Miocene long-lived lake Pebas as a stage of mollusc radiations, with implications for landscape evolution in western Amazonia

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The Miocene Pebas system was a huge (> 1 million km^2) system of long-lived lakes and wetlands that occupied most of western Amazonia between *c.* 23 and 8 Ma. Remarkable endemic radiations of molluscs and ostracods occurred in the Pebas system. The continuity of many of the endemic lineages between *c.* 17 and 9 Ma shows that the system was never fully replaced by fluvial or marine settings. Many of the endemic invertebrate groups developed an unusual range of morphologies that reflect adaptation to specific ecological stresses provided by the Pebas system, such as chemical stress, common dysoxia and high predation pressure. Mollusc diversity increased especially during the Middle Miocene. The Pebas system provided pathways for mobile marine organisms to transfer into freshwater biotopes, and at the same time obstructed exchange of terrestrial biota between the tropical Andes and the Guyana region. Short-lived, lowland aquatic corridors over northern shield regions and through the Ecuadorian Andean region almost certainly existed. The Pebas system was terminated just before the establishment of the modern Amazon system (slightly before 8 Ma), possibly coinciding with a single, wide ranging marine incursion into lowland Amazonia. With the termination of the Pebas system, the endemic mollusc fauna became largely extinct. The termination of the Pebas system provided large tracts of land for the establishment and development of terrestrial biota in western Amazonia. Subsequent diversification in lowland Amazonia has been enhanced by the edaphic heterogeneity of the Pebas Formation deposits.

Contents

Introduction

The origin of high diversity in the rainforests of lowland Amazonia has intrigued many researchers over the past 150 years. Due to the poor accessibility of this vast region, as well as the apparent lack of exposures, its geological history is poorly understood. This 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 low-

land Amazonia was repeatedly covered by savannah with forest patches (Haffer, 1969), deserts (Ab'Saber, 1982), lakes (Campbell & Frailey, 1984), seas (Nores, 1999) or just by the Amazon river system in a mostly lowland tropical rainforest setting (Irion *et al.*, 2005). The pre-Quaternary history was even more poorly understood, until recently.

A new era of geological investigations into the Neogene history of lowland western Amazonia emerged in the beginning of the 1990s. Three workers independently investigated very different aspects, and produced many new insights into the Neogene Amazonian history. Patrick Nuttall (the Natural History Museum, London, England) concluded his decade long work on western Amazonian fossil molluscs with a lengthy review (Nuttall, 1990). He concluded that fossiliferous deposits widespread in lowland western Amazonia, known as the Pebas Formation, were of a mostly Middle Miocene age, and represented a system of lakes, swamp 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 P.h.D. research, published a number of papers on the subject (Hoorn, 1993, 1994a, b; Hoorn *et al.*, 1995). She corroborated and refined the age estimates of Nuttall (1990), and reconstructed the Pebas system as marine influenced floodplain to fluviolacustrine system. Hoorn *et al.* (1995) outlined a model for the depositional history of the Amazonian region that, with some modifications (Lundberg *et al.*, 1998), still holds today. Finally, Matti Räsänen (University of Turku, Finland) and co-workers started to publish on the depositional context of Neogene sedimentary rocks of Peruvian and Brazilian Amazonia, with special emphasis on the occurrence of tidal deposits (Räsänen *et al.*, 1996). Many insights into the general depositional environments of Neogene Amazonia were gathered, but his emphasis on widespread marine influence sparked a lengthy discussion about the landscape development of western Amazonia during the Neogene (see Webb, 1996; Hoorn, 1996; Paxton & Crampton, 1996; Marshall & Lundberg, 1996). This discussion that has not yet been concluded (see Westaway, 2006 and references therein). Thus, at the beginning of the present research project, the results of which are presented in this issue, the approximate age of Neogene deposits in western Amazonia was known (through a palynostratigraphic framework) 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 system, and the type and amount of marine influence, and marine connections. Large uncertainties existed over the climate regimes, landscape structuring and development, and the role of these Miocene environments in the development of the present-day Amazonian biota. Even the age of the establishment of the modern Amazon was poorly constrained by the mid 1990s.

Oddly enough, an excellent geological and, particularly, fossil record has always been available in many areas in western Amazonia. The Miocene deposits, mainly of the Pebas Formation that commonly crop out in Peruvian and Colombian Amazonia, form an exceptionally well-preserved, rich archive that should facilitate the reconstruction of the Neogene history of western Amazonia.

Molluscs are very useful in such reconstructions for a variety of reasons. They occupy almost any biotope, from high mountains to deep seas, and contain many excellent ecological indicator groups. Furthermore, shells have good fossilization potential; they are common in the fossil record. Molluscs are important tools in palaeoecological and tapho-

nomic research, providing insights into past biotopes and depositional environments.

This volume presents seven further papers that exploit the archive provided by the Pebas fauna in order to explore various aspects of Miocene landscape development and biotic evolution, all with a clear molluscan palaeontological component. Together, these papers form the P.h.D. thesis of the author. Below, the results of the different papers are summarized and assessed in the light of scientific advances on the Neogene history of lowland Amazonia and its biota in the past decade. Finally, some of the outstanding scientific challenges concerning the evolution of Amazonian landscapes and biota are explored.

This issue

In the first paper by Wesselingh (2006a), the building blocks of the successive studies, the mollusc species of the Pebas Formation and associated deposits, are described. The Pebas fauna contains at least 158 mollusc species. Up to *c.* 90 species co-occurred in the time intervals with maximum mollusc diversity. The fauna is dominated by two families, *viz.* the Cochliopidae (86 species; 54%) and Corbulidae (23 species; 15%). These two groups are almost entirely composed of Pebasian endemics and harbour a profuse range of morphological oddities. The Pebas fauna can be characterised as aquatic, endemic and extinct. Many of the families represented by a few species in the Pebas fauna include important ecological indicator groups 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 freshwater 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. Several genera, nowadays living outside Amazonia, may have originated within the Pebas system. The stratigraphic continuity of species and lineages, at least for the late Early-early Late Miocene interval (*c.* 17-9 Ma), indicates that lakes continuously occupied the system and never were entirely replaced by rivers or the sea. The rare occurrence of marginal marine taxa indicates that the system was at sealevel and experienced occasionally diluted marine incursions.

In the second paper, Wesselingh and co-workers (Wesselingh *et al.*, 2006b) present a mollusc biostratigraphic framework for Miocene fossiliferous deposits of western Amazonia that considerably refines existing biozonation schemes. Twelve mollusc zones (indicated with MZ) are introduced, the upper eleven of which cover a time interval of approximately nine million years. Despite several efforts, not a single radiometric age estimate could be obtained for the Pebas Formation. 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, 2006c; Kaandorp *et al.*, 2006). The aerial distribution of mollusc zones in the study area (northeastern Peru, southeastern Colombia and adjacent Brazil) reveals a regional structuring of geological strata around the broad Iquitos-Araracuara anteclise. 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 provides insights into a hidden edaphic mosaic in western Amazonia.

In the third paper (Wesselingh *et al.*, 2006a), Wesselingh and co-workers investigate borehole data and samples from the Marañon basin in Peru. The regional depositional architecture of the Pebas Formation and its relationship with overlying and underlying units are investigated, as well as the type and dimensions of depositional processes and their driving mechanisms. The fossil molluscs are used in this study in order to correlate between wells and for assessing depositional environments. The Pebas system forms a continuum with the fluvially dominated Oligocene Chambira 'system' before and the modern Amazon system afterwards. The Oligocene Chambira system was deposited under more pronounced seasonal and likely more arid conditions than today. Around *c.* 23 Ma (Early Miocene), climate shifted towards the modern wet tropical conditions. The area 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 sealevel) 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 Milankovitch scale of precipitation/erosion cycles and eustatic sealevel variation. By the early Late Miocene (*c.* 9 Ma), fluvial activity increased as a result of increased Andean tectonic activity and the modern Amazon system became established. From exposures 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).

In the fourth contribution of this issue (Wesselingh *et al.*, 2006c), landscape and ecosystem structuring and diversity are investigated on (geological) small time scales. Sedimentary facies, molluscan composition and taphonomy, and stable isotope geochemistry were studied in a single exposure, Santa Rosa de Pichana (Loreto, Peru). Three complete sequences were studied, containing a succession of transgressive, highstand and regressive/prograding facies. The sequences possibly represent obliquity or precession cyclicity (*c.* 23-42 kA; Wesselingh *et al.,* 2006a). 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. The salinity discrepancies between ichnofossil and mollusc/isotope data are not resolved, and are interpreted to result either from a subtle temporal separation of the ichnofossils and the mollusc fossils or from supralimital evolution of taxa that produced the ichnofossils in freshwater settings. The stable isotope signatures are used as an additional tool in the evaluation of reworking of shell faunas.

The Pebas system staged spectacular ostracod and mollusc diversifications. The evolutionary ecological context of these radiations is explored by Wesselingh (2006b) in the fifth paper for the numerically dominant corbulid bivalves. The Pebasian corbulid

fauna is composed of seven genera yielding 24 species. 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 prior to the establishment of the Pebas system. Nevertheless, 19 species (belonging to five genera) are considered as Pebasian endemic corbulids. These species were hugely successful in the Pebas system; they make up more than half of the Pebas fauna in terms of abundance. The endemic Pebasian corbulids harbour a spectacular array of morphologies. Some morphological characters, such as thick, convex shells in some species, may have deterred significant 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 molluscivoran fish, such as sciaenids. However, the shells are often thickened at the anterior margin, away from potential predators. Such selective 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 are interpreted in terms of adaptation to recurring lowered oxygen levels in the Pebas system. 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.

In the sixth paper (Wesselingh *et al.,* 2006d), the fossil molluscs of the Late Miocene Solimões Formation of western Brazilian Amazonia are reviewed, in order to understand the termination of the Pebas system and the onset of modern Amazonian fluvial environments. The Solimões Formation deposits are renowned for their rich vertebrate faunas. They are of Late Miocene age and slightly post-date the Pebas Formation. From these deposits Räsänen *et al.* (1996) first described tidal deposits that sparked the debate on marine influence in the Neogene of western Amazonia (Räsänen *et al.*, 1996; Webb, 1996; Marshall & Lundberg, 1996; Hoorn, 1996; Paxton & Crampton, 1996; Gingras *et al.*, 2002a, b; Hoviskoski *et al.*, 2005; Rebata *et al.,* 2006; Westaway, 2006, to name but a few of the contributors). A mollusc fauna of only 13 species is described from the Solimões Formation, seven of which are pearly freshwater mussels. The 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 Solimões fauna lived at the time of the onset of the modern Amazon *c.* 8 Ma ago. By that time the endemic Pebas mollusc fauna must have vanished.

In the final paper (Wesselingh & Salo, 2006), faunal development within the Miocene Pebas system, faunal affinity with other areas and the role of the Pebas system in shaping modern Amazonian diversity are explored. The Pebas system formed a huge barrier for the exchange of terrestrial biota between the emergent tropical Andean zone and the Guyana craton areas for prolonged periods, and at the same time provided an interface for the evolution and establishment of marine biota into the Amazonian freshwater biotopes. The Pebas system was the stage for remarkable mollusc and ostracod

radiations. Mollusc radiations intensified during the Middle Miocene, possibly linked to the expansion of the Pebas system into intracratonic areas in the eastern part of the Solimões basin. 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 most likely disappeared at the end of the Pebas system. If this was due to a short, but geographically extensive, marine ingression or just by a transition towards fluvial settings of the modern Amazon system is still unclear. The termination of the Pebas system made an area of more then one million square kilometres available for colonization of terrestrial biota. Through uplift, fluvial depositional and erosional processes the area previously occupied by the Pebas system developed into a highly heterogeneous edaphic mosaic landscape that enhanced subsequent diversifications. All faunal evidence indicates the Pebas system was connected to tropical marine areas; no faunal support is found for direct biogeographic connections with the Parana basin in the south.

Advances in the understanding of the Neogene history of Amazonia

Insight into the Neogene history of Amazonia has improved dramatically 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 is dated at slightly before 8 Ma (Dobson et al., 1997, 2001; Harris & Mix, 2002). The role of regional tectonic processes and settings in forcing this event also has become increasingly clear through various studies in the Colombian (Cooper et al., 1995; Villamil, 1999; Rojas, 2002), Ecuadorean (Steinmann et al., 1999) and Peruvian (Rousse et al., 2003) Andes. 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.

The Miocene Amazonian salinity debate has intensified and diversified. Faunal and geochemical evidence has consistently concluded that most of western Amazonia during the Miocene was dominated by freshwater settings at sealevel (Vonhof et al., 1998, 2003; Wesselingh et al., 2002, 2006c; Kaandorp et al., 2006). In contrast, a number of recent studies based on ichnofossils and tidal depositional features have argued for the common presence of mesohaline and higher salinities (Räsänen et al., 1996; Gingras et al., 2002a, b; 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; Latrubesse et al., 1997; Wesselingh et al., 2006d). However, Gingras and colleagues also uncovered many brackish trace fossil assemblages and tidal depositional facies within exposures 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; Wesselingh et al., 2006c). 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 (Vonhof et al., 1998, 2003; Wesselingh et al., 2002, 2006c; Kaandorp et al., 2006), I believe that the

depositional environment was mostly a freshwater system. The presence of marine ichnofossils in the Pebas Formation (in the strict sense) is 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 (Wesselingh, 2006a, b) and is a common phenomenon in long-lived lake faunas (Wesselingh, in press). However, subtle temporal separation of mollusc communities and brackish ichnofossil communities within the Pebas Formation cannot be ruled out.

Very few radiometric ages have been established for lowland Amazonian deposits in the past decade (Campbell *et al.*, 2001; Hermoza, 2005). Many more radiometric ages have become available for geological units in intramontane basins 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 lake/wetland system during the early Late Miocene. Together with new radiometric ages for Paleogene units (Hermoza, 2005), they formed the basis of an age calculation model by Wesselingh *et al.* (2006a) that indicated the Pebas system to have existed between *c.* 23 and 9 Ma. 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 similar to those of today, existed in western Amazonia *c.* 16 Ma (Kaandorp *et al.*, 2003, 2005). The transition from a seasonal climate with pronounced dry season to a wetter climate has been calculated by Wesselingh *et al.* (2006a) to have occurred around 23 Ma ago. 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 the present-day tropical rainforest belt and savannah belt to the north were, in effect, in place during the Middle Miocene.

In the past decade, the combination of fossil occurrences and DNA analyses of extant fish taxa provided potent new insights into the role of Miocene western Amazonia in shaping modern (fish) biodiversity of tropical South America. Studies, such as those on the Miocene catfish of northern Venezuela (Lundberg & Aguilera, 2003), Miocene-extant freshwater stingrays (Lovejoy *et al.*, 1998, 2006), and other possible marine-derived and obligate freshwater fish taxa of tropical South America (Albert *et al.,* 2006; Lovejoy *et al.,* 2006), have shown the important role the Pebas system played in the evolution of the modern tropical South American fish faunas. The Pebas system provided, for example, a pathway for marine fish taxa to become adapted to and established into freshwater biotopes. At the same time, marginal marine molluscs failed to become established in freshwater biotopes. This feature is attributed by Vermeij & Wesselingh (2002) and Wesselingh & Salo (2006) to a number of ecological barriers in the Pebas system, such as common dysoxia, salinity stress and high predation pressures. These favoured the evolution of a highly specialized, endemic mollusc fauna, and prevented the establishment of marginal marine taxa in the Pebas system. Fish studies also added many new insights into the organisation of catchment areas in northwestern South America that underwent drastic reorganisations in the past 23 Ma as a result of Andean tectonics.

For various different Amazonian terrestrial groups, molecular clock age estimates have been produced, consistently showing major diversifications to have occurred during the Neogene in tropical South America (references in Wesselingh & Salo, 2006).

In the past decade, insights into groups other than molluscs from the Pebas Formation and associated deposits have increased as well. Ostracod faunas of the Pebas Formation have been described (Muñoz Torres *et al.*, 1998, 2006), as well as those of the slightly younger Solimões Formation of Brazil (Ramos, 2006). The development of the ostracod fauna in the Miocene of western Amazonia mirrors that of the molluscs; large radiations of endemic species within the Pebas system which became largely replaced by modern fluvial ostracod groups during deposition of the Late Miocene Solimões Formation.

A first inventory of pebasian fish taxa was published by Monsch (1998). It showed the presence of marine to strictly freshwater groups. Large vertebrate faunas (including fishes and reptiles) have been described from coeval deposits of the Magdalena basin (aquatic taxa treated in Lundberg, 1997; Langston & Gasparini, 1997; Wood, 1997), northern Venezuela (at the time linked with lowland Amazonia; aquatic taxa treated in Lundberg & Aguilera, 2003; Aguilera & Rodrigues de Aguilera, 2004; Dahdul, 2004) and slightly younger deposits of the Acre and Amazonas regions of Brazil (Latrubresse *et al.*, 1997; Carvalho *et al.*, 2002; Malabarba & Dutra, 2002; Gayet *et al.*, 2003). These works have shown that major modern Amazonian aquatic groups were present and well diversified in the Miocene, and that the area between northern Venezuela and the Acre territory in Brazilian Amazonia, including the Magdalena basin of Colombia, formed a single biogeographic zone during the Miocene, that also included the Pebas system.

A model for landscape evolution and biotic development in western Amazonia

In Figure 1, a model for landscape evolution and biotic development of aquatic mollusc faunas in western Amazonia is summarised. During the Late Eocene (Fig. 1A; *c.* 45-34 Ma), the foreland basins to the west of Iquitos were occupied by a shallow marine embayment. Fossil faunas from this interval are scarce, poorly allocated and appear to contain marine molluscs, such as the mitriform gastropod *Mitricaulus incarum* Pilsbry,

Fig. 1. A model of landscape evolution and biotic development in western Amazonia. ▶
Stratigraphic model from Wesselingh *et al.* (2006a). Note that age uncertainties for many of the unit-boundaries are typically one or two Ma. The block diagrams cover an area in northern Peruvian Amazonia approximately between the Corrientes River in the west and Pebas in the east. River courses, shorelines and landscapes are conjectural. Grey triangles indicate regional hiatuses, many more of which must exist in the time interval after 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 8 Ma. Key: Priab. = Priabonian; Aquit. = Aquitanian; Langh. = Langhian; Serra. = Serravallian; Mess. = Messinian; Qua. = Quaternary; CM = Clay Member; Su1 = Subunit 1.
At (B), *Sheppardiconcha colombiana* (from Wesselingh, 2006a, fig. 255). This freshwater cerithioidean is from younger intervals, but resembles poorly identified freshwater certhioideans reported in literature as well as seen in borehole samples (pers. obs.). The bivalve at (E) is *Pachydon obliquus*, the most common endemic Pebasian species (specimen data in Wesselingh, 2006a). The gastropod representing elevated salinities is *Nassarius? reductus* (data in Wesselingh, 2006a). The pearly freshwater mussel at (H/I) is *Diplodon* sp. from the Nanay River near Iquitos (data in Kaandorp *et al.*, 2006).
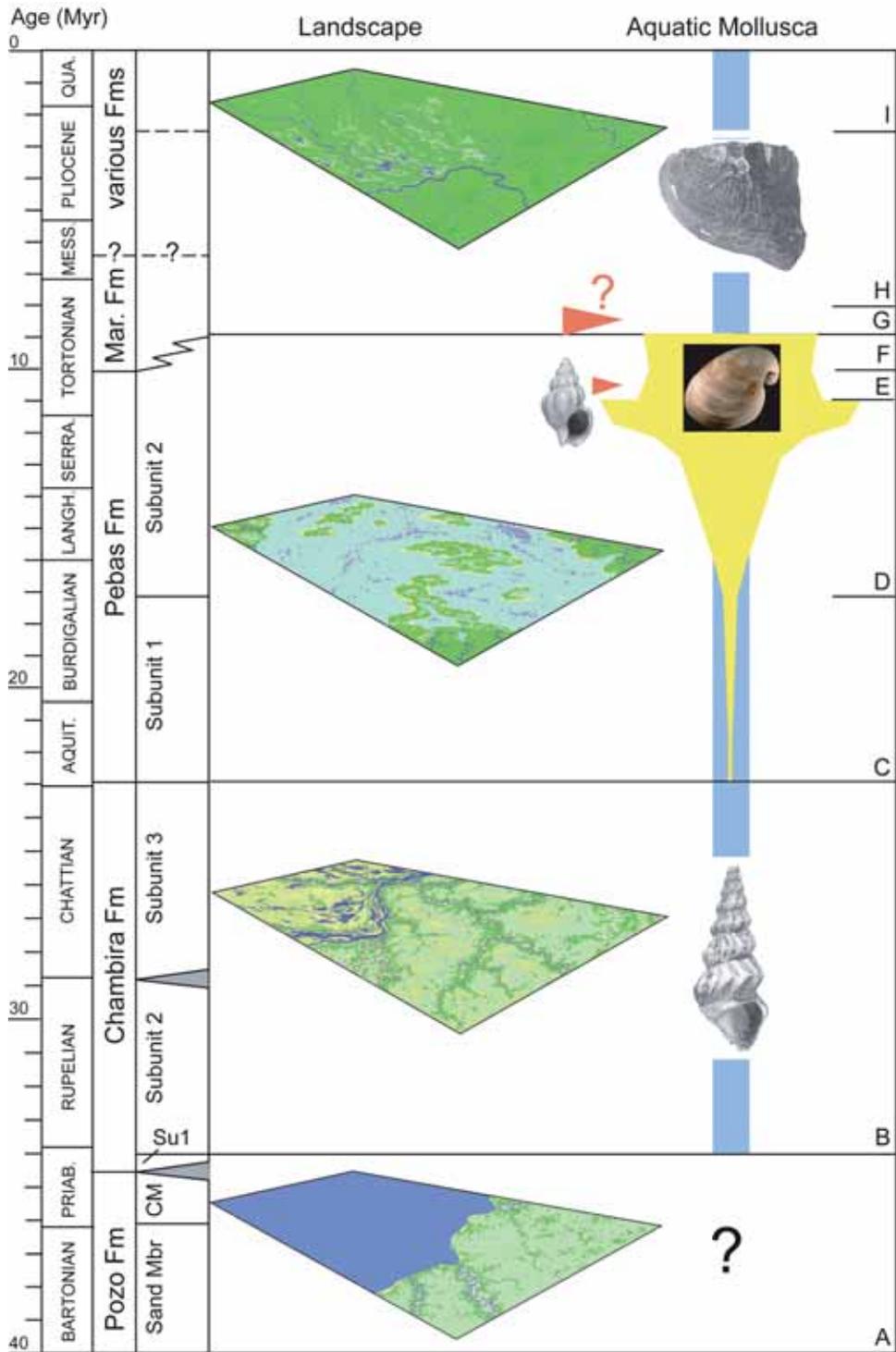
1944. Coeval deposits containing planktonic foraminifera indicative of open marine settings have been reported from the adjacent Oriente basin in Ecuador (Tschopp, 1953).

During the Oligocene (Fig. 1B: *c*. 34-23 Ma), the region was occupied by a trunk river system that flowed northwards towards the Caribbean (the Chambira system). From the low-lying Andes in the west, river belts in otherwise seasonally flooded back swamps emptied into this river. From the east, rivers joined draining lowlands and craton areas. The trunk river system may have been very low lying and may have experienced some intermittent tidal influence. The climate was pronouncedly seasonal and probably dryer than today. Mollusc faunas from this interval are scarce, but include poorly identified cerithioid gastropods, corbiculid clams and pearly freshwater mussels.

In the Early to early Late Miocene (Fig. 1C-F: *c*. 23-9 Ma), the region became mostly submerged and transformed into a continually shifting mosaic of lakes, wetlands and river belts, the Pebas system. In the early phase of this system (C), faunas were dominated by fluviolacustrine taxa, and few corbulid and cochliopid species occurred. Possibly, the area experienced episodic, widespread fluvial or marginal marine influences that restrained faunal diversifications. From *c*. 17 Ma onwards, an endemic fauna (the Pebas fauna) diversified to reach maximum diversity levels near *c*. 12 Ma (D). Coinciding with some marginal marine influence (E), diversity dropped somewhat, but remained high in the final stages of the Pebas system (F). The region experienced a wet tropical monsoon climate.

A drastic reorganization of the landscapes occurred in the early Late Miocene, some 8-9 Ma (Fig. 1G). In a short time interval, fluvial landscapes fed by the uplifting Andean hinterland to the west replaced 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 marine trace fossils, including *Thalassinoides*, *Planolites*, *Chondrites*, *Scolicia*, *Skolithos*, *Arenicolites* and *Teichnus* (Rebata *et al.*, 2006). Such a marine incursion would have enhanced the decline of the endemic Pebas fauna before the change towards fluviolacustrine settings. Unfortunately, no mollusc faunas have been preserved in these possible marine settings. The demise of the Pebas system made large tracts of land available for colonization of terrestrial biota.

From *c*. 8-2.6 Ma (Fig. 1H) the landscape 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 probably remained wet and rainforest occupied most of the area. Modern fluviolacustrine mollusc faunas became established. Increased glacioeustasy, as well as broad uplift of the area, forced rivers into increasingly entrenched valleys in the last 2.6 Ma (Fig. 1I), with the exception of the foreland basin zone, where aggrading megafans persisted. During the Quaternary, edaphic heterogeneity increased through uplift and denudation, and the modern landscapes developed.

Outlook and concluding remarks

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 less well understood than that of the Miocene. From the Late Neogene – Quaternary period few deposits are available for study that are typically fluvial and lack fossils almost entirely. 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 sealevels drops facilitated entrenchment of the rivers into valleys? Was the region always wet after 8 Ma? On what scales did drainage reorganizations occur in lowland Amazonia? How did edaphic heterogeneity develop? Again, 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 8 million years and assess possibilities for the development of the modern Amazonian biota. From radar images of the highest interfluvial parts in Brazilian Amazonia (for example, between the Içá 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 many 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 documented, 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, their evolution. Study of the early parts of the Pebas system (MZ1-MZ4 intervals), for which good exposures 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, 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 palaeogeographic situation in adjacent areas, and especially the Llanos basin in the north (Colombia-Venezuela), and the development of its fauna during the Middle Miocene, are completely unexplored and have great scientific potential. 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 fauna of western Amazonia emerges. During deposition of the Leon Formation, the Llanos basin experienced widespread marine settings (Cooper *et al.*, 1995; Rojas, 2002), but also may have episodically experienced widespread freshwater settings allowing for Pebasian taxa to become established there as well. The organisation of the Pebas and the Llanos system during the Miocene might resemble that of the Caspian and the Black Sea during the Quaternary. From the Early Quaternary on, the Caspian Sea continually experienced endemic molluscan evolution (and diversifications). Episodically, the inland brackish Caspian Sea was connected to the Black Sea and Caspian taxa became established there. However, the Black Sea underwent repeated episodes of freshening as well as occupation by marine settings, driving the Caspian taxa repeatedly to extinction. Most of the Caspian taxa occurred typically for short periods in the Black Sea and often occupied marginal habitats. On the other hand, it is almost certain that many of the endemic Caspian taxa originated from that same Black Sea region during the Early Quaternary, and it is distinctly possible that the latter acted as a donor region for the Caspian faunas afterwards, although the focus of diversification remained in the Caspian Sea itself (Wesselingh, in press and references therein). For the Llanos basin, very few exposures are available and no coordinated study as to the macropalaeontology from borehole data has been undertaken to date. The large size and the intermediate location between the Pebas system in the south and the marine realm in the north are very similar to the position of the Black Sea between the Caspian Sea and the marine realm during the Quaternary. 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 basins may have provided short-lived corridors for the exchange of Pebasian and Pacific (freshwater) 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).

Molluscan palaeontological investigations of the Miocene Pebas Formation of western Amazonia has provided many new insights into the history of the modern Amazon system and its biota, as is shown by contributions in this volume. Other lines of research corroborate many of the new finds. However, many, large uncertainties on the history of this vast and wonderful region remain to be addressed.

Acknowledgements

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