

# The stratigraphy and regional structure of Miocene deposits in western Amazonia (Peru, Colombia and Brazil), with implications for late Neogene landscape evolution

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A biozonation based on molluscs is proposed for Miocene deposits of western Amazonia (Peru, Colombia and Brazil), commonly referred to as the Pebas Formation. The new zonation refines existing pollen zonations and provides a key for the quick assessment of the stratigraphic position of Neogene deposits in the field. The regional distribution of twelve mollusc zones reveals a structuring of geological units around the broad Iquitos-Araracuara anticline. 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. Based on this work a biostratigraphic framework for Miocene deposits of western Amazonia, including fossiliferous deposits from adjacent basins (Putumayo, Llanos and Magdalena basins in Colombia), is proposed.

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## Introduction

The stratigraphy of Neogene deposits of western Amazonia is poorly constrained due to the scarcity of radiometric dates. Miocene strata, known as Pebas and/or

Solimões Formation (further indicated as Pebas Formation), cropping out along rivers in western Amazonia of northeast Peru, southeast Colombia and the adjacent border zone of Brazil, are renowned for their rich fossil faunas (Nuttall, 1990; Wesselingh *et al.*, 2002). The stratigraphic framework for the Pebas Formation has been based on pollen zones that were correlated with (dated) marine successions in the Caribbean (Hoorn, 1993, 1994b). Pebas Formation outcrops in Colombian and Peruvian Amazonia were attributed by Hoorn (1994b) to three pollen zones covering an interval between late Early and early Late Miocene. The relationship of the Pebas Formation with underlying and overlying geological units is poorly defined (see, *e.g.*, Hoorn, 1993; Wesselingh *et al.*, 2006a), although the formation itself is highly characteristic, with predominantly blue fossiliferous siltstones and claystones, and lignites. Strata yielding a Pebas type of mollusc fauna (characterised by endemic corbulid and cochliopid species; Wesselingh, 2006) cover an area over a million km<sup>2</sup> in Colombian, Peruvian, Ecuadorian and Brazilian Amazonia (Wesselingh *et al.*, 2002). In this paper, we use the fossil molluscs to erect a refined biozonation for the Pebas Formation. This zonation is based on outcrop work, but was found to be compatible with borehole successions from the region (Wesselingh *et al.*, 2006a). We discuss the stratigraphic relationships of the Pebas Formation with spatial and temporal adjoining formations, and reveal a structuring of the subsurface in the Amazon lowlands of Peruvian Loreto, Colombian Amazonas and neighbouring areas.

The area where fieldwork was carried out spans northeast Peru, southeast Colombia and the adjacent border areas of Brazil (Fig. 1a). The area is located in the transition zone of the lower western margin of the Guyana Shield in the north, the intracratonic Solimões basin in the southeast, the Acre pericratonic/foreland basin in the south and the Marañon foreland basin in the west (Fig. 1b). The major part of this transition zone consists of a subsurface 'platform' overlying cratonic basement, with a Neogene cover typically of a few hundred metres only. This platform, called the Amazonas basin in southeast Colombia, defies tectonic classification. Since a major basin east of the Solimões basin in Brazil is also called the Amazonas basin, the Colombian Amazonas basin and adjacent areas that form a shallow sedimentary platform-like rim along the northern margin of the Solimões and Acre basins and to east of the Putumayo, Oriente and Marañon basins are grouped and indicated here as the 'Caqueta platform' (see below).

Palaeozoic and Precambrian sedimentary and metamorphosed rocks of the Guyana Shield are found northeast of the study area. This region is characterised by low ridges and hills formed by the basement with poorly mapped and understood depressions filled with Miocene fluvial units (Hoorn, 1994a; 2006). To the southeast the surface is formed by Pliocene fluvial strata and Quaternary fluvial aggradational plains (Rosetti *et al.*, 2005). Most of the basement outcrops are surrounded by Miocene fluvial units, but in some areas, such as the lower Caqueta area at the Colombian-Brazilian border, the Pebas Formation lies directly on these basement rocks (Maia *et al.*, 1977). This craton area is bounded by the Caqueta platform to the south and southeast, and the Putumayo basin to the west.

The Caqueta platform is not a basin in the classical sense, but merely a pericratonic zone with a thin (up to *c.* 300 m) Neogene cover on craton basement in its northern and eastern parts. In the western zone of this platform, thick series of Paleogene, Mesozoic and Palaeozoic strata develop below the Neogene cover. The strata are thickening towards the Andean mountain front (Sanz Parra, 1974; Balkwill *et al.*, 1995; Marocco, 1995).

The Caqueta platform has experienced tectonic uplift in the past 10 Ma (Balkwill *et al.*, 1995; Roddaz *et al.*, 2006). The southwestern zone of this platform (Iquitos-Napo region) has been part of the active foreland basin during the Cretaceous and early Paleogene. The present-day active zone of subsidence is more restricted toward the west, leaving an area that belongs neither to the foreland basin nor to the craton zone; for convenience, it is here included in the Caqueta platform. To the north and east the Caqueta platform is bounded by the lower western margin of the Guyana Shield and to the south it gradually merges into the Acre and Solimões basins. The platform extends along the whole northern margin of the Solimões basin in Brazil, and towards the Marañón, Oriente and Putumayo basins in the west (Fig. 1b). Most of the fieldwork area is located on this platform.

The Solimões basin is an east-west elongate intracratonic basin that forms the western part of the Solimões megashear, a series of basins that originated in the Palaeozoic and were episodically active during the Phanerozoic (Caputo, 1991; Hoorn, 1993). In the subsurface, the basin is dotted by basin thresholds, commonly termed 'arches' (but see discussion in Wesselingh & Salo, 2006, about this term). The maximum thickness of the Cainozoic infill in the basin (referred to as Solimões Formation or Group in Brazil that includes the Pebas Formation) is *c.* 400 m (dell'Arco *et al.*, 1977). To the east, the Solimões basin is separated from the (Brazilian) Amazonas basin by a basin threshold termed the Purus arch (a slightly bending north-south structure located at *c.* 62/63°W). The boundary between the Solimões basin and the Acre basin to the west is either defined at a basin threshold (which has been confusingly named the Carauari arch (Caputo, 1991) and Iquitos arch (Maia *et al.*, 1977; see discussion below)) or at a poorly defined, northwest-southeast trending basin threshold located at approximately 72°W (Iquitos 'arch' of Caputo, 1991). We follow the basin boundaries proposed by the latter.

The Marañón basin is the northern Peruvian part of the Subandean foreland basin that continues as the Oriente basin in Ecuador and Putumayo basin in Colombia. To the southeast it grades into the Acre basin (Brazil). The Marañón basin is separated from the peri-intramontane Ucayali basin in the south by an Andean thrust sheet that is expressed as low mountains (*e.g.*, Sierra de Divisor) and partially located in the subsurface (in the Requena region, Peru). The architecture of the Miocene deposits in the Marañón basin is treated in Hermoza (2005) and Wesselingh *et al.* (2006a). Pebas Formation thickness can reach up to *c.* 1000 m in the Marañón basin.

### Material & methods

Samples from 74 localities, collected during fieldwork of the first author in 1991 and 1996 were assessed (Appendix 1; see maps in Wesselingh *et al.*, 2002). These localities are located in northeast Peruvian Loreto and adjacent southeast Colombia (Fig. 1a, indicated as fieldwork area). A single locality (San Juan RioSeco) from Central Colombia was sampled by F.P.W. in 1996. Samples from two localities in southern Colombian Amazonia were collected by C.H. in 1989. Additionally, material held in museum collections and collected by other researchers from 25 localities was studied, in order to broaden the geographic coverage of this study (see Appendix 2 for details of localities). Thus, the study includes Miocene faunas from larger parts of inland northwest South America (Fig. 1a).

Several of the outcrops used in this study have been studied for palynology by Hoorn (1993, 1994a, b), providing us with palynological stratigraphic references. For descrip-

tions and illustrations of mollusc species, the reader is referred to Wesselingh (2006).

For the present paper, only the presence and absence of taxa are recorded and grouped. Benthic molluscs are notably good (palaeo-)environmental recorders. The drawback of this is that they are usually considered to be poor time-indicators. In the Pebas system, the simultaneous evolution in many endemic mollusc (and ostracod) lineages (Wesselingh, 2006; Muñoz Torres *et al.*, 2006), as well as relatively high extinction rates (or within lineages replacement rates), provide relative high numbers of potential zonation points and lower the possibility of diachronism.



Fig. 1a. Localities treated in this paper. Inset is fieldwork area. Background modified from [www.photojournal.jpl.nasa.gov](http://www.photojournal.jpl.nasa.gov).



### Molluscan zones

Twelve mollusc zones are proposed, one of which is void. These zones are assigned MZ1-MZ12 (MZ= molluscan zone).

#### MZ1: *Aylacostoma ava* Range Zone

The MZ1 is characterised by the occurrence of *Aylacostoma ava* (Pilsbry & Olsson, 1935). From literature and study of museum collections, it appears that *Dyrus laciranus*



Fig. 1b. Structural geological units discussed in this paper. Key: CB = Cuenca basin; CBB = Chaco basin; MB = Magdalena basin; OB = Oriente basin; PB = Putumayo basin; RBESC = Rio Branco-Essequibo Corridor; SAZ = Subandean zone; SM = Serrania de la Macarena; UB = Ucaiyali basin. The boundary between the Acre and Solimões basins follows Caputo (1991). The topographic background of this figure (and of other figures) is taken from [www.photojournal.jpl.nasa.gov](http://www.photojournal.jpl.nasa.gov).

(Pilsbry & Olsson, 1935) might form a second co-occurring biostratigraphic indicator. Both the fauna from the Middle Magdalena basin referred to in literature as the 'La Cira fauna' (or fauna from the 'La Cira Beds' or 'La Cira Formation'; Wheeler, 1935) as well as that from the Santa Teresa Formation (Nuttall, 1990; de Porta, 1966; Gómez *et al.*, 2003) from the west flank of the Colombian Eastern Cordillera fall within this zone. Apart from the two stratigraphic indicators, the fauna includes common *Pachydon hettneri* (Anderson, 1928), *Pachydon cebada* (Anderson, 1928), *Charadreon eucosmius* (Pilsbry & Olsson, 1935) and various species of pearly freshwater mussels (Pilsbry & Olsson, 1935). In a single sample studied in the ANSP from San Juan de Arama (southern Llanos basin), presumably from the Leon Formation, *A. ava* was encountered as well.

### **MZ2: *Dyris denticulatus* Range Zone**

The MZ2 is characterised by the following stratigraphic indicator species; *Dyris denticulatus* Wesselingh, 2006, *Cochliopina? colombiana* (Nuttall, 1990), *Aylacostoma lataguensis* (Nuttall, 1990), *Sheppardiconcha lataguensis* Nuttall, 1990, and *S. colombiana* (Nuttall, 1990). Abundant (but stratigraphically not exclusive) species are *Tryonia semituberculata* (Nuttall, 1990), *Dyris lataguensis* Wesselingh, 2006, and *Pachydon hettneri* (Anderson, 1928). The MZ2 contains the first occurrence date (FOD) of *Tryonia semituberculata* (Nuttall, 1990) and *Exallocorbula dispar* (Conrad, 1874). Important last occurrence dates (LODs) are those of *Pachydon hettneri* (Anderson, 1928) and *P. cebada* (Anderson, 1928). The La Tagua Beds of the Colombian Putumayo basin (Nuttall, 1990) are assigned to MZ2. Also, some poorly documented samples studied in the ANSP from the southern Llanos and Putumayo basins (Colombia) should be placed in this biozone (see Appendix 2). MZ2 faunas have also been found in wells studied from the Pastaza-Marañon foreland basin (Wesselingh *et al.*, 2006a).

### **MZ3: void zone**

The MZ3 is introduced to bridge the faunal gap between the MZ2 and MZ4. We have not collected samples that can be attributed to this zone ourselves. Samples studied superficially from the Putumayo basin (located in the ANSP, see discussion below and Appendix 2) contain faunas with both *Pachydon hettneri* (Anderson, 1928) and *P. obliquus* Gabb, 1869. Because it was impossible to evaluate the quality of the samples (are they from single horizons or localities?) and the region has been inaccessible due to guerrilla activity for additional collecting, we have decided to establish a void zone that will need to be elaborated in the future. If the studied samples are of good quality, then the LOD of *Pachydon hettneri* (Anderson, 1928), *Pachydon cebada* (Anderson, 1928) and *Sheppardiconcha colombiana* Nuttall, 1990, might be extended to the MZ3 that furthermore might yield the FOD of *Pachydon obliquus* Gabb, 1869, and *Pachydon carinatus* Conrad, 1871. Localities assigned to MZ3 lay in the Colombian Putumayo basin. A single locality along the Ecuadorian Curaray River also might be attributed to this zone (Appendix 2).

### **MZ4: *Toxosoma carinatum* Range Zone**

This interval is characterised by the presence of *Toxosoma carinatum* Wesselingh, 2006. The MZ4 contains amongst others the FOD of *Neritina ortonii* Conrad, 1871, *Dyris hauxwelli* Nuttall, 1990, *D. tricarinata* (Boettger, 1878), *Toxosoma ovatum* Wesselingh, 2006, *T. globosum* Wesselingh, 2006, and *Pachydon andersonae* Wesselingh, 2006. An important

LOD is that of *Dyris lataguensis* Wesselingh, 2006. The MZ4 crops out in Peruvian Loreto along the Amazon River and lower Napo River north of Iquitos and at some places more upstream along the Napo River.

#### **MZ5: *Diplodon indianensis* Range Zone**

This zone is characterised by the presence of *Diplodon indianensis* Wesselingh, 2006, and *Sheppardiconcha solida* Wesselingh, 2006. Both species are typical of marginal lacustrine associations (Wesselingh *et al.*, 2002). Additionally, the presence of *Sioliella carinata* Wesselingh, 2006, and the absence of *Toxosoma carinatum* Wesselingh, 2006, in the lacustrine associations is also typical of this zone. Major LODs are those of *Tryonia semituberculata* (Nuttall, 1990), *Toxosoma ovatum* Wesselingh, 2006, *T. globosum* Wesselingh 2006, *Sioliella carinata* Wesselingh, 2006, *S. littoridinaeformis* Wesselingh, 2006, *Cochliopina? convexa* Wesselingh, 2006, and *Pachydon maaikae* Wesselingh, 2006. Outcrops assigned to MZ5 are found along the Napo River and the Amazon River north of Iquitos.

#### **MZ6: *Onobops? iquitensis* – *Onobops communis* Interval Zone**

The MZ6 is characterised by the occurrence of *Onobops? iquitensis* Wesselingh, 2006, and the absence of *Onobops communis* Wesselingh, 2006. This zone contains LOD of *Onobops elongoides* Wesselingh, 2006, and *Charadreon eucosmius* (Pilsbry & Olsson, 1935). FODs include those of *Onobops? iquitensis*, *Sioliella woodwardi* (Kadolsky, 1980), *Toxosoma eboreum* (Conrad, 1871), *Tropidebora tertiana* (Conrad, 1874), and *Cochliopina? bourguyi* (Roxo, 1924). Outcrops assigned to this zone are known from Iquitos, as well as the lower part of the Nanay and Momon rivers.

#### **MZ7: *Dyris pebasensis* Range Zone**

This zone is characterized by the occurrence of *Feliconcha reticulata* Wesselingh, 2006, *Dyris pebasensis* Wesselingh, 2006, *Dyris microbispiralis* Wesselingh, 2006, and *Sioliella crassilabra* (Kadolsky, 1980). The FODs of many species are recorded, including those of *Dyris acicularis* Wesselingh, 2006, *Littoridina pebasensis* (Conrad, 1874), *Sioliella bella* (Conrad, 1874), *Charadreon semiglabrum* Wesselingh, 2006, and *Ostomya carinata* Wesselingh, 2006. Important LODs include those of *Onobops iquitensis* Wesselingh, 2006, *Sioliella woodwardi* (Kadolsky, 1980) and *Sheppardiconcha tuberculifera* (Conrad, 1874). The MZ8 is known from south of Iquitos in a zone from Puerto Almendras on the Nanay River to Tamshiyacu on the Amazon River, and along the Amazon River between Pebas and Beiruth.

#### **MZ8: *Dyris lanceolatus* Range Zone**

This zone is characterized by the occurrence of *Dyris lanceolatus* Wesselingh, 2006, *Onobops minimissimus* Wesselingh, 2006, *O. microconvexus* Wesselingh, 2006, *Sioliella fusiiformis* Wesselingh, 2006, and *Hemisinus kochi* (Bernardi, 1856). The latter species occurs nowadays in rivers of eastern Brazil, but has not been found in other stratigraphic intervals within the Pebas Formation. Important LODs include *Tryonia scalarioides tuberculata* (de Greve, 1938), *Dyris regularis* Wesselingh, 2006, *Dyris hershleri* Wesselingh, 2006, *Sioliella saloi* Wesselingh, 2006, *Littoridina pebasana* (Conrad, 1874) and *Ostomya carinata* Wesselingh, 2006. Important FODs include *Tryonia scalarioides scalarioides* (Etheridge, 1879), *Feliconcha feliconcha* Wesselingh, 2006, *Dyris carinatus* Wesselingh, 2006, *Toxosoma*

*denticulatum* Wesselingh, 2006 and *Sioliella umbilicata* Wesselingh, 2006. MZ8 localities are found along the Itaya River south of Iquitos, along the Amazon from Beiruth to the Colombian border (Loreto, Peru), as well as in the lower Caqueta area (Colombia; Appendix 2).

#### **MZ9: *Pachydon trigonalis* – *Dyris tricarinatus* Concurrent range Zone**

The MZ9 is characterised by the co-occurrence of *Pachydon trigonalis* Nuttall, 1990 and *Dyris tricarinatus* (Boettger, 1878). *Longosoma fusiforme* Wesselingh & Kadolsky in Wesselingh, 2006, and *Iolaea amazonica* van Aartsen & Wesselingh, 2005, have so far only been found in samples assigned to the MZ9 zone. Their very rare occurrence makes them, however, not very suitable as stratigraphic indicator species. *Sheppardiconcha septencincta* (Roxo, 1937), so far only found in MZ10 deposits within the Pebas Formation, is also known from younger deposits of the Brazilian Solimões Formation (Wesselingh *et al.*, 2006c). Seven species (*Corbula cotuhensis* Wesselingh & Anderson in Wesselingh, 2006, *Macoma* sp. in Wesselingh, 2006, *Thais woodwardi* (Roxo, 1924), *Nassarius reductus* Vermeij & Wesselingh, 2002, *Odostomia nuttalli* and *O. cotuhensis* van Aartsen & Wesselingh, 2000, and *Iolaea amazonica* van Aartsen & Wesselingh, 2005) are associated with marine incursions that are not rare in this interval. Several of these species occur rarely in the overlying MZ10 as well. Important FODs include *P. trigonalis*, *Toxosoma grande* Wesselingh, 2006, *Dyris elongatus* Wesselingh, 2006, *Dyris bicarinatus bicarinatus* (Etheridge, 1879), and *Aylacostoma browni* (Etheridge, 1879). Important LODs include *Neritina ortonii* Conrad, 1871, *Tryonia minuscula* (Gabb, 1869), *Feliconcha feliconcha* Wesselingh, 2006, and *Dyris tricarinatus* (Boettger, 1878). MZ9 localities are found along the Amazon north of Nauta (Loreto, Peru), in at least one locality at the Javari River (Loreto, Peru) and around the Cotuhé River (Amazonas, Colombia).

#### **MZ10: *Dyris mattii* – *Tryonia minuscula* Interval Zone**

The MZ10 is characterised by the occurrence of *Dyris mattii* Wesselingh, 2006, and the absence of *Tryonia minuscula* (Gabb, 1869). The former has its LOD in this zone, together with species such as *Feliconcha feliconcha* Wesselingh, 2006, and *Dyris carinatus* Wesselingh, 2006. Within MZ10, *Pachydon obliquus* Gabb, 1869, has become replaced by *P. trigonalis* Nuttall, 1990, as the dominant bivalve species. MZ10 localities are found along the Amazon River and tributaries in the south tip of the Trapecio Amazónico Colombiano, in outcrops and wells near the Yavari River in Brazil, in one locality on the east bank of the Amazon River south of Tamshiyacu (Loreto, Peru: Nuevo Valentin) and in one locality along the Iça River in Brazil (Ipiranga: Appendix 2).

#### **MZ11: *Pachydon obliquus* - *Dyris megacarinata* Concurrent range Zone.**

The MZ11 is characterised by the co-occurrence of *Dyris megacarinata* Wesselingh, 2006, and *Pachydon obliquus* Gabb, 1869. In this zone, *Littoridinops? amazonicus* Wesselingh, 2006, and *Dyris megacarinata* Wesselingh, 2006, have their FOD. Major LODs are those of *Pachydon carinatus* Conrad, 1871, *P. obliquus* Gabb, 1869, *P. tenuis* Gabb, 1869, *Dyris acicularis* Wesselingh, 2006, *D. carinata* Wesselingh, 2006, *Toxosoma denticulatum* Wesselingh, 2006, *Littoridina crassa* (Etheridge, 1879) and *Sioliella umbili-*



*cata* Wesselingh, 2006. MZ11 associations are known only from the Amazon banks of southeast Colombia. They occur in the upper part of outcrops near Puerto Nariño and in outcrops to the southeast.

### **MZ12: *Dyris bicarinatus sofiensis* Range Zone**

Characterised by the occurrence of *Dyris bicarinatus sofiensis* Wesselingh, 2006. This zone is found only in the most southeastern outcrop along the Colombian Amazon at Santa Sofia. The outcrop at Benjamin Constant (Brazil) also should be attributed to this zone (Appendix 2).

## **Stratigraphic framework**

Figure 2 presents the species occurrences in the studied samples. Figure 3 presents a stratigraphic framework for fossiliferous deposits of western Amazonia. Figure 4 illustrates some of the most important stratigraphic indicator species. The absence of radiometric dates in the Pebas Formation makes the proposed stratigraphic framework open to uncertainty concerning absolute ages. The framework is based on the following assumptions.

1. Base of *Verrutricolporites* zone at Oligocene-Miocene boundary and the strata bearing La Cira faunas in the Magdalena valley located in the top of that zone (Nuttall, 1990).
2. Age of *Psiladiporites* zone late Early-early Middle Miocene (Hoorn, 1993).
3. Age of *Crassoretitriletes* zone Middle Miocene (Hoorn, 1993).
4. Age of *Grimsdalea* zone late Middle- early Late Miocene (Hoorn, 1993).
5. Termination of the Pebas system before the establishment of the modern Amazon at c. 8 Ma (Dobson *et al.*, 1997; 2001; Harris & Mix, 2002).
6. Molluscan zones within pollen zones assumed to represent equal periods of time.

These assumptions yield a number of uncertainties or are, in the case of assumption 6, certainly invalid. Also, the absence of fossil occurrences that are located in the *Retitricolporites* zone, as well as the lack of an age estimate for the base of that zone, introduce a number of uncertainties about the age estimates for the earlier intervals. Therefore, the age estimates of this stratigraphic framework are approximations only.

The La Cira fauna (found in the La Cira and Santa Teresa formations of the western foothills of the Eastern Cordillera as well as in the Leon Formation of the Llanos basin, the latter yielding younger faunas as well; Appendix 2) contains the oldest occurrences of *Pachydon* and *Dyris* in South America. Older fossiliferous formations in the Magdalena basin, such as the Oligocene Mugrosa Beds and Eocene Los Corros Beds lack *Pachydon* and *Dyris* species (Nuttall, 1990). It is therefore assumed that the Pebas radiation started with the La Cira/Santa Teresa faunas (Wesselingh & Macsotay, 2006).

The Pebas system must have terminated with the establishment of the modern Amazon system c. 8 million years ago (Hoorn *et al.*, 1995; Dobson *et al.*, 1997, 2001; Harris & Mix, 2002). However, it appears that the Pebas fauna became already replaced by fluvial faunas in western Amazonia around 9 Ma (Wesselingh *et al.*, 2006c). The age of the youngest Pebas faunas cannot be established more precisely than early



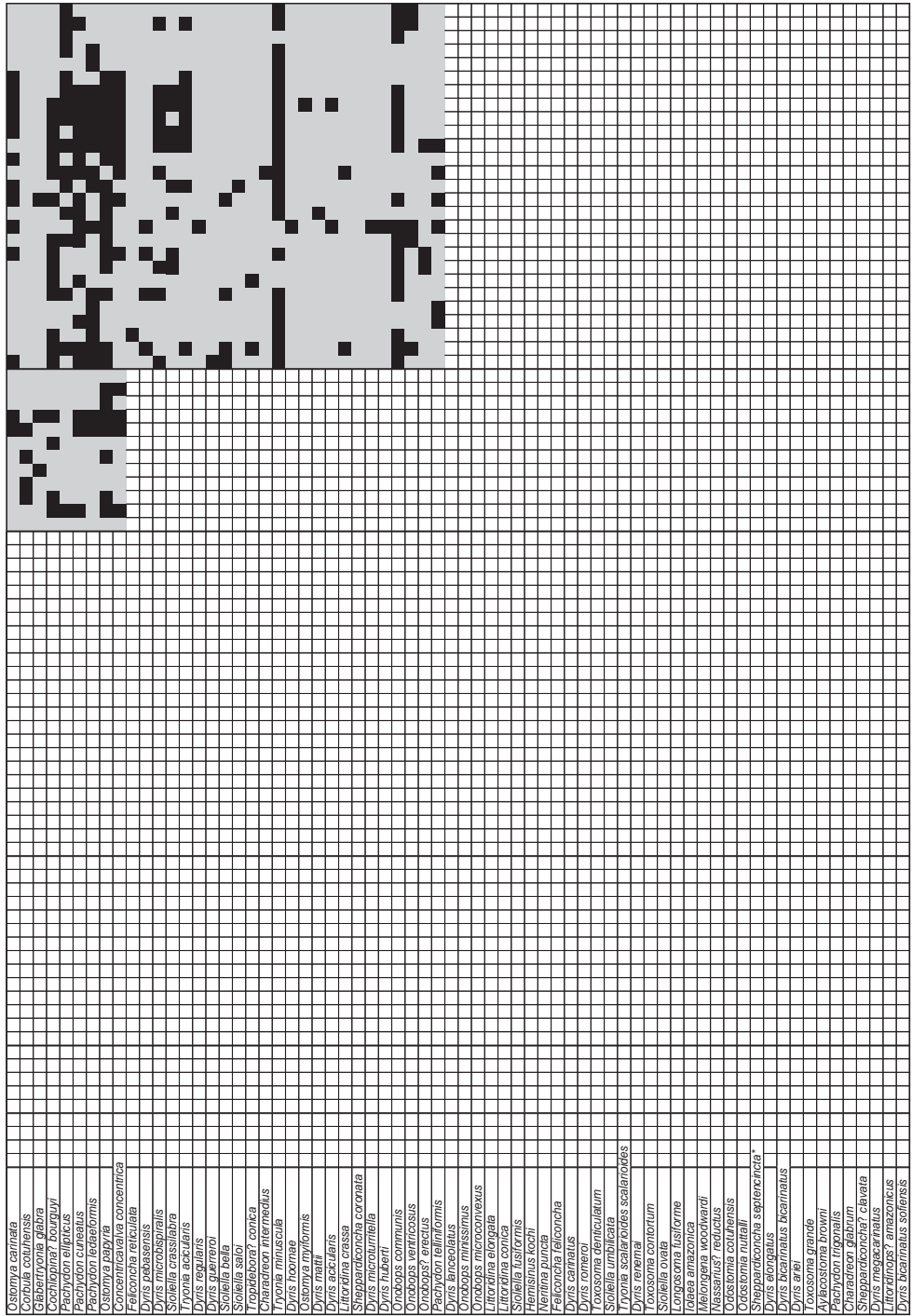


Fig. 2. (continued).







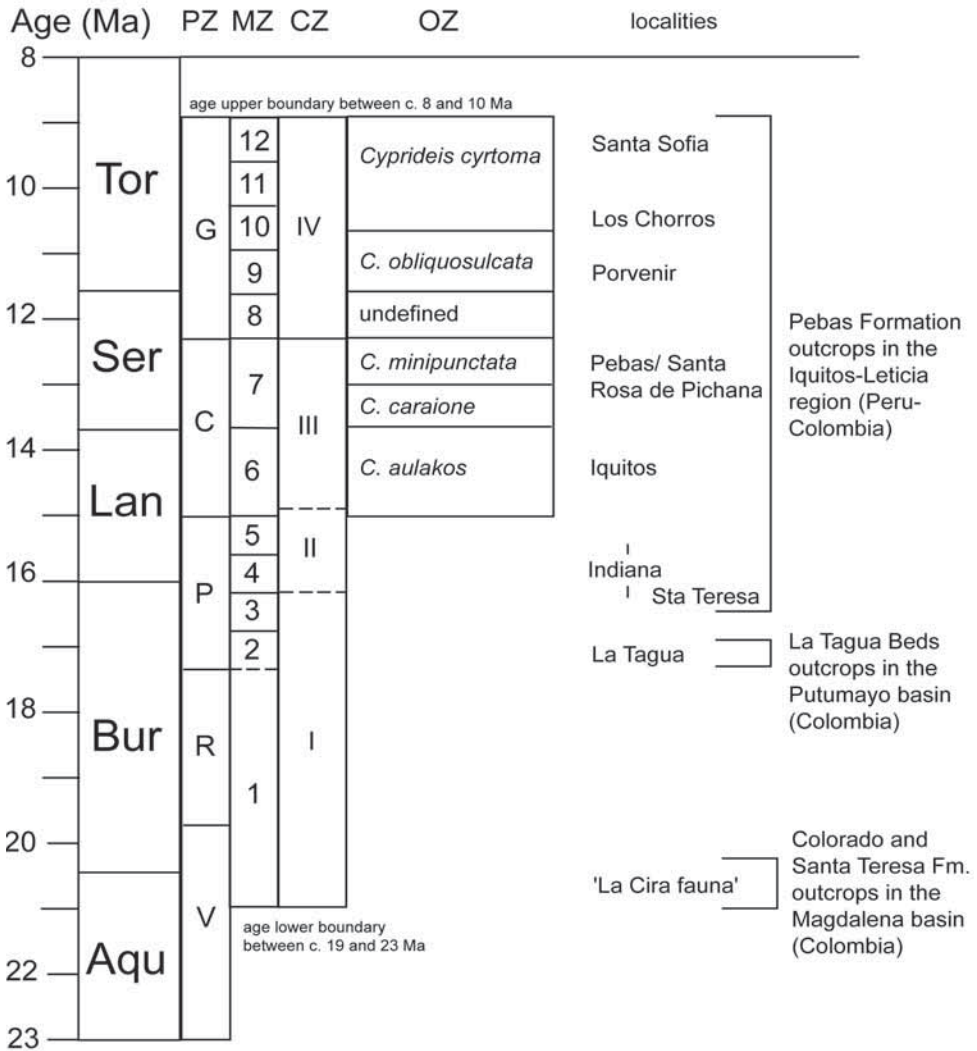
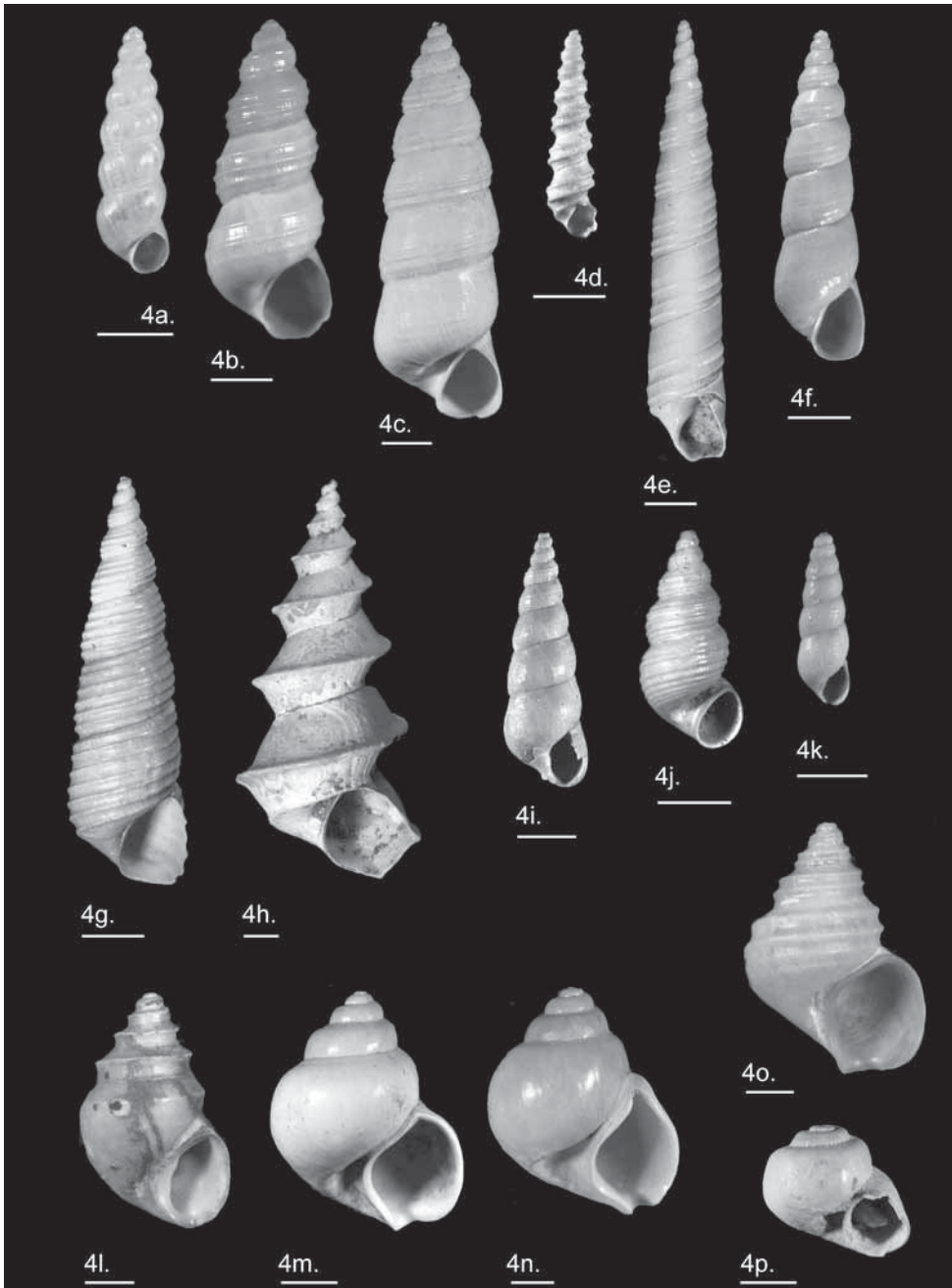


Fig. 3. Stratigraphic framework for the Pebas Formation and related fossiliferous deposits. Stage boundaries from Gradstein *et al.* (2004). Key: Aqu = Aquitanian, Bur = Burdigalian, Lan = Langhian, Ser = Serravallian and Tor = Tortonian; PZ = pollen zones (Hoorn, 1993, 1994a, b; see Wesselingh *et al.*, 2006a, fig. 2, for explanation) with attribution of MZ1 from Nuttall (1990); MZ = mollusc zones (this work); CZ = crude mollusc zones (Wesselingh *et al.*, 2006a); OZ = ostracod zones (Muñoz-Torres *et al.*, 2006). We have not seen mollusc faunas from localities located in the *Retitricolporites* pollen zone (R). Uncertainties of age estimates typically about +/- 1 Ma in the upper part and +/- 2 Ma in the lower part.

Fig. 4a-p. Stratigraphic indicator species. Specimen data (including collection abbreviations) in Wesselingh (2006). Scale bar = 1 mm. a, RGM 456 538, *Tryonia minuscula* (Gabb, 1869). b, RGM 456 417, *Dyris tricarinata* (Boettger, 1878). c, INGEMMET TN34, *Dyris pebasensis* Wesselingh, 2006. d, RGM 456 485, *Dyris microbispinalis* Wesselingh, 2006. e, RGM 456 568, *Dyris lanceolatus* Wesselingh, 2006. f, RGM 456 472, *Dyris mattii* Wesselingh, 2006. g, RGM 456 633, *Dyris bicarinatus sofiensis* Wesselingh, 2006. h,



RGM 456 394, *Dyris megacarinatus* Wesselingh, 2006. i, RGM 456 554, *Dyris denticulatus* Wesselingh, 2006. j, INGEMMET TN60, *Onobops communis* Wesselingh, 2006. k, RGM 456 534, *Onobops iquitensis* Wesselingh, 2006. l, RGM 456 380, *Toxosoma carinatum* Wesselingh, 2006. m, RGM 456 324, *Sioliella crassilabra* (Kadolsky, 1980). n, INGEMMET TN04, *Sioliella fusiformis* Wesselingh, 2006. o, RGM 456 337, *Sioliella carinata* Wesselingh, 2006. p, RGM 456 521, *Cochliopina? colombiana* (Nuttall, 1990).

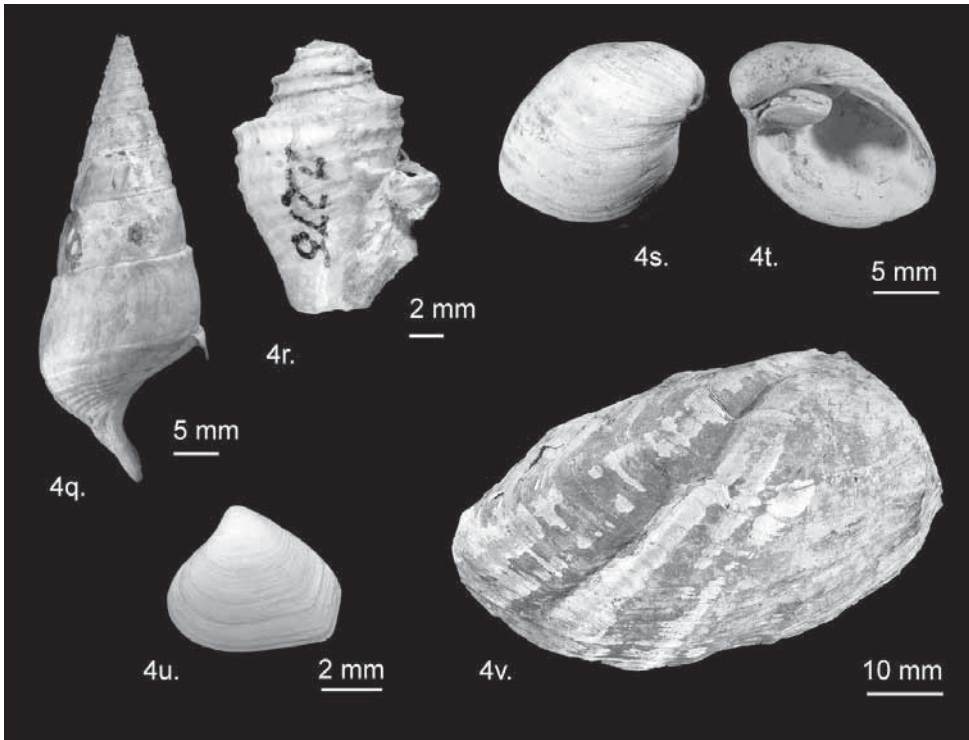
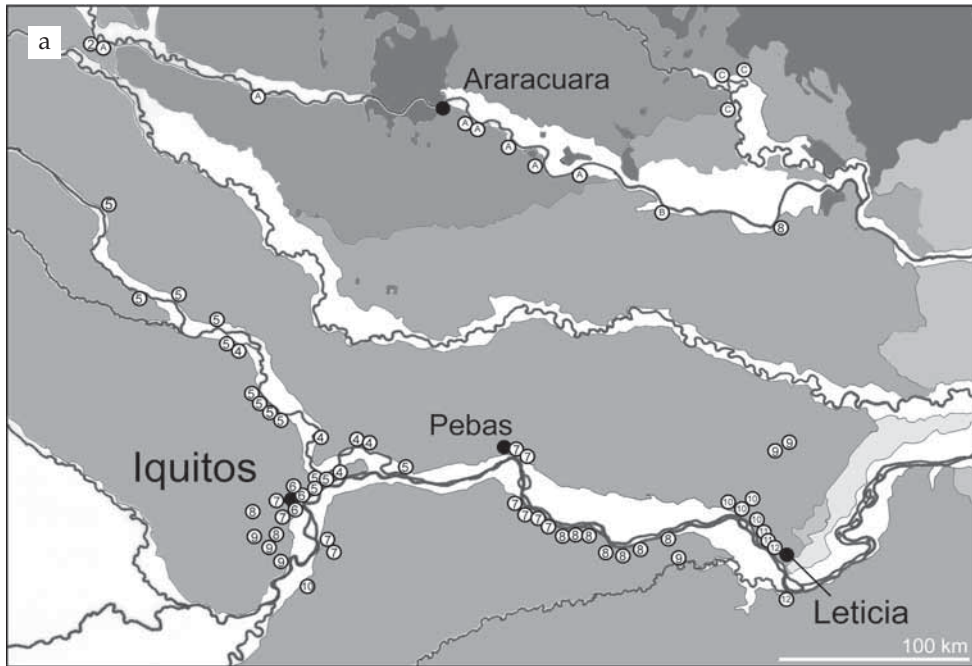


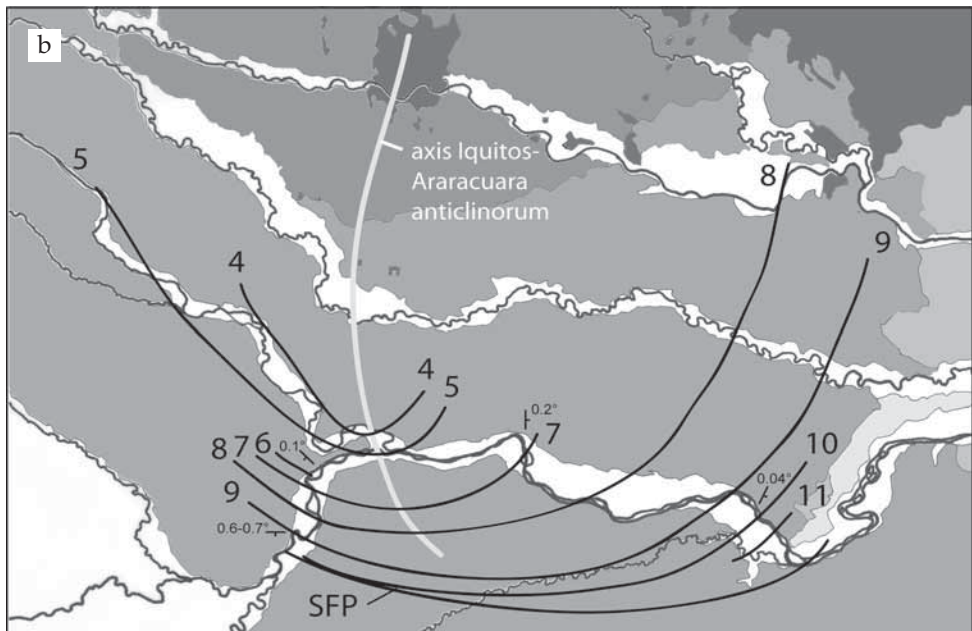
Fig. 4q-u. Stratigraphic indicator species. Specimen data (including collection abbreviations) in Wesselingh (2006). q, INGEMMET TN51, *Sheppardiconcha clavata* Wesselingh, 2006. r, ANSP n.n., *Aylacostoma ava* (Pilsbry & Olsson, 1935). s, t, RGM 456 192, *Pachydon obliquus* Gabb, 1869. u, RGM 456 406, *Pachydon trigonalis* Nuttall, 1990. v, RGM 456 391, *Diplodon indianensis* Wesselingh, 2006.

Fig 5. a, Distribution of mollusc zones in Pebas Formation outcrops in western Amazonia. Numbers refer to mollusc zones. Characters refer to pollen zones (Hoorn, 1994a, 2006). Key; a = *Retitricolporites-Psiladiporites/Crototricolpites* zones; b = *Crassoretitriletes* zone; c = *Grimsdalea* zone. Northern limit of outcrops of Pebas Formation in Colombia adapted from Hoorn (1994a). Eastern limit of outcrop of Pebas/Solimões Formation adapted from Rosetti *et al.* (2005). Note that the zone where the Pebas Formation is present near the surface, thin (typically <10 m) late Neogene and Quaternary fluvial deposits can be present. These have not been indicated. In the Tigre-Nauta area, as well as south of the Javari River, younger Neogene deposits ('Nauta Formation', upper Solimões Formation) have been included in the Pebas/Solimões Formation. b, Spatial distribution of stratigraphic zones. The southernmost line (SFP) indicates the southern boundary of occurrences of Pebas-type of fossils in outcrops. Direction of dip is very crudely only.





- |                               |                                  |
|-------------------------------|----------------------------------|
| Late Quaternary floodplains   | Pebas/Solimões/Marañon Formation |
| Quaternary terrace formations | Mariñame/Apaporis Sand Unit      |
| Iça Formation                 | Paleozoic/Precambrian basement   |



Madre de Dios Formation (Räsänen *et al.*, 1996; Campbell *et al.*, 2001; Gingras *et al.*, 2002; Hoviskoski *et al.*, 2005). Radiometric ages of  $9.01 \pm 0.28$  Ma (Campbell *et al.*, 2001) and  $9.31 \pm 3.4$  Ma,  $8.8 \pm 3.2$  Ma and  $7.91 \pm 1.2$  Ma (Hermoza, 2005) from these latter deposits are in agreement with the early Late Miocene age of the upper parts of the Pebas Formation. Another corroboration for the age estimates is the correlation of the occurrence of *Aylacostoma browni* in the Mangan Formation of the Cuenca basin (dated between 11.5 and 8.3 Ma; Steinmann *et al.*, 1999) with its occurrence in MZ9 up to MZ12 in the Pebas Formation.

### Regional distribution of stratigraphic zones

Mollusc zones to which outcrops are assigned (Fig. 5a; Appendix 2) show a clear regional pattern in their distribution that reveals the structure of the subsurface in the fieldwork area. In several long sections we observed very low structural dips that confirm the regional trends depicted in Figure 5b. In general, mollusc zones are located from old to young along transects, and the very low angle dips measured in field sections also conform the regional dip. Within series of outcrops, structural undulations have been observed of a few metres. Only slightly to the west, along the Ecuadorian Curaray, a locality yielded a fauna that is older than might be expected (Fig. 6; Appendix 2). However, seismic surveys in that area (Balkwill *et al.*, 1995) show locally strong folding and doming of Neogene deposits in the subsurface near the outcrop along the Curaray River.

The distribution of mollusc zones in the fieldwork area reveals a broad anteklise-like structure, with younger strata outcropping to the southwest and southeast. The axis of this structure is located near the Napo-Amazon confluence and plunges from there to the southeast. Towards the north the axis appears to connect to basement outcrops in the vicinity of Araracuara in Colombia (Fig. 5b). The structure is indicated here as the Iquitos-Araracuara anteklise.

Outcrops assigned to the oldest mollusc zones (MZ1-3) are known only from the Intra- and Subandean zones of Colombia, the Oriente basin of Ecuador, and the Marañon and Ucayali basins of Peru (Appendix 2; Wesselingh *et al.*, 2006a). However, organic-bearing horizons in the lower part of the Pebas/Solimões Formation studied in Brazilian wells (Hoorn, 1993; Leite, pers. comm.) contain pollen assemblages representing wetland settings during the Early Miocene (approximately the MZ1-MZ3 time span), indicating that the early 'Pebas' system already occupied larger pericratonic regions as well.

Although most of the Pebas Formation mollusc zones (MZ4-MZ9) appear to be restricted to the fieldwork area, well data from the Pastaza area in Peru (Wesselingh *et al.*, 2006a), samples seen from Brazilian wells in the Solimões and Acre basins (unpublished data), as well as two outcrops in the Peruvian Andean zone (Fig. 6; Appendix 2) indicate a wide geographic distribution of these zones. The two youngest zones (MZ11-MZ12) have been found only in the eastern part of the fieldwork area. This implies that the Pebas system originated in the Andean foreland basin zone in response to Andean uplift (indicated by heavy mineral content of the sedimentary rocks as well as low amounts of Andean pollen types). It rapidly expanded over the cratonic edge occupying the entire study area as a vast wetland and only during the (early) Late Miocene did it become replaced by overlying fluvial units from the west.

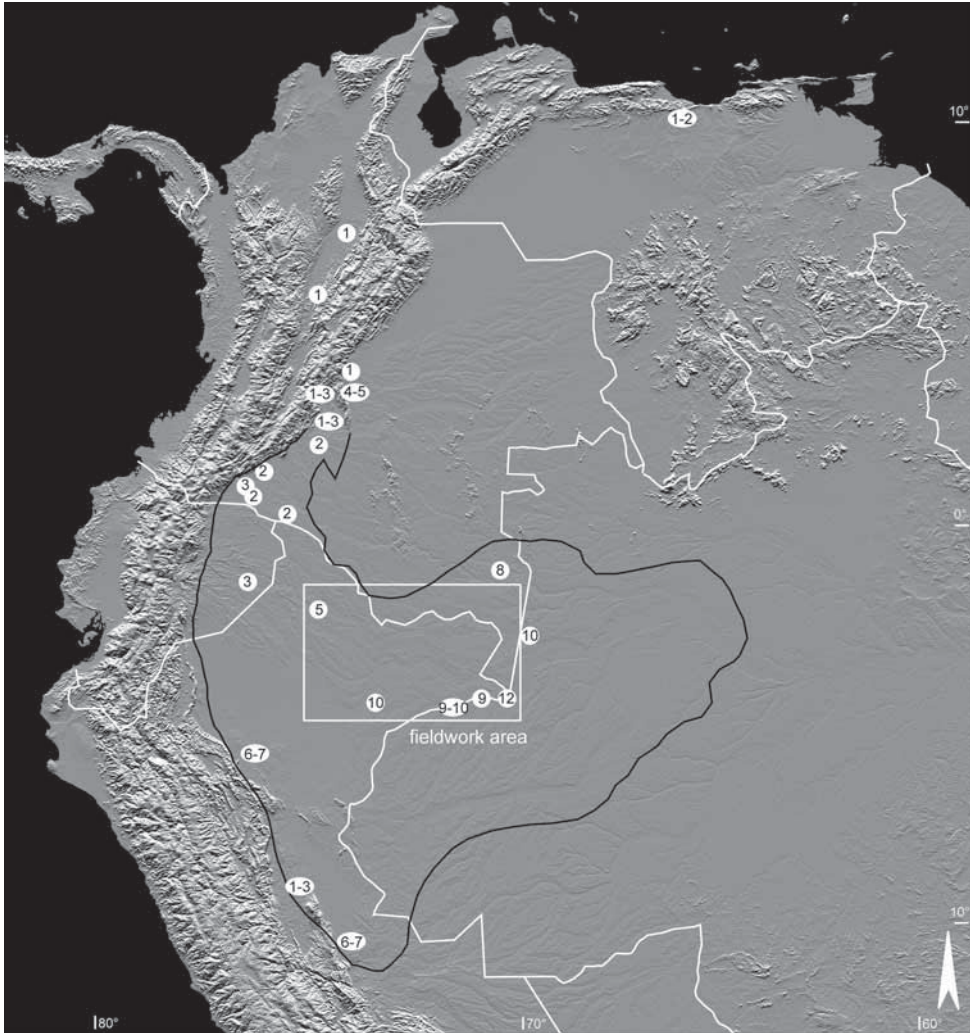


Fig. 6. Spatial distribution of stratigraphic zones outside the fieldwork area (see Appendices 1 and 2 for data). The black line depicts the limits of the Pebas system (following Wesselingh *et al.*, 2002).

## Discussion

Considerable scientific debate exists over the amount of marine influence in the Pebas system (see Wesselingh *et al.*, 2002, 2006b; Gingras *et al.*, 2002; Vonhof *et al.*, 1998, 2003, for different opinions). When it comes to the molluscs, marine influence is shown by the presence of marine taxa and by a marine signal in their strontium isotope ratios (Vonhof *et al.*, 1998, 2003; van Aartsen & Wesselingh, 2000, 2005; Vermeij & Wesselingh, 2002). The fauna and the strontium isotope ratios point in concert to maximum salinities of c. 5 per mil in only very few layers that are restricted to the MZ9 zone. Marginal marine molluscs occur very rarely in other intervals (especially in MZ10), but they are

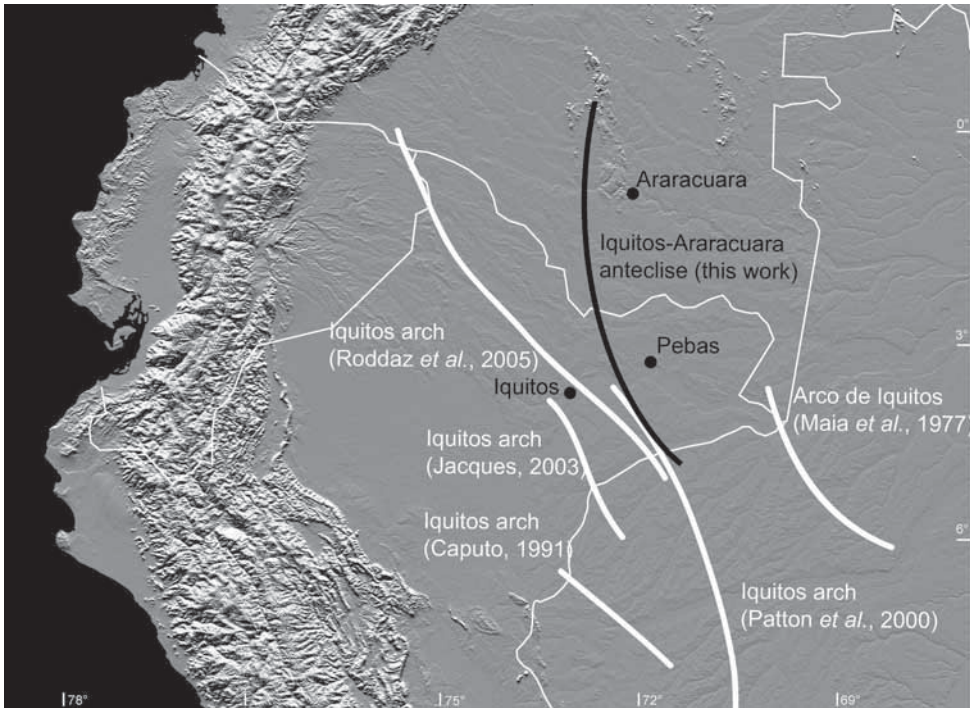


Fig. 7. The location of the Iquitos arch as proposed by various authors and the location of the Iquitos-Araracuara anteclise as proposed in this work.

usually diminutive and the strontium isotope ratios show no elevated salinities in such specimens.

The Iquitos-Araracuara anteclise is apparent from the surface distribution of mollusc zones. It is tempting to consider this structure to be the so-called 'Iquitos arch'. The exact location of the Iquitos arch has shifted in various publications over the past decades over hundreds of kilometres (Fig. 6). The Arco de Iquitos of Maia *et al.* (1977) was based on the mapping of the depth of the basement from borehole data. The basin threshold they called the Arco de Iquitos was later renamed (Caputo, 1991) as the Carauari arch. The location of the Iquitos arch by Patton *et al.* (2000) was a mere interpretation to fit a zoogeographical break these authors encountered in the Juruá valley. The Iquitos arch as proposed by Caputo (1991) was based on a combination of seismic surveys and gravimetric data. The background for the Iquitos arch of Jacques (2003) is unclear. The latest documentation of the Iquitos arch by Roddaz *et al.* (2006) shows a line following from Iquitos along the Napo to the northwest (Fig. 7). This is based on a zone of positive magnetic anomalies. The Iquitos arch is defined by Roddaz *et al.* (2006) as an anticlinal structure, separating different post-Pebasian formations on the western and eastern flanks. Although the lineament of positive anomalies seems real, the anticline interpretation is not compatible with the surface architecture of the mollusc zones. Possibly, the northwest-southeast gravity lineament reflects extinct (Mesozoic-Paleogene) forebulge remains in the subsurface. The lineament is located in an area where



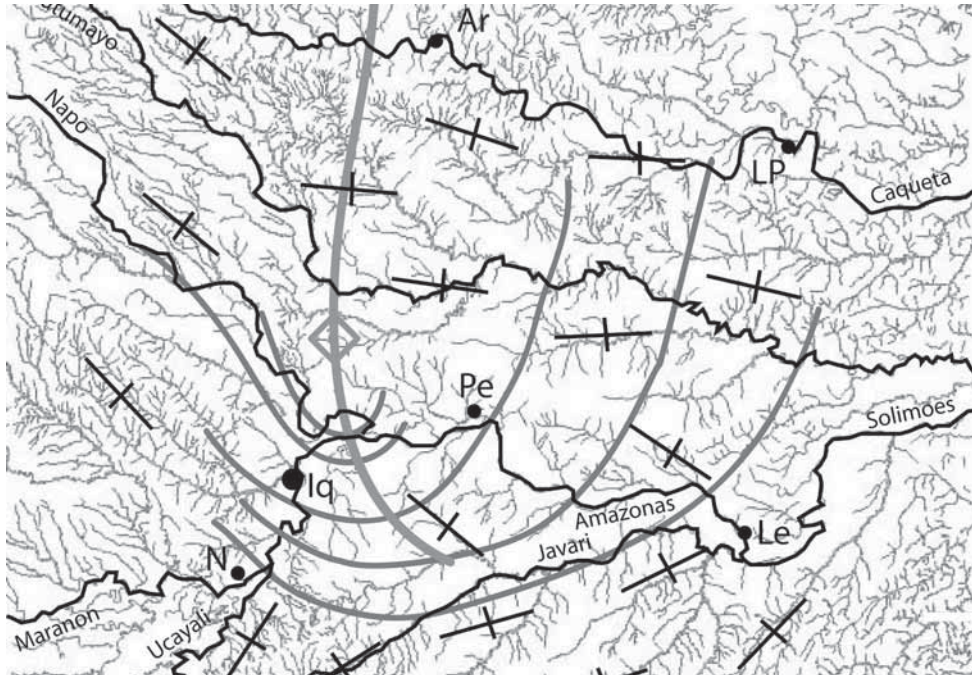


Fig. 8. Geological architecture in the study area and river courses. The dark lines are isochronous mollusc zones, in light grey the axis of the Iquitos-Araucara antecline, and in dark grey are the main and secondary directions of second and lower order rivers. The background figure with the river patterns has been made available by M. Roddaz. Key: Ar = Araucara; Le = Leticia; LP = La Pedrera; Pe = Pebas; Iq = Iquitos; N = Nauta). Rivers in active fluvial areas (in the Amazon valley and the Pastaza fan upstream Nauta) have no relationship with the architecture of subsurface Neogene units.

Palaeozoic and Precambrian basement dips steeply away into the foreland basin zone.

There is an apparent match of directions of second and lower order rivers and the structure of the Pebas zones (Fig. 8). In the western part of the fieldwork area (Napo-Tigre area extending to the Tamshiyacu River), rivers trend clearly northwest-southeast, conforming the trend of the beds with the mollusc zones. In the area between the Boca Napo/Pebas and the Yavari rivers trend east-northeast to west-southwest, also matching the trends of the MZ outcrop belts. The Boca Napo (the winding, and odd, lower 100 km of the Napo River above its confluence with the Amazon River) appears to be located in the axis of the antecline. These patterns suggest that the structure of the basement and the Miocene strata underlying the fieldwork area has had considerable influence in the determination of the course of second and lower order rivers since the Late Miocene Andean and pericratonic uplift.

### Conclusions

A mollusc biozonation is proposed for Miocene deposits of northwestern Amazonia, with emphasis on the Pebas Formation. The Pebas system originated in the Sub-

Andean region in the Early Miocene, and rapidly expanded to the east to cover pericratonic and cratonic areas. Only near the end, during the early Late Miocene, the system was replaced from the west by the transcontinental Amazon River system. Marine influence based on the combined occurrence of marine mollusc taxa and indicative strontium isotope ratios representing oligohaline salinities is restricted to a single mollusc zone only. The geographical distribution of mollusc zones reveals a large structure, the Iquitos-Araracuara antecline. This structure does not conform the location of the 'Iquitos arch' of other authors. Second and lower order river courses in the fieldwork area appear to conform the general directions of the mollusc zone outcrop belts.

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### Appendix 1: Locality data

Coordinate estimates indicated with GNS are estimates from the NGA Geographic Names Server (<http://gnswww.nga.mil/geonames/GNS/index.jsp>). Collection abbreviations: ANSP, Academy Natural Sciences, Philadelphia, U.S.A.; CAS, California Academy of Sciences, San Francisco, U.S.A.; INGEMMET, Instituto Geológico, Minero y Metalúrgico, Lima, Peru; NMNH, National Museum of Natural History, Washington, D.C., U.S.A.

#### Colombia, Cundinamarca dept.

*San Juan RioSeco* – Quebrada RioSeco, 1 km upstream from bridge, c. 1.5 km north-east of San Juan.

#### Colombia, Caqueta dept.

*Betania* – Vereda Betania, Finca de Alberto Montoya, 200 m from the school at well, Municipio de San Vicente del Caguan, c. 2°20'N; 74°43'W (GNS). Leg. J. Saldariaga, 1991. La Tagua Beds (now included in Pebas Formation).

#### Colombia, Putumayo dept.

*La Tagua* – c. 0°03'S; 74°40'W (GNS). Leg. M.C. Hoorn, 1987. Outcrop in south bank of Caqueta River at the village. La Tagua Beds (now included in Pebas Formation).

#### Colombia, Amazonas dept.

All localities are assigned to the Pebas Formation. Coordinates estimated from local topographic maps.

*Buenos Aires* – Outcrop in south bank of Cotuhé River, below village, c. 70°25'W; 3°23'S. Leg. F.P. Wesselingh, 9-1991.

*Los Chorros I* – Outcrop north bank Loreto-Yacu River, at confluence with Amazon River, c. 70°22'W; 3°46'S. Leg. F.P. Wesselingh, 9-1991.

*Los Chorros III* – Outcrop north bank Amazon River, c. 1.3 km east of Los Chorros I, c. 70°21'W; 3°46'S. Leg. F.P. Wesselingh, 9-1991.

*Macedonia* – Outcrop in north bank Amazon River, c. 500 m west of landing stage, c. 70°15'W; 3°48'S. Leg. F.P. Wesselingh, 9-1991.

*Mocagua I* – Outcrop in north bank Amazon River, below school, c. 70°17'W; 3°48'S. Leg. F.P. Wesselingh, 9-1991.

*Mocagua II* – Outcrop in north bank Amazon River, c. 1 km east of Mocagua I, c. 70°17'W; 3°48'S. Leg. F.P. Wesselingh, 9-1991.

*Mocagua III* – Outcrop in north bank Amazon River, c. 300 m east of Mocagua II, below land house, c. 70°17'W; 3°48'S. Leg. F.P. Wesselingh, 9-1991.

*Puerto Nariño I* – Outcrop north bank Loreto-Yacu River, c. 1 km east of port, c. 70°22'W; 3°46'S. Leg. F.P. Wesselingh, 9-1991.

*Salado del Pamaté* – Outcrop in Salado (well), c. 2 km east of Quebrada Pamaté, c. 70°23'W; 3°23'S. Leg. F.P. Wesselingh, 9-1991.

*Santa Sofia* – Outcrop in north bank Amazon River, c. 3 km northwest of village below land-house, at northwestern tip of Isla Santa Sofia, c. 70°09'W; 3°57'S. Leg. F.P. Wesselingh, 9-1991.

*Villareal* – Outcrop in north bank Amazon River, at landing stage, c. 70°13'W; 3°50'S. Leg. F.P. Wesselingh, 9-1991.

*Zaragoza* – Outcrop in north bank Amazon River, 300 m east of landing stage, c. 70°11'W; 3°52'S. Leg. F.P. Wesselingh, 9-1991.

### Peru, Loreto dept.

All localities are assigned to the Pebas Formation. Coordinates estimated from radar maps (IFG, 1984) unless stated otherwise.

*Barradero de Omagua I* – Outcrop in east bank Itaya River, below village, c. 73°23'W; 4°10'S. Leg. F.P. Wesselingh, 13-9-1996.

*Beiruth* – Outcrop in south bank Amazon River below village, c. 71°28'W; 3°53'S. Leg. F.P. Wesselingh, 27-8-1996.

*Boca Momon* – Outcrop in north bank Rio Momon, 300 m upstream from confluence with Nanay River, c. 73°15'W; 3°41'S. Leg. F.P. Wesselingh, 12-8-1996.

*Boca Napo I* – Outcrop in north bank of Napo River, c. 2 km east of confluence Rio Socosani, 100 m west of church on hill, c. 72°53'W; 3°17'S. Leg. F.P. Wesselingh, 23-9-1996.

*Buen Pasa I* – Outcrop in east bank Napo River, c. 1 km east of village, near confluence with stream, c. 73°11'W; 3°15'S. Leg. F.P. Wesselingh, 30-9-1996.

*Buen Pasa II* – Outcrop in east bank Napo River, 800 m east of village, c. 73°11'W; 3°15'S. Leg. F.P. Wesselingh, 30-9-1996.

*Chimbote I* – Outcrop in south bank of Amazon River, c. 0.5 km west of village, c. 70°45'W; 3°55'S. Leg. F.P. Wesselingh, 26-8-1996.

*Chimbote III* – Outcrop in south bank of Amazon River, c. 1.5 km west of village, c. 70°46'W; 3°55'S. Leg. F.P. Wesselingh, 26-8-1996.

*Condor* – Outcrop in south bank Amazon River, c. 71°41'W; 3°44'S. Leg. F.P. Wesselingh, 29-8-1996.

*Copal Urco I* – Outcrop in east bank Napo River, 500 m south of confluence with Rio Urco, c. 23°47'W; 2°20'S. Leg. F.P. Wesselingh, 26-9-1996.

*Fortaleza* – Outcrop in south bank Napo River, W-end of exposure, c. 73°36'W; 2°31'S. Leg. F.P. Wesselingh, 29-9-1996.

*Indiana I* – Outcrop in west bank Amazon River, 200 m N of port, c. 73°02'W; 3°29'S. Leg. F.P. Wesselingh, 7-8-1996.

*Indiana II* – Outcrop in west bank Amazon River, 3.1 km south of village, 150 m N of Barradero de Mazan, c. 73°05'W; 3°31'S. Leg. F.P. Wesselingh, 8-8-1996/15-8-1996.

*Indiana III* – Outcrop in west bank Amazon River, 1.2 km south of port, c. 73°03'W; 3°30'S. Leg. F.P. Wesselingh, 8-8-1996.

*Indiana IV* – Outcrop in west bank Amazon River, 1.4 km south of port, 200 m south of Indiana III. Leg. F.P. Wesselingh, 8-8-1996; 1-9-1996.

*Indiana V* – Outcrop in west bank Amazon River, 1.65 km south of port, 250 m south of Indiana IV, at stair to tourist lodge. Leg. F.P. Wesselingh, 8-8-1996.

*Indiana VI* – Outcrop in west bank Amazon River, 1.9 km south of port, 250 m south of Indiana V. Leg. F.P. Wesselingh, 8-8-1996.

*Indiana VII* – Outcrop in west bank Amazon River, 2.3 km south of port, 400 m south of Indiana VI, at stream inlet. Leg. F.P. Wesselingh, 8-8-1996.

*Iquitos-Itaya* – Outcrop in west bank Itaya River, 500 m south of port of Belem, at factory, c. 73°15'W; 3°46'S. Leg. F.P. Wesselingh, 13-8-1996.

*Iquitos Puerto Ganso-Azul* – Outcrop in harbour, below market, at 'grifos', c. 73°11'W; 3°45'S. Leg. F.P. Wesselingh, 10-1991.

*Itaya III* – Outcrop in east bank Itaya River, c. 73°23'W; 4°05'S. Leg. F.P. Wesselingh, 13-9-1996.

*Mayoruna II* – Outcrop in south bank Amazon River 200 m south of confluence with Rio Nuevo Octubre, c. 71°12'W; 3°58'S. Leg. F.P. Wesselingh, 27-8-1996.

*Mishana* – Outcrop in south bank Nanay River, 100 m west of landing stage, c. 73°29'W; 3°52'S. Leg. F.P. Wesselingh, 10-1991.

*Nueva Paleta II* – Outcrop in south bank Napo River, 1 km east of Nueva Paleta I, 2 km west of Negro Urco, c. 73°25'W; 3°00'S. Leg. F.P. Wesselingh, 30-9-1996.

*Nuevo Horizonte I* – Temporary road cut (east wall) Iquitos-Nauta road, km 45.2 (from Iquitos), in village, c. 73°25'W; 4°05'S. Leg. F.P. Wesselingh, 10-1991.

*Nuevo Horizonte II* – Temporary road cut (east wall) Iquitos-Nauta road, km 45.4 (from Iquitos), 200 m south of village, c. 73°25'W; 4°05'S. Leg. F.P. Wesselingh, 16-9-1996.

*Nuevo Horizonte III* – Temporary road cut (west wall) Iquitos-Nauta road, km 43 (from Iquitos), c. 2 km N of village, c. 73°26'W; 4°02'S (73°26'2''W; 4°02'16''S. GPS). Leg. F.P. Wesselingh, 16-9-1996.

*Nuevo Horizonte IV* – Temporary road cut (west wall) Iquitos-Nauta road, km 42 (from Iquitos), c. 500 m N of outcrop Nuevo Horizonte III. Leg. F.P. Wesselingh, 16-9-1996.

*Palo Seco* – Outcrop in west bank Itaya River, c. 73°22'W; 4°00'S. Leg. F.P. Wesselingh, 13-9-1996.

*Pebas III (Quebrada Pijoyal)* – Outcrop in north bank Amazon River, 350 m east of naval base Pijoyal (base at 3°20'S, 71°50'W). Leg. F.P. Wesselingh, 31-8-1996.

*Pebas VI (Ave Maria III)* – Outcrop in north bank Amazon River, 900 m east of naval base Pijoyal (base at 3°20'S, 71°50'W). Leg. F.P. Wesselingh, 31-8-1996.

*Pebas IV (Pijoyal II)* – Outcrop in north bank Amazon River, 250 m east of naval base Pijoyal (base at 3°20'S, 71°50'W). Leg. F.P. Wesselingh, 31-8-1996.

*Pebas IX (Ave Maria II)* – Outcrop in north bank Amazon River, 1350 m east of naval base Pijoyal (base at 3°20'S, 71°50'W). Leg. F.P. Wesselingh, 21-8-1996.

*Pebas XI (Santa Julia II)* – Outcrop in north bank Amazon River, 1650 m east of naval base Pijoyal (base at 3°20'S, 71°50'W). Leg. F.P. Wesselingh, 22-8-1996.

*Pebas XIII (Santa Julia IV)* – Outcrop in north bank Amazon River, 2250 m east of naval base Pijoyal (base at 3°20'S, 71°50'W). Leg. F.P. Wesselingh, 23-8-1996.

*Pebas XVII (Tarma)* – Outcrop in north bank Amazon River, 6500 m east of naval base Pijoyal, c. 71°47'W; 3°22'S. Leg. F.P. Wesselingh, 23-8-1996.

*Porvenir Amazon II* – Outcrop in west bank Amazon River, 50 m north of southernmost outcrop in village, 73°22'19''W; 4°13'44''S (GPS). Leg. F.P. Wesselingh, 5-9-1996.

*Porvenir Amazon IV* – Outcrop in west bank Amazon River, 250 m north of Porvenir Amazon II. Leg. F.P. Wesselingh, 5-9-1996.

*Puerto Almendras* – Outcrop in east bank Nanay River, 25 m north (downstream) of port, c. 73°22'W; 3°49'S. Leg. F.P. Wesselingh, 15-9-1996 (F835). Outcrop at port. Leg. F.P. Wesselingh, 10-1991 (F73).

*San Antonio/ Itaya II* – Outcrop in west bank Itaya River, at north side village, c. 73°23'W; 4°01'S. Leg. F.P. Wesselingh, 13-9-1996.

*San Francisco* – Outcrop south bank Amazon River, c. 71°43'W; 3°43'S. Leg. F.P. Wesselingh, 29-8-1996.

*San Lorenzo* – Outcrop in south bank Napo River, at cape 100 m west of village at east end of exposure, c. 1 km east of Fortaleza, c. 73°35'W; 2°32'S. Leg. F.P. Wesselingh, 29-9-1996.

*San Miguel de Cochiquinas* – Outcrop in south bank Amazon River, c. 1.5 km downstream from confluence Rio Cochiquinas, c. 71°36'W; 3°47'S. Leg. F.P. Wesselingh, 28-8-1996.

*Santa Elena I* – Outcrop in south bank Amazon River, 1 km west of Santo Tomas Amazonas, c. 71°23'W; 3°52'S. Leg. F.P. Wesselingh, 27-8-1996.

*Santa Elena II* – Outcrop in south bank Amazon River, 500 m west of Santa Elena I, c. 71°23'W; 3°52'S. Leg. F.P. Wesselingh, 28-8-1996.

*Santa Elena III* – Outcrop in south bank Amazon River, 600 m west of Santa Elena II, c. 71°24'W; 3°53'S. Leg. F.P. Wesselingh, 28-8-1996.

*Santa Elena/Tamshiyacu* – Outcrop in south bank of Quebrada Tamshiyacu, c. 73°05'W; 4°04'S. Leg. F.P. Wesselingh, 22-9-1996.

*Santa Julia* – Outcrop in north bank Amazon River, 2550-2650 m east of naval base Pijoyal (base at 3°20'S, 71°50'W). Leg. F.P. Wesselingh, 10-1991/31-8-1996.

*Santa Rosa de Pichana* – Outcrop west bank Amazon River, c. 200 m south of confluence with Rio Pichana, c. 71°46'W; 3°40'S. Leg. F.P. Wesselingh, 30-8-1996; R.J.G. Kaandorp & H.B. Vonhof, 1998.

*Santa Teresa I* – Outcrop west bank Amazon River below village, c. 73°00'W; 3°29'S. Leg. F.P. Wesselingh, 1-9-1996; 7-8-1996.

*Santa Teresa IIa* – Outcrop in west bank Amazon River, 200 m north of village, at stream inlet, c. 73°00'W; 3°29'S. Leg. F.P. Wesselingh, 7-8-1996.

*Santa Teresa Tacsha* – Outcrop in west bank Napo River, c. 2 km below confluence with Rio Tacsha Curaray, c. 73°33'W; 2°50'S. Leg. F.P. Wesselingh, 29-9-1996.

*Santo Tomas/ Amazonas* – Outcrop in south bank of Amazon River, at west tip of Isla San Isidro, c. 71°22'W; 3°52'S. Leg. F.P. Wesselingh, 27-8-1996.

*Santo Tomas/ Nanay* – Outcrop in west bank Nanay River, c. 1 km westnorthwest of port of Bellavista Nanay, c. 73°15'W; 3°41'S. Leg. F.P. Wesselingh, 3-8-1996.

*Socosani I* – Outcrop in north bank Napo River, 200 m west of confluence with Rio Socosani, c. 72°56'W; 3°16'S. Leg. F.P. Wesselingh, 1-10-1996.

*Tamshiyacu* – Outcrop in east bank Amazon River, 500 m east of port, c. 73°09'W; 4°01'S. Leg. F.P. Wesselingh, 2-9-1996; 8-9-1996.



## Appendix 2: Other material studied

### Colombia, Meta dept.

*Rio Bravo* – Circa 3°10′-3°44′N; 74°18′-75°56′W (GNS). Leg. Shell. Coll. ANSP. MZ4-MZ5, based on the occurrence of *Pachydon obliquus* Gabb, 1869, *P. ledaeformis* (Dall, 1872), *P. carinatus* Conrad, 1871 (an elongate, slightly bilobed form only seen in MZ4-MZ5 samples from Peruvian Loreto), *P. erectus* Conrad, 1871, and *Exallocorbula dispar* (Conrad, 1874). Unnamed beds.

*Rio La Cal* – Quebrada Natania, c. 3°32′N; 73°46′W (GNS). Leg. O. Reny, Shell. Coll. ANSP. MZ3, based on the occurrence of *Pachydon cf. obliquus*, *P. cf. hettneri* (Anderson, 1928), *P. cf. carinatus* and *P. cf. erectus*. Unnamed beds.

*Rio Guayeburo* – Circa 2°36′-3°14′N; 72°47′-75°30′W (GNS). Leg. unknown. Coll. ANSP. MZ1-MZ3, based on the occurrence of *Pachydon hettneri*. Sample indicated with ‘San Fernando Formation’ (now assigned to Leon Formation).

*El Guape* – Circa 3°10′N; 74°19′W (GNS). Leg. ?O. Reny, Shell. Coll. ANSP. MZ1-MZ3, based on the occurrence of *Pachydon hettneri* and *P. cf. cebada* (Anderson, 1928). Unnamed beds.

*Rio Guape* – Circa 3°10′-3°31′N; 73°45′-74°19′W (GNS). Leg. ?O. Reny, Shell. Coll. ANSP. MZ1-MZ3, based on the occurrence of *Pachydon hettneri* and *P. cf. cebada*. Unnamed beds.

*San Juan de Arama* – Circa 3°24′N; 73°49′W (GNS). Leg. Shell. Coll. ANSP. MZ1, based on the occurrence of *Aylacostoma ava* (Pilsbry & Olsson, 1935). ‘San Fernando Formation’ (now assigned to Leon Formation).

### Colombia, Caqueta dept.

*Rio Heroru* – Also known as Rio Tuña, c. 1°30′N; 73°55′W (GNS). Leg. unknown. Coll. ANSP. MZ3, based on the occurrence of *Pachydon cf. obliquus*, *P. hettneri*, *P. cf. carinatus* and *P. cf. cebada*. Unnamed beds.

*Rio Ortegua* – Circa 0°43′N; 75°16′W (GNS). Leg. unknown. Coll. ANSP. MZ3, based on the occurrence of *Pachydon hettneri*, *P. cf. obliquus* and *P. cf. cebada*. Unnamed beds.

*Macagua* – Circa 0°56′N; 75°32′W (GNS). Leg. O. Reny, Shell. Coll. ANSP. MZ3, based on the occurrence of *Pachydon hettneri*, *P. cf. erectus* and *P. cf. carinata*. Unnamed beds.

*Rio Pescado* – Circa 1°13′-2°24′N; 74°56′-75°31′W (GNS). Leg. A.A. Olsson, Standard Oil. Coll. ANSP. MZ2, based on the occurrence of *Pachydon hettneri*, *P. cf. erectus*, *P. cf. cebada*, *Sheppardiconcha colombiana* (Nuttall, 1990), *S. cf. lataguensis* Nuttall, 1990, and *Dyris denticulatus* Wesselingh, 2006. Unnamed beds.

### Colombia, Putumayo dept.

*Rio Mecayas* – Circa 0°28′-0°59′N; 75°12′-75°20′W (GNS). Leg. unknown. Coll. ANSP. MZ1-MZ3, based on the occurrence of *Pachydon hettneri*. Unnamed Beds.

*Jose Maria Hernandez* – Quebrada Jose Maria, c. 0°53′N; 77°37′W (GNS). Leg. A.A. Olsson, Texas Oil Company. Coll. ANSP. MZ2, based on the occurrence of *Shepp-*

*ardiconcha colombiana*, *S. lataguensis*, *Aylacostoma* cf. *lataguensis* (Nuttall, 1990), *Pachydon* cf. *cebada*. Unnamed Beds.

### Colombia, Amazonas dept.

*Puerto Caiman* – Outcrop on the south bank of the Caqueta River, c. 01°34'05"S; 070°01'59"W (GNS). Leg. M.C. Hoorn, 1987. Zone MZ8, based on the occurrence of *Feliconcha feliconcha* Wesselingh, 2006, *Dyris regularis* Wesselingh, 2006, *Littoridina conica* Wesselingh, 2006, and *Sioliella saloi* Wesselingh, 2006.

### Peru, Loreto dept.

*Canamá* – North bank of Rio Yavarí, c. 80 km upstream from Benjamin Constant. Leg. B. Brown. Coordinates 5°38'35"S; 72°05'23"W (see Nuttall, 1990, p. 327). Coll. BMNH. MZ9, based on the occurrence of *Aylacostoma browni* (Etheridge, 1879), *Toxosoma grande* Wesselingh, 2006, *Pachydon trigonalis* Nuttall, 1990, *Tryonia scalarioides scalarioides* (Etheridge, 1879) and *Neritina puncta* (Etheridge, 1879).

*Três Unidos* – Circa 4°42'S; 71°13'W, north bank of Rio Yavarí, c. 80 km west-southwest from Canamá (Nuttall, 1990, p. 329). Leg. Oliveira & Carvalho, 1924, fauna published in Roxo 1924. MZ9-MZ10, based on the occurrence of *Aylacostoma browni*, *Toxosoma grande*, *Nassarius reductus* Vermeij & Wesselingh, 2002, and *Melongena woodwardi* (Roxo, 1924).

*Puerto Elvira* – Circa 2°02'04"S; 74°33'37"W. Leg. H. Bassler, Coll. NMHM. Sample indicated with F221. MZ5, based on the occurrence of *Diplodon indianensis* Wesselingh, 2006.

*Nuevo Valentin* – Outcrop in north bank Quebrada Valentin, c. 73°10'W; 4°11'S (O. Coomes pers. comm.). Leg. O. Coomes, 10-1996. MZ10 based on the occurrence of *Pachydon trigonalis* (dominant), *Aylacostoma browni*, and *Dyris carinatus* Wesselingh, 2006.

*Puerto Miguel* – Section along the Rio Paranapura, west of Yurimaguas (no details given). Chambira Formation (Sanchez *et al.*, 1997). MZ6-MZ7 based on the occurrence of *Sioliella woodwardi* (Kadolsky, 1980, coll. INGEMMET)

*7 de Julio* – 73°07'W; 4°23'S (GPS). Leg. H. Tuomisto, K. Ruokolainen and J. Vormisto, 1997. MZ8 based on the occurrence of *Dyris pebasensis* Wesselingh, 2006.

### Peru, Ucayali dept.

*Shepahua* – Outcrop in east bank of Rio Urubamba, below the community of Bufo Pozo. Coordinates (GNS): 73°04'W; 11°10'S. Sample studied at INGEMMET (1996). Contamana II or Contamana III Formation (Romero Pittman, 1997). MZ6-MZ7 based on the occurrence of *Toxosoma eboreum* (Conrad, 1874).

### Peru, Huanuco dept.

*Rio Pachitea 1* – Station 269, 2 miles (c. 3 km) downstream from Isla de Santa Isabel, c. 9°35'S; 74°35'W (Singewald, 1928). MZ1-MZ3, based on the occurrence of *Pachydon hettneri* (*Corbicula* spec. indet. in Pilsbry, 1944, p. 146, pl. 11, fig. 36) and *P. cebada* (pl. 11, fig. 34 as Bivalve indet.). Leg. J. Singewald, 1926. "Red Beds".

*Rio Pachitea 2* – Station 154, about 1 mile (c. 1.5 km) upstream from Quebrada Sun-garillo, c. 9°14'S; 74°35'W (Singewald, 1928). MZ1-MZ3, based on the occurrence of *Pachydon cebada* (*Corbula arcana* Pilsbry, 1944, p. 149, pl. 11, fig. 38). Leg. J. Singewald, 1926. "Red Beds".

#### **Ecuador, Pastaza dept.**

*Rio Curaray* – 47 km west (straight line) from confluence with Rio Cononaco. Leg. J.J. Dozy, 1942. Coll. CAS. Curaray Formation. MZ3, based on *Sheppardiconcha colombiana* and *Dyris orton* Gabb, 1869.

#### **Brazil, Alto Amazonas dept.**

*Benjamin Constant* – Outcrop in east bank of Javari River at port, c. 4°21'S; 70°02'W (GNS). Leg. M.C. Hoorn, 1987. Pebas Formation. MZ12, based on the occurrence of *Dyris bicarinatus sofiaensis* Wesselingh, 2006.

*Ipiranga* – South bank of Rio Iça, c. 2°59'S; 69°35'W: Nuttall, 1990, p. 359). Solimões Formation. Leg. unknown. MZ10, based on the occurrence *Pachydon trigonalis* (dominant), *Aylacostoma browni* and *Dyris carinatus*.