecture of the outcropping geological strata.

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- The wide variety of successive depositional environments as well as the smectite component in the clay minerals deposited in the Pebas lake system has resulted in a widely variable but generally nutrient rich geological unit. The presence of heterogeneous Pebas Formation sediments near the surface in large areas in western Amazonia facilitated increased edaphic heterogeneity that sustain high diverse plant communities.

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