Cainozoic Research, 1(1-2) (2001), pp. 35-81, November 2002

Lake Pebas: a palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia

F.P. Wesselingh[1,7], M.E. Räsänen[2], G. Irion[3], H.B. Vonhof[4], R. Kaandorp[4], W. Renema[1], L. Romero Pittman[5] & M. Gingras[6]

[1]*Nationaal Natuurhistorisch Museum, P.O. Box 9517, NL-2300 RA Leiden, the Netherlands; e-mail: wesselingh@naturalis.nnm.nl*
[2]*Department of Geology, University of Turku, SF 20014 Turku, Finland*
[3]*Senckenberg Meeresforschungsinstitut, D 26382 Wilhelmshaven, Germany*
[4]*Department of Earth Sciences, Vrije Universiteit, de Boelelaan 1085, NL-1081 HV Amsterdam, the Netherlands*
[5]*INGEMMET, Avenida Canada 1470, San Borja, Lima 12, Peru*
[6] *Department of Geology, University of New Brunswick, P.O. Box 4400, Fredericton-NB E3B#5A3, Canada*
[7]*Biodiversity Centre, University of Turku, SF 20014 Turku, Finland*

Received 20 February 2001; revised version accepted 19 February 2002

The taxonomic composition and palaeoecological signature of molluscan faunas from the Miocene Pebas Formation of Peruvian Amazonia are assessed. The Pebas fauna is almost entirely made up of extinct, obligate aquatic taxa, and is dominated in numbers of species and specimens by endemic cochliopine hydrobiid gastropods and pachydontine corbulid bivalves. Molluscan assemblages are defined and linked to depositional environments. Isotope data from the shells indicate freshwater settings during deposition of the Pebas Formation, with the exception of a few incursion levels that were deposited under oligohaline-mesohaline conditions. Faunal and isotope geochemical data point to a large, long-lived freshwater lake system at sea level with swamps and deltas, open to marine settings in the north (Llanos Basin). Sedimentological data and ichnofossils point to (restricted) marine settings. These different interpretations are discussed, and it is concluded that faunas (including ichnofabrics) from evolutionary isolated and long-lived systems cannot be assessed in a straightforward actualistic mode, using taxa from non-long-lived environments for comparison. Aspects of Lake Pebas are compared with modern depositional environments. Lake Pebas is among the largest and longest-lived lake complexes in Phanerozoic history; it was an important stage for the evolution of endemic molluscan and ostracod faunas. It may have played some role in the transition of marine biota to Amazonian freshwater environments during the Miocene, and likely was an important, hitherto unrecognised, dispersal barrier for terrestrial organisms in northwest South America during the Miocene.

Key words: Palaeoecology, molluscs, Miocene, Amazonia, Pebas Formation, community palaeoecology, long-lived lake, Lake Pebas.

Introduction

In 1869, the American palaeontologist W.M. Gabb reported on a remarkable fossil molluscan fauna from Pebas in Peruvian Amazonia. All but one of the species described by Gabb were new, and the assemblage bore but little resemblance to any modern South American fauna. Almost all species were extinct, but the exquisite preservation of the fauna led Gabb to believe that the fossils were of relatively recent age. Gabb described several taxa whose relatives at present occur in settings with fluctuating salinities, others that are marine, and still others with a freshwater affinity. The question arose in what kind of environment the Pebas molluscs had lived, and given the inferred presence of marine taxa (the gastropod genera *Turbonilla* and *Mesalia* and the bivalve *Corbula*), the origin of marine settings in lowland Amazonia, far away from modern coastal areas, was questioned. Gabb's work was the first of some fifteen papers dealing with the remarkable fossil molluscs from the Pebas Formation of western Amazonia. Different authors came up with different interpretations of the environment that sustained these unusual faunas (terrestrial, freshwater, brackish and/or marine settings) and the origin of possible marine influence (Pacific, southern Atlantic, eastern Atlantic approximately through the course of the present-day Amazon River, and Caribbean).

In 1990, Patrick Nuttall published his seminal monograph on the Neogene molluscs from western Amazonia and adjacent regions (Nuttall, 1990a). He clarified much of the systematic uncertainties that complicated age estimates and environmental interpretations. Based on a meticulous region-wide stratigraphic correlation he assigned a Middle Miocene age to the fauna. Nuttall (1990a) interpreted the depositional environment in Miocene western Amazonia as a continually shifting pattern of streams, swamps and lakes of varying salinity, with marine influence from the north (Caribbean). Nuttall's age assignments were confirmed and refined by Hoorn (1993, 1994a, b) on the basis of pollen. Hoorn concluded that the Pebas Formation included at least three pollen zones, spanning an age between late Early Miocene and early Late Miocene (*c.* 17-10 Ma). Based on pollen and sediments, Hoorn (1994a) interpreted the depositional environment as 'fluviolacustrine with some marine influence'.

The discovery of supposed Miocene tidal deposits in Brazilian Acre (Räsänen *et al.*, 1995) led Webb (1995) to interpret Miocene western Amazonia as part of an intracontinental seaway that would have occupied all major sedimentary basins of inland South America. Webb's views provoked severe criticism (*e.g.*, Hoorn, 1996; Paxton *et al.*, 1996; L.G. Marshall & Lundberg, 1996). Nevertheless, more tidal deposits have been discovered since then in Peruvian Amazonia (Rebata, 1997; Räsänen *et al.*, 1998), and in the Pebas Formation. The predominantly endemic molluscan and ostracod faunas (Nuttall, 1990a; Wesselingh, 1993; Whatley *et al.*, 1996; Muñoz-Torres *et al.*, 1998; Vonhof *et al.*, 1998) conflict with an interpretation as a possible interior seaway environment as proposed by Räsänen *et al.* (1995) and Webb (1995), as well as with fluvio-lacustrine conditions as proposed by Hoorn (1993, 1994a, b). Based on strontium, carbon and oxygen isotopes, as well as on fauna, Vonhof *et al.* (1998) concluded that the Pebas Formation had been deposited in a lacustrine system, occasionally reached by marine incursions. A Caribbean (northerly) origin of the incursions as proposed by Nuttall (1990a) and Hoorn (1994b; see also Hoorn *et al.*, 1995) was supported by these faunal and isotope data. The ostracod fauna from the Pebas Formation was studied by Whatley *et al.* (1996), who proposed a low energetic athalassic (inland-sea) environment, based on the taxonomic composition and exceptional preservation of the ostracod fauna. Compilations of Pebas molluscan taxa autecological signatures, such as provided by Nuttall (1990a, table 2) and Vonhof *et al.* (1998, table 1) show an admixture of (inferred) ecological preferences. Almost all species from the Pebas Formation are extinct, and several of the genera dominating the fauna are extinct or have survived as relics only (Wesselingh, 2000), limiting their actualistic ecological use. This has complicated insight into the environmental system in which these faunas lived.

The aim of the present paper is to assess the palaeoenvironment in which the Pebas Formation was deposited, based on a palaeoecological analysis of molluscan samples from individual shell-bearing horizons. Palaeoenvironments should be reconstructed by integrating faunal, sedimentological and isotope data, which method is employed here. Finally, implications for landscape evolution and biotic evolution in Miocene western Amazonia are discussed.

Material and methods

Fossil-bearing sediment samples, collected (in 1996) in outcrops of Pebas Formation deposits in Peruvian Loreto, were weighed and washed (minimum sieve mesh 0.3 mm). Sampling locations are given in Appendix 1. Samples typically weighed about 1 kg. A total of 285 samples were assessed for taxonomic composition. The geographic distribution of 'Pebas' and contemporanous non-marine faunas is shown in Figure 1. The age of the samples is between late Early Miocene and early Late Miocene (Figure 2; see Hoorn 1993, 1994a).

The Pebas Formation is referred to as a lithostratigraphic unit comprising predominantly turquoise-blue smectitic clays; immature, feldspar-rich, usually grey sands, and brown-black organic clays and lignites. The formation is characterised by 3-7 m thick, predominantly coarsening-upwards (CU) cycles, the brilliantly turquoise smectite-rich clays, as well as the common occurrence of lignitic intervals (Räsänen *et al.*, 1998). The Pebas Formation is extremely rich in fossils, often beautifully preserved, *e.g.* molluscs, ostracods, wood fragments as well as fish, amphibian and reptilian remains.

In Peru, this formation is properly known as the Pebas Formation (see *e.g.*, Räsänen *et al.*, 1998). The Curaray Formation of eastern Ecuador (Tschopp, 1953; Baldock, 1982) is the time equivalent of the Pebas Formation. In Colombian Amazonia, deposits formerly referred to as 'Terciario inferior Amazonico' were attributed by Hoorn (1994b) to the Pebas Formation. The La Tagua Beds (Nuttall, 1990a; Hoorn, 1994b) are included in the Pebas Formation as well. In Brazil, Pebas Formation deposits have usually been included in the Solimoes Group/Formation, an informal unit comprising a plethora of western Brazilian Amazonian Cainozoic strata (*e.g.*, Maia *et al.*, 1977), but some authors (Costa, 1981; Petri & Fulfaro, 1983) have indeed distinguished the Pebas Formation as such in Brazil.

In the present paper we use the terms 'lowermost', 'lower', 'middle' and 'upper' Pebas Formation loosely; all in lower case, in order not to be confused with 'Lower', 'Middle' and 'Upper' in lithostratigraphic usage. For the Pebas Formation, 'lower', 'middle' and 'upper' correspond to the *Psiladiporites/Crototricolpites* Concurrent Range, *Crassoretitriletes* Acme and *Grimsdalea* Interval zones of Hoorn (1993), respectively (Figure 2). 'Lowermost' refers to all deposits deemed to be older than the Peruvian localities studied by Hoorn, and includes the La Tagua Beds of southern Colombia.

Figure 1. Distribution of Pebas molluscan faunas and the probable maximum limits of the Pebas system (dashed line). Filled circles are faunas checked by the authors, open circles are unconfirmed reports. Black triangles are contemporaneous non-marine molluscan occurrences checked by the authors, open triangles are unconfirmed contemporaneous non-marine molluscs. Encircled triangles are contemporaneous molluscan faunas that have species in common with the Pebas fauna. Distribution of Pebas Formation deposits in Colombia is adapted from Hoorn (1994b), with a westerly extension into the Putumayo Basin. Approximate distribution of Curaray Formation in Ecuador follows Tschopp (1953) and Baldock (1982); distribution of the Pebas Formation in Brazil follows Petri & Fulfaro (1983). Peruvian localities are those from Nuttall (1990a), Wesselingh (Appendix 1 here) and Romero-Pittman (1997).

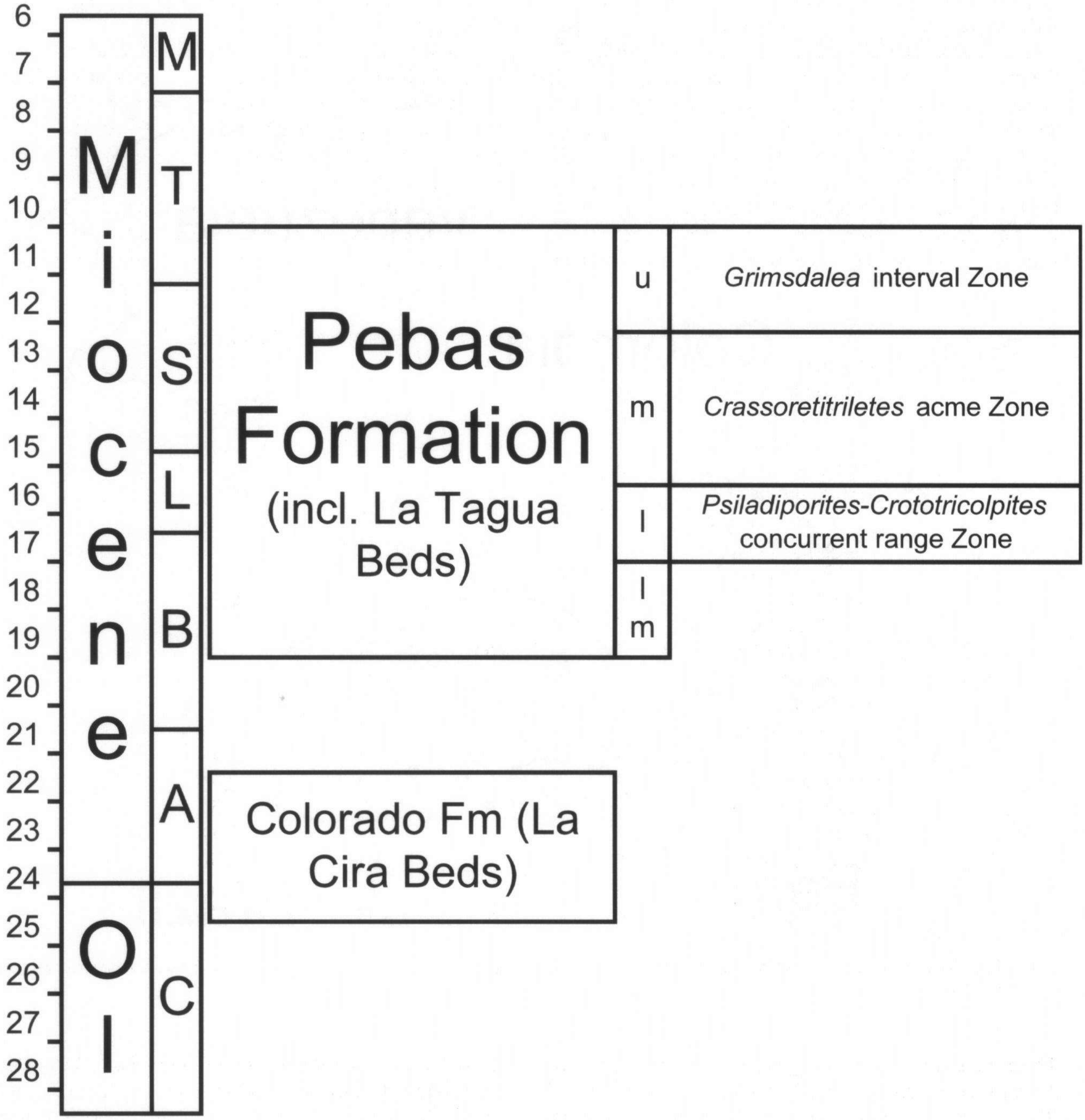

Figure 2. Stratigraphic framework for the Pebas Formation and geological units discussed in this paper. Ol Oligocene, M Messinian, T Tortonian, S Serravallian, L Langhian, B Burdigalian, A Aquitanian, C Chattian, u upper, m middle, l lower, lm lowermost; the timescale is after Berggren *et al.* (1995).

The systematic status of numerous molluscan taxa in our material is uncertain. More than half of the fauna is undescribed (Appendix 2). The Pebas molluscan fauna also contains several species flocks, further complicating species-based analyses. By using taxonomic groups, some of which contain single species while others include several genera, we have attempted to overcome the systematic uncertainties. Classification procedures are outlined in Appendix 2. The senior author (FPW) has estimated abundances for each of the taxa groups. Categories were logarithmically chosen (0%, >0-1%, >1-2%, >2-4%. >4-8% etc.). The use of this type of categories, a slight modification of the so-called 'octave scale', is discussed in Smith (1999). The 'octave scale' has the great advantage that data do not suffer the closed sum effect in statistical analyses and that inherent noise and minor variation within the data set are suppressed, leaving only the basic major signals (Smith, 1999). It cannot be overemphasised that these methods deliver only a crude insight into faunal composition and abundances. The samples were subjected to a variety of statistical analyses. In the present paper results of Ward clustering methods using Euclidean distances were subjected to indicator-species analysis as described in Dufrêne & Legendre (1997). Following those authors, indicator values over 30 were considered to be meaningful. Analyses were run on PC-ORD, version 4 (McCune & Mefford, 1999). In order to discuss (dis-)similarity between assemblages, Pearson's similarity coefficients for the average composition of each of the assemblages were calculated using SPSS version 8.0.

Subjecting the taxa/sample matrix to Ward clustering using Euclidean distances produced five clusters of samples that are described as assemblages below. Indicator-species analysis (Dufrêne & Legendre, 1997) was applied. An R-mode cluster analysis was also performed. A few species-groups were found to cluster tightly. Pearson's correlation coefficients were computed for these combinations. This produced three groups that yield taxa that cluster together and show a correlation of over 0.4.

	genera	species	species%	abundance %
Neritidae	1	4	3,0	0,9
Ampulariidae	1	1	0,7	0,0
Cochliopinae	15	75	56,0	28,2
Pachychilidae	2	7	5,2	0,6
Thiaridae	3	5	3,7	0,7
perimarine taxa				0,1
Melongenidae	1	1	0,7	
Nassariidae	1	1	0,7	
Pyramidellidae	1	3	2,2	
Pulmonata				0,7
Planorbidae	2	2	1,5	
Ferrissidae	1	1	0,7	
Acavidae	1	1	0,7	
Bulimulidae	1	1	0,7	
indet. family	1	1	0,7	
Corbiculidae	1	1	0,7	0,1
Sphaeriidae	2	2	1,5	0,1
Dreissenidae	1	2	1,5	1,6
Hyriidae	2	3	2,2	0,4
Mycetopodidae	1	2	1,5	0,3
Tellinidae	1	1	0,7	0,0
Pachydontinae	6	20	14,9	66,5

Table 1. Taxonomic composition (estimated numbers of species per (sub)family) and estimated molluscan abundance (percentages) of the Pebas fauna.

The groups are (A) *Pebasia* group + *Ostomya* group, (B) *Neritina roxoi* group + Pachychilidae + Thiaridae and (C) *Corbicula* + perimarine taxa. These three groups are used as additional descriptors for the assemblages.

Stable isotope analyses were run on 109 shells from seven different levels following analytical procedures described in Vonhof *et al.* (1998). Five of the levels are from Santa Rosa de Pichana, the remaining two are from outcrop Tamshiyacu (see Appendix 1). Both outcrops are located in the upper part of the *Crassoretitriletes* Acme Zone, characterised by the occurrence of the gastropod *Sioliella bella* (Conrad, 1874), and are of Middle Miocene age. Entire or slightly damaged shells were homogenised prior to analyses, in order to provide a 'mean' isotopic signature for the shells.

For exploring within-shell isotopic variation a specimen each of the bivalves *Diplodon longulus* Conrad, 1874 (Nuevo Horizonte, Loreto dept., Peru, level 366; M. Räsänen Colln), and *Pachydon erectus* Conrad, 1871 (Santa Rosa de Pichana, Loreto dept., Peru; collected from surface of outcrop at the fossiliferous interval from which samples 533-536 were taken, F. Wesselingh Colln, 1996) were sampled along growth increments. The Nuevo Horizonte specimen is of late Middle to early Late Miocene age (*Grimsdalea* Interval Zone). Within-shell isotope profiles of the fossil shells were compared to isotope profiles of two bivalve shells from the present-day Amazonian floodplains. These are *Anadontites trapesialis* (Lamarck, 1819) from a floodplain lake on Isla Indiana (F. Wesselingh Colln, 1996; 73°30' W, 3°32'S) and *Diplodon* sp. from the Itaya River, southwest of Iquitos (Kaandorp & Vonhof Colln, 1998; 73°16'W, 3°45'S). Salinities are given in practical salinity units (psu).

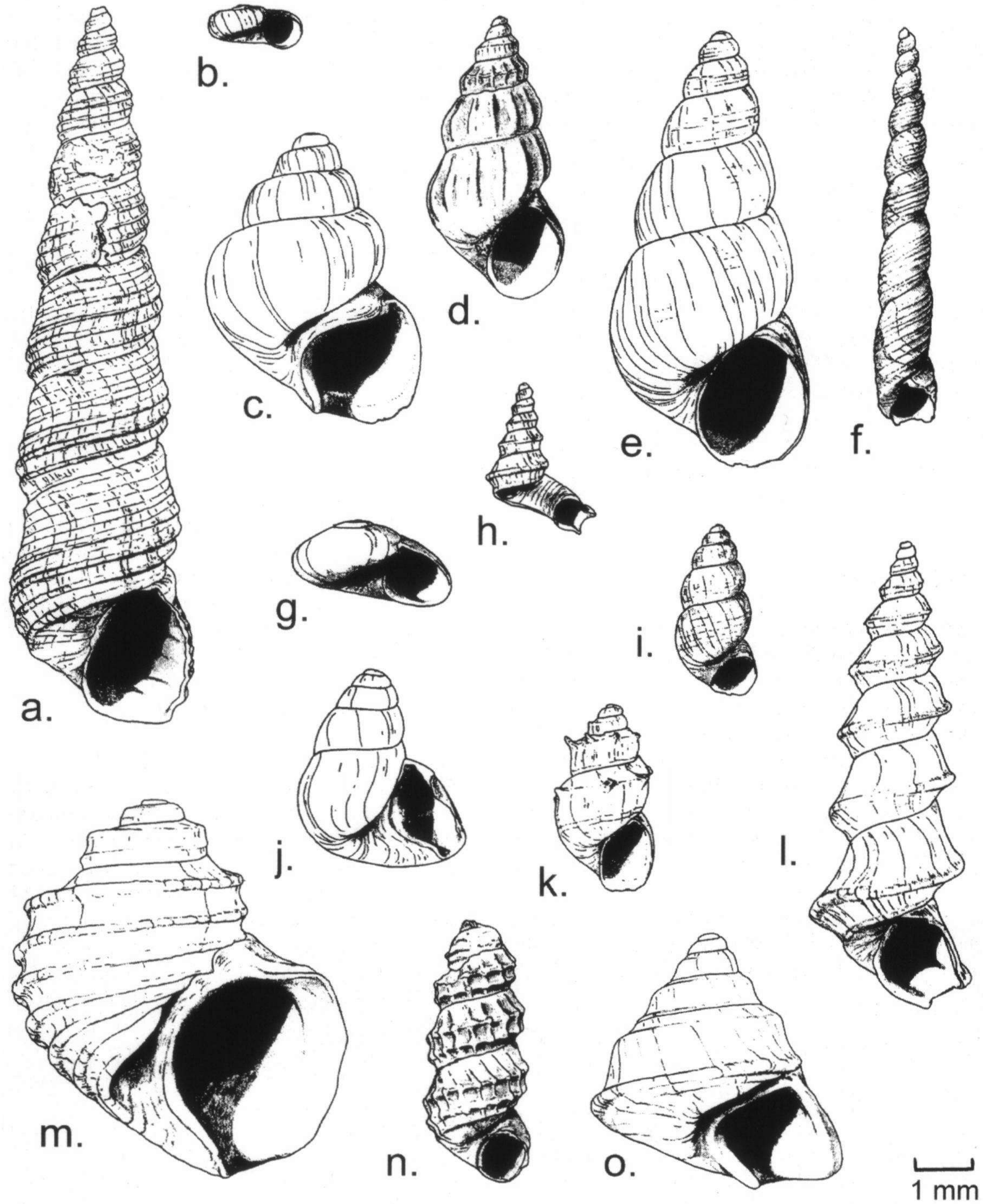

Figure 3. Morphological diversity in Pebasian cochliopines. Scale bar represents 1 mm.

A- RGM 456 000; *Dyris* sp., Macedonia, Amazonas dept., Colombia;
B- RGM 456 001; *Nanivitrea hauxwelli* (Nuttall, 1990a), Indiana, Loreto dept., Peru;
C- RGM 456 002; *Sioliella* sp., Santa Teresa, Loreto dept., Peru;
D- RGM 456 003; *Tryonia* sp., Santa Sofia, Amazonas dept., Colombia;
E- RGM 456 004; *Dyris ortoni* (Gabb, 1869), Macedonia, Amazonas dept., Colombia;
F- RGM 456 005; *Dyris* sp., Chimbote, Loreto dept., Peru;
G- RGM 456 006; *Nanivitrea degrevei* (Nuttall, 1990a), Santa Julia, Loreto dept., Peru;
H- RGM 456 007; genus and species indet., Nuevo Horizonte, Loreto dept., Peru;
I- RGM 456 008; ?*Onobops* sp., Santa Sofia, Amazonas dept., Colombia;
J- RGM 456 009; *Toxosoma* sp., Mocagua, Amazonas dept., Colombia;
K- RGM 456 010; *Pyrgophorus* sp., Santa Teresa, Loreto dept. Peru;
L- RGM 456 011; *Dyris* sp., Nuevo Horizonte, Loreto dept., Peru;
M- RGM 456 012; *Sioliella bella* (Conrad, 1874), Puerto Almendras, Loreto dept., Peru;
N- RGM 456 013; *Tryonia tuberculata* (de Greve, 1938), Santa Julia, Loreto dept., Peru;
O- RGM 456 014; *Tropidobora tertiana* (Conrad, 1874), Iquitos Puerto Ganso Azul, Loreto dept., Peru.

Clay mineralogy analyses were run on twenty-seven samples from stratigraphic intervals covering the three pollen zones defined by Hoorn (1993); analytical procedures are described in Räsänen *et al.* (1998). The abbreviation RGM refers to the collections of the Department of Cainozoic Mollusca, Nationaal Natuurhistorisch Museum, Leiden (the Netherlands; formerly Rijksmuseum voor Geologie en Mineralogie).

Composition of the fauna

The estimated number of species and abundance of families in the Pebas fauna are given in Appendix 3 and summarised in Table 1. The entire Pebas fauna contains at least 135 species, 59 of which have been described previously. The taxonomic work is in progress, so these numbers serve as indications only. In numbers of species the Cochliopinae (55.6%) and Pachydontinae (14.1%) dominate. Other common groups in numbers of species include Neritidae (3.0%), Pachychilidae (5.2%), Thiaridae (3.7%) and Unionoidea (Hyriidae and Mycetopodidae, 3.7%).

In estimated abundance, Pachydontinae (66.5%) dominate, followed by Cochliopinae (28.2%). All other groups together make up only an estimated 5.3% of the molluscan fauna.

Trophic and life habit characteristics of faunal elements

* Neritidae (4 species)

Extant species of *Neritina* are mostly hard-substrate dwellers, some are mud-dwellers. Some species are obligate freshwater inhabitants, whereas others are found in brackish lagoons, and still others occur in tidal pools on rocky shores (Rodriguez, 1963; Russell, 1941; von Cosel, 1986). The latter tolerate salinity changes from freshwater to hypersaline. Mangrove-inhabiting *Neritina* cling to roots and may experience periodic drought. Various coastal neritids withstand large temperature and salinity fluctuations (Russell, 1941). Neritids are algal grazers and browsers as well as scavengers (Gittenberger & Janssen, 1998). Pebasian *Neritina ortoni* Conrad, 1871 is characterised by its flared outerlip and velatiform outline (Nuttall, 1990a). Possibly these were adaptations for living on muddy bottoms.

* Ampullariidae (1 species)

Ampullariid snails are very rare in the Pebas Formation. Today, these amphibious snails occur abundantly in floodplains of Amazonia, where they litter areas that experience regular flooding. Ampullariids feed on aquatic vegetation, and are extremely salt-intolerant (von Cosel, 1986).

* Cochliopinae (*c.* 75 species)

The Cochliopinae outnumbers any other group in the Pebas fauna in number of species. Many of these, and some of the genera as well, are undescribed and appear endemic to Miocene deposits of western Amazonia (Nuttall, 1990a; Wesselingh, 1993). Some speciose genera, such as *Dyris* and *Sioliella* (referred to as *Eubora* by earlier authors) currently occur as relics only (*Dyris amazonicus* (Haas, 1949) and *Sioliella effusa* Haas, 1949 in the lower Tapajos River of central Brazil; Wesselingh, 2000), restricting their value as uniformitarian ecological markers. Other genera, represented by low numbers of species in the Pebas Formation, such as *Pyrgophorus* and *Nanivitrea*, are widespread in modern freshwater settings of the tropical Americas (Hershler & Thompson, 1992). Some cochliopine genera are known only from the Pebas Formation (e.g., *Toxosoma*, *Tropidobora*, *Liosoma*). Other Pebasian species are tentatively assigned to extant neotropical genera known from outside Amazonia (*e.g.*, *Lithococcus* and *Onobops*), but this is in need of systematic confirmation. The Pebas Formation is unusually rich in hydrobiid taxa as well as morphotypes (Figure 3), including planorbiform, naticiform, trochiform, turritelliform, turbonilliform, and hydrobiform species. Such an excessive morphological diversity is known from long-lived lake environments (*e.g.*, Lake Ohrid, Lake Baikal, Caspian Sea, Miocene Lake Pannon; see Boss, 1978; Müller *et al.*, 1999, amongst others). Morphological features found in the Pebasian cochliopines, such as the trend towards open coiling, miniaturisation as well as gigantism (the smallest hydrobiids are barely 2 mm, whereas the largest exceed 21 mm in height) and the diverse array of sculptural elements are known to occur in long-lived lake gastropod faunas (see *e.g.*, Boss, 1978; Gorthner, 1992). The functionality of these is not always clear (Gorthner, 1992). The denticulation seen in *Toxosoma* is known only from one other hydrobiid genus (*Hemistomia* Crosse, 1872), known from New Caledonia and Lord Howe Island; Haase & Bouchet, 1998). To our knowledge, siphon-like structures, as seen in most species of *Sioliella*, *Tropidobora* and *Toxosoma*, occasionally including a second adapical sinus in some species of *Sioliella*, are a unique feature for hydrobiid snails. Extant cochliopine snails occur in aquatic habitats ranging from high-altitude freshwater streams to brackish coastal settings (Hershler & Thompson, 1992). Most species are detritivores, some are grazers. Cochliopinae includes epifaunal and semi-infaunal dwellers.

* Pachychilidae (7 species)

The Pachychilidae comprises neotropical freshwater dwellers that graze on algae. They are dioecious (Nuttall, 1990a; Glaubrecht, 1996). Extant pachychilids (*e.g.*, *Doryssa* and *Pachychilus*) are mostly substrate dependent, which might be related to feeding and egg-deposition. Five species of *Sheppardiconcha* and two undescribed species tentatively assigned to *Doryssa* are Pebas Formation representatives of this family. The supraspecific classification of *Doryssa* is uncertain (Glaubrecht, 1996).

* Thiaridae (5 species)

Thiaridae are represented by two genera in the Pebas Formation, *viz.* *Aylacostoma* and *Hemisinus*. A third genus, *Charadreon* (to which *Longiverena eucosmius* Pilsbry & Olsson, 1935 should be assigned), is tentatively placed in this family, but its assignment needs further investigation. Extant species of *Hemisinus* are widely distributed in freshwater ecosystems of the Caribbean and northern South America (Nuttall, 1990a; Glaubrecht, 1996). Some species of *Hemisinus* have been reported to tolerate temporal saline conditions (Glaubrecht, 1996). The genus *Aylacostoma* comprises various extant species living in rivers and other freshwater habitats in eastern Brazil (Nuttall, 1990a). One species of *Charadreon*, *C. ruginosum* (Morelet, 1849), lives in Guatemalan lakes. Like pachychilids, thiarid snails are (sub-)tropical freshwater dwellers that graze on algae and organic detritus.

* Melongenidae (1 species)

Melongena woodwardi (Roxo, 1924) occurs in marine incursion levels in the upper Pebas Formation only (Vonhof *et al.*, 1998; Vermeij & Wesselingh, 2002). Melongenid gastropods are marine to perimarine carnivores that feed on barnacles, other molluscs or carrion. They can withstand reduced salinities but are not known from freshwater settings.

* Nassariidae (1 species)

A species of *Nassarius* is known from marine incursion intervals in the upper Pebas Formation (Vonhof *et al.*, 1998, fig. 2-1; Vermeij & Wesselingh, 2002). Nassariids are primarily carnivores or scavengers living in marine and brackish environments, and have been reported to tolerate meso- to oligohaline conditions (Cernohorsky, 1984; Gittenberger & Janssen, 1998). They are not known from freshwater environments.

* Pyramidellidae (3 species)

Three species of *Odostomia* have been found in the upper part of the Pebas Formation in levels containing other indicators of marine influence (van Aartsen & Wesselingh, 2000). Pyramidellids are parasitic snails, living on and in molluscs and other invertebrates. Pyramidellid species are known from a range of salinities (as low as oligohaline), but have not been reported from freshwater environments.

* Planorbidae (3 species)

Helisoma is an extremely rare constituent of the Pebas fauna, represented by two species. Specimens tentatively attributed to *Drepanotrema* were found in a single sample only. Planorbids are limited to freshwater environments, both permanent and ephemeral. They feed on organic detritus, algae, and decaying plant material (Baker, 1945). The scarcity of planorbids in the Pebas Formation contrasts markedly with the abundance of this group in modern South American freshwater ecosystems.

* Ferrissiidae (1 species)

Only a single species (?*Hebetancylus* sp.) is known from the Pebas Formation (Nuttall, 1990a, p. 261). Some fragments attributable to this species have been recognised in two of the samples assessed for the present paper. Ferrissiid gastropods (*Laevapex* and *Hebetancylus* spp.) are common in aquatic environments of white-water floodplains (floodplains of rivers draining the Andes) of central Amazonia (Irmler, 1975), where they feed on detritus and occasionally on fungi.

* Acavidae (1 species)

Pebasiconcha immanis Wesselingh & Gittenberger, 1999 is a huge, extinct terrestrial snail (up to 26 cm in height), whose extant relatives live on trees and on the ground in neotropical forest environments, where they feed on plant material (*e.g.*, leaves). *Pebasiconcha* is restricted to the Miocene of western Amazonia, and is not rare in Pebas Formation deposits.

* Orthalicidae (2 species)

Orthalicus linteus (Conrad, 1874) is known only from the Pebas Formation (Nuttall, 1990a); it is a rare constituent of the fauna. A second, unidentified, species tentatively attributed to this family has been found in a single sample. Extant species of *Orthalicus* are widespread in neotropical forests, where they occur on the forest floors and in trees and feed on leaves, lichens etc.

* Dreissenidae (2 species)

Species of *Mytilopsis* are epifaunal, hard substrate-dependent, byssally attached filter feeders. Often, specimens form aggregates or clumps (Nuttall, 1990b). Clumps of *Mytilopsis* were found on a few occasions in the Pebas Formation deposits. Extant species of *Mytilopsis* are found in fresh, brackish and occasionally hypersaline settings (Nuttall, 1990b). Some *Mytilopsis* occurrences have been reported from far inland (*e.g.*, Figueiredo-Alvarenga & Ricci, 1989), indicating an obligate freshwater existence for these. These mussels are able to colonise both fast-running and relatively stagnant waters.

* Pearly freshwater mussels: Mycetopodidae (2 species) and Hyriidae (3 species)

Pearly freshwater mussels are semi-infaunal filter feeders that are restricted to freshwater ecosystems, such as lakes, streams and rivers. During reproduction, juveniles undergo a parasitic stage on fish. This way they gain their distribution prior to a rather immobile adult life stage. Nowadays, these mussels are widespread in many freshwater habitats of South America, including Amazonia (Nuttall, 1990a). These taxa are not able to withstand salt water. Pearly freshwater mussels are a common constituent of the Pebas fauna; they were found in nearly one third of the samples, but their numbers are low (0.8% of estimated abundance).

* Corbiculidae (1 species)

Species of the semi-infaunal genus *Corbicula* occur in many freshwater systems in South America, but appear to have been lacking in the Amazon system, until introducted recently (pers. obs.). Unlike the corbiculid *Polymesoda*, which lives in oligohaline and mesohaline habitats in northern South America (Rodriguez, 1963; von Cosel, 1978), neotropical *Corbicula* appears entirely restricted to *freshwater* ecosystems (*e.g.*, W.B. Marshall, 1927; Lange de Morretes, 1949). Recent immigrant species of *Corbicula* in South America may tolerate a wide range of salinities (Darrigan, 1992). It is somewhat surprising that the rare *Corbicula* valves found in the Pebas Formation usually occur in samples containing indicators of marine influence, wheras strontium isotope measurements on the corbiculid shells (H. Vonhof, unpublished data) point to a freshwater habitat. The few samples in which *Coribula* have been found also contain freshwater taxa, such as cerithioideans, pointing to a mixed origin of faunas in them. Corbiculids are mainly filter feeders but have been also reported to be facultative deposit feeders (Way *et al.*, 1990). *Corbicula* is common in Miocene fossiliferous deposits of the tropical Andean region (see *e.g.*, Nuttall, 1990a), but a very rare constituent of the Pebas fauna.

* Sphaeriidae (2 species)

Sphaeriids are very rare in the Pebas Formation. They are represented by two species only, one assigned to the genus *Eupera*, the other to *Pisidium*. These tiny nutclams are obligate freshwater inhabitants. The habitat of sphaeriids ranges from ephemeral and small-bodied freshwater settings to large lakes, where they live at or in bottoms, or clogged on the vegetation (Gittenberger & Janssen, 1998). Sphaeriids are filter feeders, but Amazonian sphaeriids have been reported to feed on small detritus particles and occasionally on fungi (Irmler, 1975). Sphaeriids do not survive in salt water.

* Tellinidae (1 species)

Macoma sp. has been found at a single marine incursion level in the Pebas Formation only (Vonhof *et al.*, 1998; as *Psammotreta* sp.). Today, species of *Macoma* live in marine and marginal marine environments as infaunal deposit feeders, capable of facultative suspension feeding as well (Cadée, 1984). Minimum salinities reported for *Macoma* are 3 psu (Kuiper, 2000), comparing well with inferred maximum salinities from strontium analyses of 3-5 psu for the interval in which *Macoma* was encountered (Vonhof *et al.*, 1998). *Macoma* was not encountered in the samples studied for the present study.

* Corbulinae (1 species)

An undescribed species of *Panamicorbula* was encountered in a 'marine' interval in the Buenos Aires section of southern Colombia (Vonhof *et al.*, 1998). Those authors listed it as *Pachydon cebada* (F.M. Anderson, 1928) and *P.* cf. *ovalis* Nuttall, 1990a. The same species was illustrated by Hedberg (1936, pl. 8, fig. 4) from the Miocene of northern Venezuela. Two species of *Panamicorbula* are known from Pacific mangroves, from Mexico to Peru (L. Anderson, 1996). *Panamicorbula* has been reported from ''soft impalpable mud' in the upper (freshwater-dominated) reaches of mangroves on the Pacific side of Panama (Olsson, 1961). Fossils are known from the

Miocene and Pliocene of Venezuela and Trinidad, as well as from the Miocene of Costa Rica and the Dominican Republic (L. Anderson, 1996).

* Pachydontinae (*c.* 19 species)

The Pachydontinae is subfamily of the Corbulidae. Corbulids are semi-infaunal filter feeders (Beesley *et al.*, 1998) and are well known to tolerate dysoxic settings. In abundance the Pachydontinae dominate the Pebas fauna, in number of species they are second after the cochliopines (Table 1). Four of the six pachydontine genera that occur in the Pebas fauna (*Pachydon*, *Pebasia*, *Ostomya* and undescribed genus 1) are extinct (Nuttall, 1990a; see Appendix 2 here). These four genera appear endemic to Oligo-Miocene inland basins of northwest South America. One species is attributed to a second undescribed genus, and tentatively placed in the Pachydontinae. The sixth genus, *Anticorbula*, is a rare constituent of the Pebas fauna. Extant *Anticorbula fluviatilis* (Adams, 1860) lives in freshwater habitats of the central and lower Amazon region, as well as in rivers draining the Guyana Shield (up into the upper reaches of estuaries), mostly byssally attached to hard substrates, often nestling (Nuttall, 1990a; Leistikow & Janssen, 1997; Simone, 1999). The attached mode of life of *Anticorbula* is atypical of other Pebasian pachydontines with the possible exception of *Pebasia*. The shell torsion seen in *Pebasia* has been suggested by Savazzi & Peiyi (1992) to indicate a pleurothetic life habit and possibly a strong byssal attachment. Specimens of *Pachydon tenuis* Gabb, 1869 show moderate shell torsion comparable to forms described from extant species of *Cuneopsis* in China. This shell torsion has been attributed to a shallow burrowing behaviour (Savazzi & Peiyi, 1992). In the field, articulated valves of *Pachydon* were quite often found preserved in life position. All species of *Pachydon* appear to have been shallow burrowers, which is indicated by the presence of a very shallow pallial sinus in most specimens. *Pachydon obliquus* Gabb, 1869, the commonest species of *Pachydon* in the Pebas Formation, appears to have adapted especially well to dysoxic settings. Articulated specimens, often *in situ* or with signs of minimal transport, are found to dominate the faunas of organic-rich clayish intervals, where other pachydontine (and cochliopine) species are considerably less abundant.

The Pebas fauna is dominated by aquatic molluscs, which constitute in excess of an estimated 99.3% in abundance (the pulmonate snails accounting for the other 0.7% include both terrestrial and freshwater taxa). Nearly all of the species are restricted to the Pebas Formation, and do not occur in contemporaneous fossiliferous deposits in nearby Ecuador and Venezuela (Nuttall, 1990a). Although the taxonomic work is far from complete, it appears that only two species found in the Pebas Formation survive to the present day, *viz. Hemisinus kochi* (Bernardi, 1856) and *Mytilopsis sallei* (Récluz, 1849) (see Nuttall, 1990a).

Ecology of the Pebas fauna

salinity tolerance	
terrestrial taxa	0,4%
obligate freshwater taxa	2,5%
freshwater to oligohaline taxa	97,1%
oligohaline to hypersaline taxa	0,0%
feeding characteristics	
grazers/browsers	2,4%
suspension feeding	68,8%
detritus feeding	28,7%
scavengers/carnivores	0,1%
parasites	0,1%
life habit	
infaunal sessile	67,4%
epifaunal and semi-infaunal vagile	28,2%
epifaunal vagile	2,6%
epibyssate	1,6%

Table 2. Inferred gross ecology, feeding ecology and life habit for the Pebas fauna (based on estimated abundance of taxa in the Pebas fauna).

Endemic elements make up 90.2% of the Pebas fauna, which may be characterised as almost exclusively aquatic, endemic and extinct. Extant relatives of Pebasian taxa occur in a range of salinities, from freshwater to hypersaline. Strictly freshwater and brackish-marine taxa are rare in the Pebas fauna (Table 2). Despite the rarity of freshwater taxa (Ampullariidae, Pachychilidae, Thiaridae, *Corbicula*, Sphaeriidae, Hyriidae, Mycetopodidae) in terms of estimated abundance (2.5% of the fauna), these groups were found (in low numbers) in 54% of the samples studied. Taxa with a marine affinity (unknown to survive in freshwater settings) make up only 0.1% of the faunas studied and were found only in 5% of the samples.

The paucity or absence of extant pachydontine taxa and many of the cochliopine gastropod genera that dominate the Pebas fauna complicates an assessment of salinity based on a uniformitarian approach, which is illustrated in the large portion in Table 2 assigned to freshwater to oligohaline faunas. For similar reasons the assessment of trophic characteristics and life habit of the faunal members are subject to uncertainty. Trophic characterisation is furthermore complicated by the ability of some species to switch between feeding modes, so-called 'opportunistic feeding' (Cadée, 1984). The procedure of inferring ecological characteristics of the fauna is outlined in Appendix 2. The Pebas fauna is characterised by the predominance of sessile infaunal Pachydontinae and vagile semi-infaunal and epifaunal Cochliopinae. Substrate-dependant taxa (Neritidae, Thiaridae, Pachychilidae, Dreissenidae, ?*Pebasia* and ?*Anticorbula*) make up an estimated 4% in abundance, but representatives of these groups are found in 92% of the samples, indicating that substrate in the Pebas system (*e.g.*, shelly substrate, firmgrounds or wood) was commonly available.

	Estimated average abundance					Relative abundance					Relative frequency				
assemblage	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
n	64	52	78	83	8	64	52	78	83	8	64	52	78	83	8
Neritina ortoni group	0,2	0,6	0,2	0,5	0,0	16	33	20	31	0	39	56	53	64	0
Neritina roxoi group	0,7	0,0	0,0	0,1	3,4	31	5	4	7	53	44	12	12	14	50
Ampulariidae	0,0	0,0	0,0	0,0	0,4	17	0	0	0	83	6	0	0	0	13
Tall *Dyris* group	2,6	30,4	0,5	2,6	0,1	19	62	4	13	3	69	100	27	65	13
Small *Dyris* group	6,7	15,4	4,5	22,8	0,2	20	29	16	32	3	98	98	92	100	38
Tryonia group	10,5	4,9	1,2	3,8	11,9	31	18	8	18	25	98	83	67	92	88
Sioliella group	2,2	1,6	1,3	3,4	4,9	19	18	14	25	24	81	83	83	95	75
Other Cochliopinae	0,7	0,6	0,7	2,2	1,2	18	16	13	33	19	73	63	59	95	50
Pachychilidae	0,9	0,6	0,1	0,1	7,6	27	11	5	4	54	50	25	17	10	38
Thiaridae	0,7	0,3	0,2	0,3	12,5	19	7	5	6	63	41	13	15	13	50
Perimarine taxa	0,0	0,0	0,1	0,1	0,0	0	0	32	68	0	0	0	4	16	0
Pulmonata	0,1	0,2	0,0	0,0	23,2	4	6	1	0	88	13	13	3	1	63
Corbiculidae	0,0	0,0	0,0	0,2	0,4	2	8	7	33	51	2	4	4	12	13
Sphaeriidae	0,0	0,0	0,0	0,0	3,0	0	0	2	0	98	0	0	1	0	13
Dreissenidae	0,4	1,5	1,0	1,9	14,1	8	16	15	18	43	33	63	60	65	75
Hyriidae	0,6	0,1	0,1	0,2	7,6	20	6	5	11	58	34	15	12	23	50
Mycetopodidae	0,1	1,0	0,0	0,1	1,9	10	32	1	5	53	17	23	1	6	38
Pachydon obliquus	33,8	24,7	53,4	22,2	1,5	26	20	28	23	3	100	92	96	99	25
other *Pachydon* group	39,1	17,4	35,4	37,6	6,0	26	20	22	26	6	100	100	96	100	38
Pebasia group	0,3	0,4	0,6	1,1	0,0	14	18	22	42	4	34	48	49	83	13
Ostomya group	0,3	0,4	0,5	0,8	0,0	19	16	25	40	0	44	31	50	77	0

Table 3. Abundance, frequency and indicator values (IV) of Pebasian molluscan assemblages. *Estimated average abundance*: sum of the mean abundance of a taxon in all samples of an assemblage, corrected for 100% total. *Relative abundance*: percentage of average abundance of a given taxon in an assemblage over the average abundance of that taxon in all assemblages, expressed as a %. Note that the relative abundance is based on an octave-scale classification, and therefore occasionally differs from the estimated average abundance sample signature. *Relative frequency*: percentage of perfect indication (percentage of samples in an assemblage where the given taxon is present). *Indicator value* (IV): percentage of perfect indication based on combining the values for relative abundance and relative frequency (from Dufrêne & Legendre, 1997).

Assemblage I: *Tryonia* assemblage; Assemblage II: tall *Dyris* assemblage; Assemblage III: small *Dyris* assemblage; Assemblage IV: *Pachydon obliquus* assemblage; Assemblage V: Thiaridae-Pulmonata assemblage.

assemblage	I	II	III	IV	V
n	64	52	78	83	8
endemics	86,0	91,6	97,3	93,3	14,4
substrate-dependent taxa	3,2	3,4	2,1	4,0	37,6
infaunal taxa	73,9	43,6	89,4	61,1	17,4
obligate freshwater taxa	2,4	2,2	0,4	0,9	56,6
obligate saline taxa	0,0	0,0	0,1	0,1	0,0
Pebasia group + *Ostomya* group	0,7	0,7	1,1	1,9	0,1
Neritina roxoi group + Pachychilidae + Thiaridae	2,2	0,9	0,3	0,5	23,3
Corbiculidae and perimarine taxa	0	0	0,2	0,3	0,4

Table 4. Some average properties of the assemblages. Numbers refer to estimated percentages.

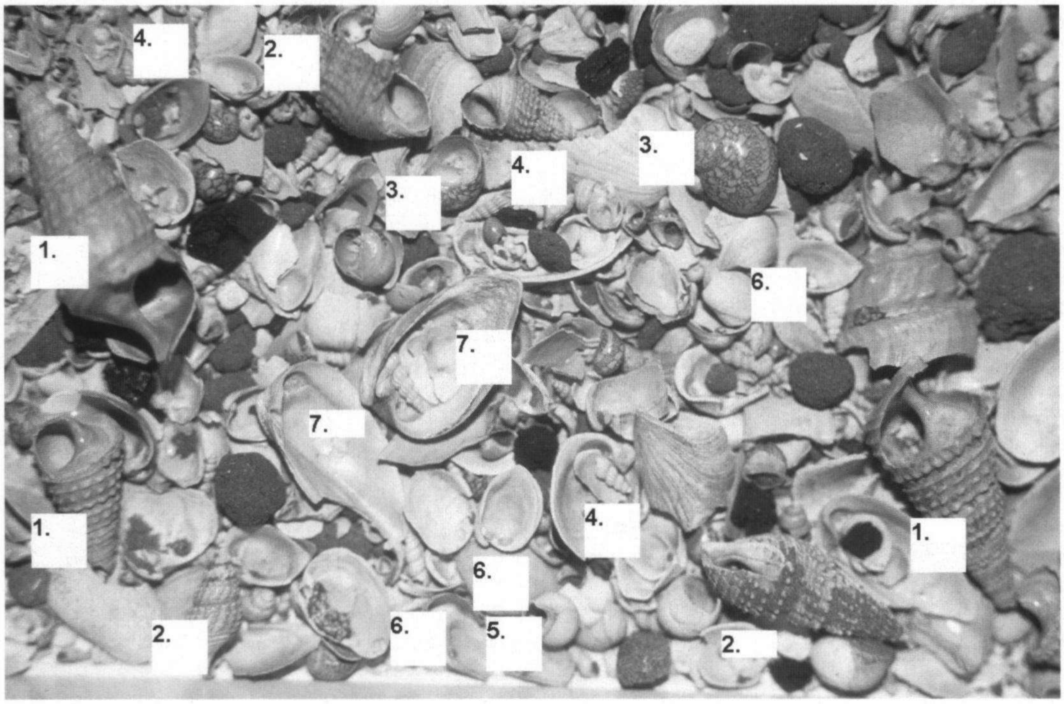

Figure 4. Example of a *Tryonia* assemblage residue. Length of valve in the centre (no. 7) is *c.* 10 mm. Sample 895 (Nueva Paleta, Napo: late Early–early Middle Miocene), containing the snails *Sheppardiconcha* spp. (1), *Charadreon eucosmius* (Pilsbry & Olsson, 1935) (2), *Neritina roxoi* de Greve, 1938 (3), the small *Tryonia* aff. *scalarioides* (Etheridge, 1879) (4), and *Sioliella* sp. (5), as well as the bivalves *Pachydon obliquus* Gabb, 1869 (6) and *P. carinatus* Conrad, 1871 (7).

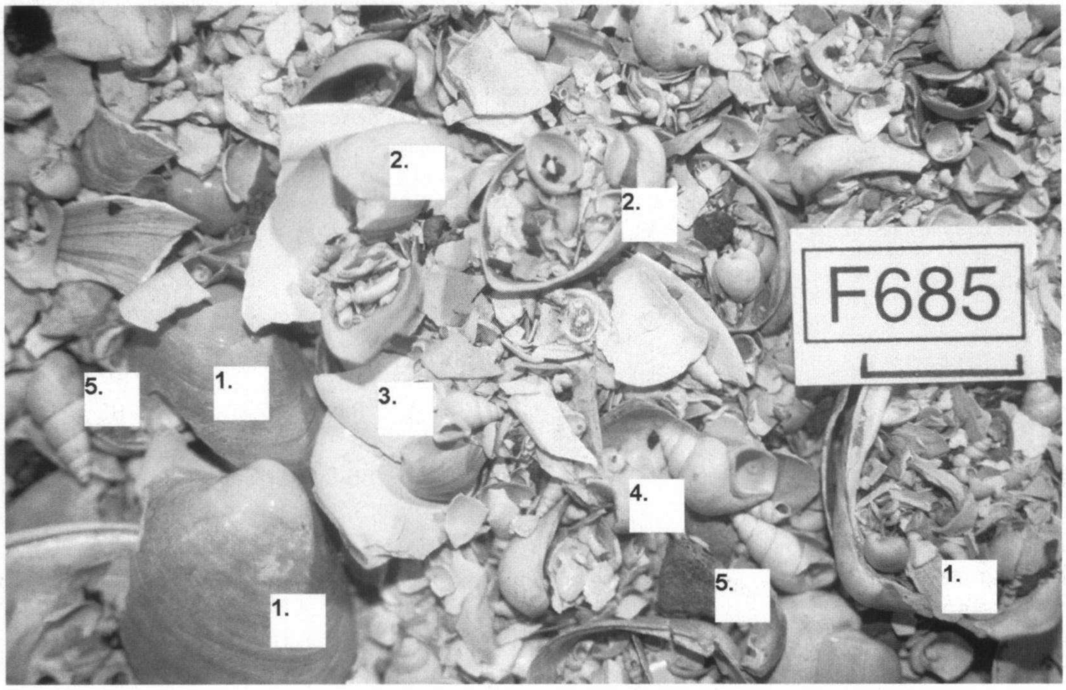

Figure 5. Example of a tall *Dyris* assemblage residue. Scale bar equals 10 mm. Sample 685 (Tamshiyacu: Middle Miocene), dominated by various species of *Pachydon*, *e.g.*, *P. tenuis* (1) and *P. obliquus* (2). Many of the *Pachydon* valves and fragments retain remains of periostracum (skin). Furthermore, small cochliopines (*Toxosoma eboreum* (3), *Sioliella crassilabra* (Conrad, 1871) (4)) and various *Dyris ortoni* (5) are present.

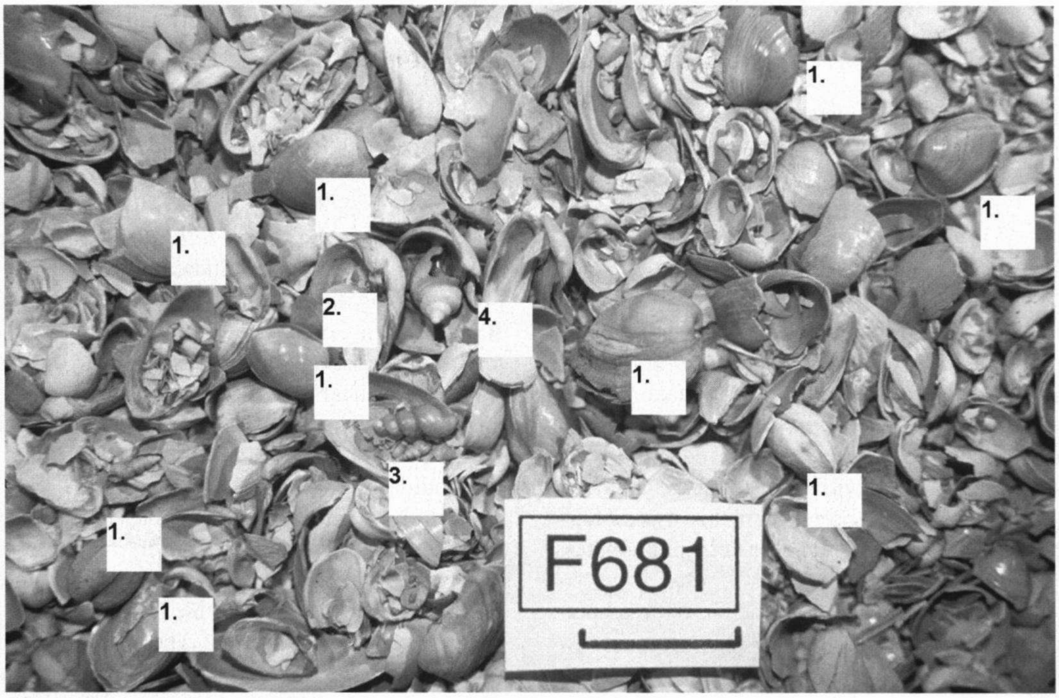

Figure 6. Example of a *Pachydon obliquus* assemblage residue. Scale bar represents 10 mm. Sample 681 (Indiana: late Early–early Middle Miocene), dominated by single valves and articulated specimens of *Pachydon obliquus* (1). The elongate valves of other species of *Pachydon* (*P. tenuis* (2) and *P.* cf. *amazonensis* (Gabb, 1869) are present. Gastropods, such as *Dyris* spp. (3) and *Sioliella* sp., (4) are rare.

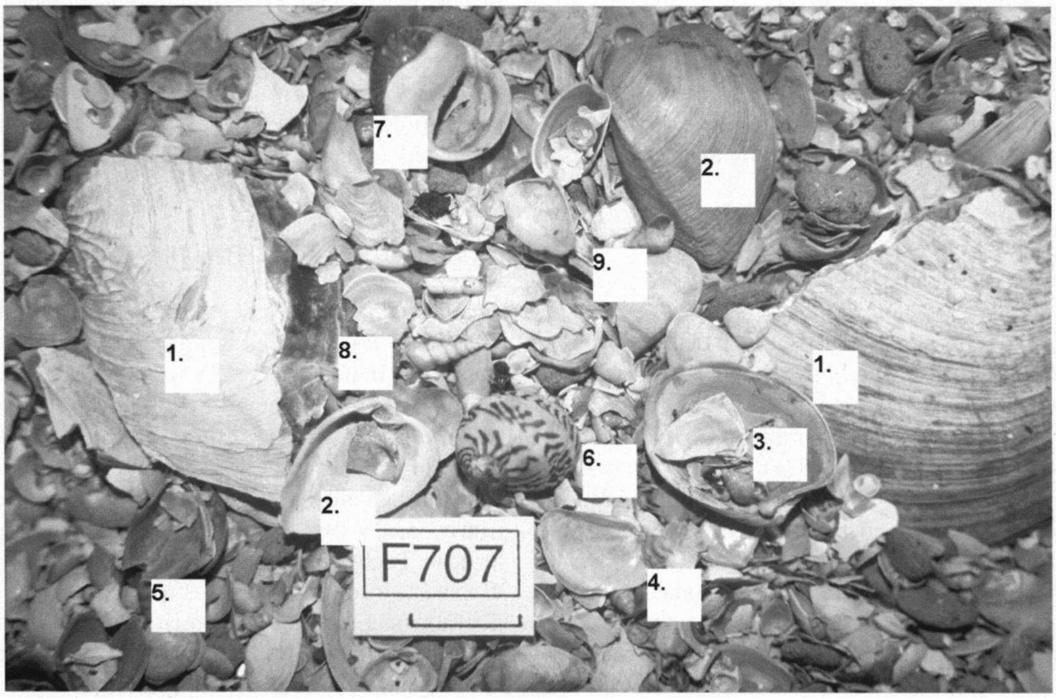

Figure 7. Example of a small *Dyris* assemblage residue. Scale bar equals 10 mm. Sample 707 (Porvenir: late Middle–early Late Miocene), being very rich in species. *Diplodon longulus* Conrad, 1874 (1), *Pachydon carinatus* (Conrad, 1871) (2), *P. tenuis* (3), *Pebasia dispar* (Conrad, 1874) (4), *Mytilopsis* cf. *sallei* (Récluz, 1849), *Neritina* sp. 1 (6), *N. ortoni* Conrad, 1871 (7), *Dyris* spp. (8) and *Toxosoma* sp. (9) are seen. *Diplodon* is usually not present in samples assigned to the small-*Dyris* assemblage.

Synecology

Five assemblages were recognised by cluster analysis. Properties of the assemblages are listed in Tables 3 and 4.

1 - *Tryonia* Assemblage (Figure 4)

Composition — This assemblage is dominated (>10% abundance) by species of *Pachydon* (*P. obliquus* and others) and of *Tryonia*. The only indicator taxon (indicator value (IV) >30) is the *Tryonia* group. This assemblage is furthermore characterised by the comparatively common occurrence of *Neritina roxoi*-group + Thiaridae + Pachychilidae. (Almost) absent from this assemblage (IV 0-1) are Ampullariidae, perimarine taxa, pulmonates, *Corbicula* and Sphaeriidae.
Ecology — Endemicity is 86.0%. The *Tryonia* assemblage is dominated by infaunal taxa (74%), contains few substrate-dependant (3.2%) and stenotypic freshwater taxa (2.4%).
Environment — Shallow lacustrine. The comparatively common occurrence of non-endemic groups compared to the other assemblages (with the exception of the Thiaridae-Pulmonata assemblage described below), is interpreted as a sign of proximity to coastal settings or fluvial influence. Given the comparatively large amounts of small and rather delicate shells of *Tryonia*, the depositional environment was possibly protected from waves and currents. The common occurrence of organic matter (inclusive of wood fragments) may be indicative of dense (aquatic) vegetation (reed swamps, floating meadows, etc.).

2 - Tall *Dyris* Assemblage (Figure 5)

Composition — This assemblage is dominated by species of *Pachydon* (*P. obliquus* and others) and both the small and tall *Dyris* groups. The only indicator taxon (IV 62) is the tall *Dyris* group, which comprises *D. ortoni* (Gabb, 1869) and *D. lintea* (Conrad, 1871). Absent from this assemblage, or nearly so, are the *Neritina roxoi*-group, Ampullariidae, Thiaridae, perimarine taxa, pulmonates, Corbiculidae, Sphaeriidae and Hyriidae.
Ecology — Endemicity is 91.6%. The abundance of infaunal taxa (43.6%) is clearly below average, that of epifaunal gastropods well above. This assemblage contains few substrate-dependant (3.4%) and stenotypic freshwater taxa (2.2%).
Environment — Often samples assigned to this assemblage are found in comparatively coarse-grained deposits (often rich in organic matter) with abundant evidence for physical disturbance (*e.g.*, waves and currents). Shoreface environments (including submerged sandbars) appear therefore the most likely setting that sustained this assemblage.

3 - *Pachydon obliquus* Assemblage (Figure 6)

Composition — This assemblage is dominated by species of *Pachydon*, and *P. obliquus* in particular. Strictly speaking, there are no indicator taxa (IV >30), but *Pachydon obliquus* comes very close to qualifying as such (IV 27). Cochliopine gastropods are rare compared to the other assemblages. Absent from this assemblage (IV 0-1), or nearly so, are Ampullariidae, the tall *Dyris* group, Pachychilidae, Thiaridae, perimarine taxa, pulmonates, Corbiculidae, Sphaeriidae, Hyriidae and Mycetopodidae.
Ecology — Endemicity is 97.3%. The *Pachydon obliquus* assemblage is almost entirely made up of infaunal taxa (89.4%) and contains few substrate-dependent (4.0%) and very few stenotypic freshwater taxa (0.4%).
Environment — Lacustrine. The abundance of infaunal bivalves and the relative paucity of mainly epifaunal hydrobiids may point to the absence of aquatic plants, and thus deposition below penetration depth of sunlight. This is no indication of depth, since light penetration is surficial in modern Amazonian waters (Furch & Junk, 1997). Also, the environment was very low energetic. Judging from the mostly organic-rich sediments from which samples assigned to the *Pachydon obliquus* assemblage have been collected, the depositional environment was characterised by widespread dysoxia. The abundance of articulated *P. obliquus* may point to the most tranquil (and deepest) depositional environments in the Pebas system, estimated to have been in the order of 10-20 metres (Räsänen *et al.*, in prep.).

4 - Small *Dyris* Assemblage (Figure 7)

Composition — This assemblage is dominated by species of *Pachydon* (*P. obliquus* and others) and the small *Dyris* group. Indicator taxa (IV > 30) are the small *Dyris* group (IV 32), the other Cochliopinae group (IV 32), *Pebasia* (IV 35) and the *Ostomya* group (IV 31). The IV for perimarine taxa is low (11), but clearly higher than in the other assemblages. Absent from this assemblage, or nearly so, (IV 0-1) are the *Neritina roxoi* group, Ampullariidae, Pachychilidae, Thiaridae, pulmonates, Sphaeriidae and Hyriidae.
Ecology — Estimated endemicity is 93.3%. This assemblage is dominated by infaunal taxa (61%), contains few hard-substrate epifaunal (4.0%) and stenotypic freshwater taxa (0.9%).
Environment — Lacustrine (with rarely some marine influence). The common occurrence of well-preserved fragile shells, such as small species of *Dyris* and *Ostomya* points to very low-energy conditions, that might occur *e.g.* below fair-weather wave base.

5 - Thiaridae-Pulmonata Assemblage (Figure 8)

Composition — This assemblage is dominated by species of *Tryonia*, Thiaridae, pulmonates and Dreissenidae. Indicator taxa (IV > 30) are Thiaridae (IV 31), pulmonates (IV 55) and Dreissenidae (IV 32). Absent from this assemblage, or nearly so, (IV 0-1) are the *Neritina ortoni* group, both small and tall *Dyris* groups, perimarine taxa, *Pachydon obliquus*, *Pebasia* and species of *Ostomya*. The other *Pachydon* group is rare and has a very low indicator value compared to other assemblages.
Ecology — Estimated endemicity is with 14.4% very low compared to the other assemblages. The Thiaridae-Pulmonata assemblage also contains few (17.4%) infaunal taxa (compared to 67% for the overall fauna) but is rich in substrate-dependent (37.6%) and predominantly composed of stenotypic freshwater taxa (56.6%).
Environment — Fluviolacustrine-deltaic (river channels, floodplain lakes and swamps, seasonally flooded forests) and/or swamp. This assemblage contains only subordinate amounts of endemic Pebasian taxa. The assemblage includes groups that can be found in present-day Amazonian aquatic environments, such as ampullariids, pulmonates, freshwater cerithioideans, pearly freshwater mussels and sphaeriids.
Four of the five assemblages are dominated by cochliopine gastropods and pachydontine bivalves and characterised by very high rates of endemicity. The mean faunal composition of these four assemblages shows great similarity (similarity coefficients of average composition between .64 and .94), and their limits are not well defined. The fifth assemblage (Thiaridae-Pulmonata assemblage) is very different from the other four (similarity with the other four assemblages between -.01 and -.20). The endemicity of the Pebas fauna, and the wide range of morphological 'oddities' point to an isolated long-lived aquatic setting (either lake or inland sea; see discussion below). Boss (1978) distinguished two ecological groups which he referred to as 'moeities', in ancient (= long-lived) lake molluscan faunas.

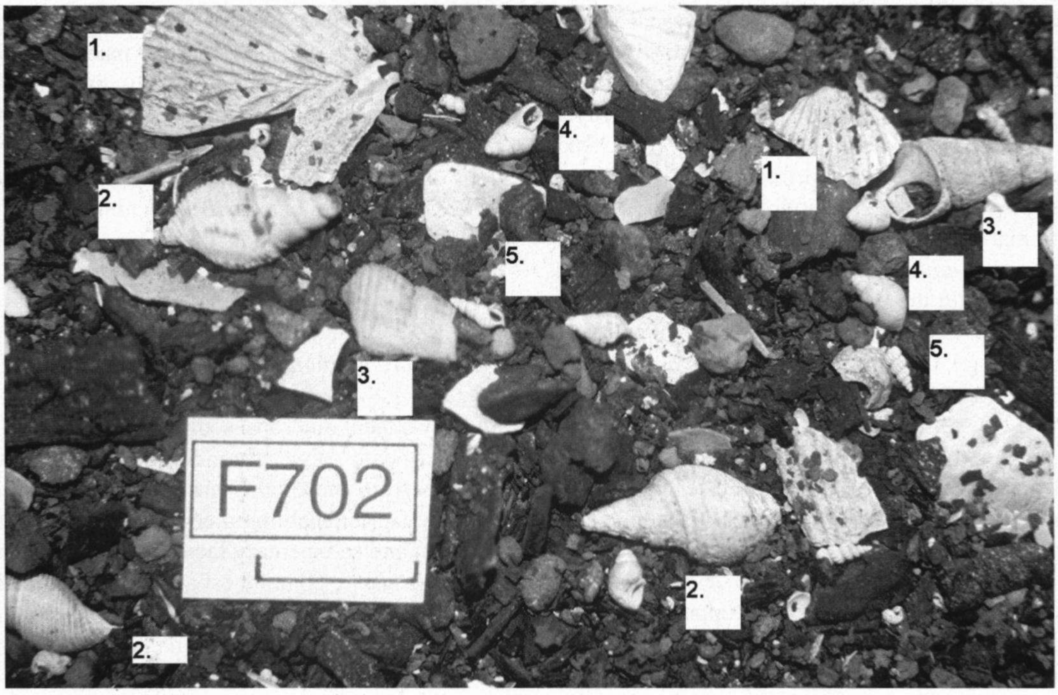

Figure 8. Example of a Thiaridae-Pulmonata assemblage residue. Scale bar represents 10 mm. Sample 702 (Porvenir: late Middle–early Late Miocene) is composed mostly of lignite/wood fragments. Molluscs belong mainly to cosmopolitan freshwater groups, such as the pearly freshwater mussel ?*Castalia* sp. (1) and the freshwater cerithioideans *Aylacostoma browni* (Etheridge, 1879) (2) and *Sheppardiconcha* sp. indet. (3). *Toxosoma* sp. indet. (4) and *Tryonia scalarioides* (5) are considered to be Pebasian endemics, and make up only subordinate amounts in samples assigned to the Thiaridae-Pulmonata assemblage.

One consists mostly of endemic elements and is restricted to lakes proper, the second contains various amounts of molluscan species with a wider distribution and is found in peripheral habitats of the lake. The four lacustrine assemblages contain percentages of endemics ranging from 86.0 to 97.3% (estimated abundance), and may therefore be assigned to Boss's lake moeity. The Thiaridae-Pulmonata assemblage, with its low percentage endemics (14.4% of estimated abundance) typically falls into Boss's peripheral moeity. The lacustrine moeity (97% of the samples) predominates markedly within the studied faunas.

Molluscan distribution and depositional environments

Sedimentary facies (and interpreted depositional environments) are shortly characterised in order to provide a framework for exploration of molluscan distribution in the different depositional environments represented by the Pebas system.

Sedimentary facies and ichnofossils

Pebas Formation deposits are dominated by small-scale (3-7m) generally coarsening-up parasequences (Räsänen *et al.*, 1998) reflecting drowning, maximum flooding, and shoaling. An ideal parasequence overlies sand or lignite strata. The basis of a parasequence is commonly a thin sandish interval, occasionally containing reworked bioclasts such as shells and wood fragments, overlying a wave ravinement surface. Commonly, this zone is characterised by marine trace fossils, such as *Asterosoma* and (well-developed) *Ophiomorpha* (Räsänen *et al.*, 2000). These ichnofossils in the Pebas Formation are large, and the ichnodiversity is high compared to ichnodiversity in non-marine settings. Upwards, the sediments turn rapidly into clays that are interpreted as maximum flooding intervals. These clays usually contain *in situ* (or nearly so) molluscan faunas (bivalves found in life position, either articulated or isolated valves found in close proximity). Often these clays directly overlie the basal contact, resulting in completely CU (coarsening-up) parasequences.

The clays grade upwards into lower shoreface clay-sand alternations and are topped by upper shoreface sands or lignites. Upwards-coarsening intervals of the sedimentary succession are consistently burrowed by brackish/marine ichnofauna, locally to a very high degree. Rarely to moderately bioturbated mud intervals are indicative of stressed (restricted) conditions (Räsänen *et al.*, 2000). Shelly faunas are not very common in these coarsening-up portions of the parasequences.

Parasequences can be incompletely or imperfectly developed. Most of the sands in the upper portions of the parasequences were formed along shorefaces and occasionally they represent beach settings (Räsänen *et al.*, 1998). Overlying lignites are sometimes separated from the underlying sandy interval by a thin (<0.5 m) organic-rich clay interval, representing slack deposition in back-barrier settings. Evidence for occasional emergent conditions (*i.e.*, rare palaeosols, mostly root traces) is found in the top parts of these parasequences. Almost every parasequence is capped by a *Glossifungites* surface. This ichnologic feature is related to burrowing (in this case of thalassinidean shrimps) in compacted substrates in meso-polyhaline settings and is often associated with transgressive erosion surfaces (Räsänen *et al.*, 2000).

Less common in the Pebas Formation, but nevertheless occurring regularly, are channel-like structures. These channels (up to *c.* 10 m in depth) are characterised by inclined heterolithic stratification, and commonly include structures that indicate tidally influenced subaquatic deposition (Räsänen *et al.*, 1995, 1998). Tidal deposits have been documented from the upper Pebas Formation (*i.e.*, in intervals also containing marine palynofloras and faunas; see Rebata, 1997; Räsänen *et al.*, 1998). Tidal deposits have now also been recognised in the middle and lower portions of the Pebas Formation (Räsänen & Irion, unpubl. data).

As a whole the sedimentary facies occurring in the Pebas Formation point to shallow, open aquatic (brackish to shallow marine) settings with intermittent shoals and occasionally beach/swamp/deltaic depositional environments. The difference between maximum flooding surfaces and the topmost part of the parasequences is usually between 3 and 7 m, which may give some indication for the maximum depth of the system (although some metres should be added to take into account compaction). Organic-rich maximum flooding horizons may reflect periods of extensive drowning and larger maximum depths (probably in the order of a few of tens of metres).

Molluscan distribution

For seventeen outcrops sedimentological and palaeontological data have been combined. Sixty molluscan samples from these outcrops could be assigned to sedimentary facies, enabling a comparison of molluscan distribution and sedimentary facies (Table 5).

Molluscs are commonest at the base of parasequences (intervals overlying ravinement surfaces, maximum flooding and lower shoreface intervals), but are quite rare in upper shoreface intervals.

Samples directly overlying the base of a parasequence (usually a wave ravinement) are dominated by *Pachydon obliquus* (42.1%) and the other *Pachydon* group (28.2%). Pebasian endemics dominate these samples (96.5%), but a few terrestrial and strictly freshwater groups (3.0%) occur as well. Samples from the maximum flooding intervals (including 'organic-rich' maximum flooding intervals, as well as the lowermost shoreface intervals) are very similar to the samples at the base of the parasequence. In the maximum flooding intervals, molluscan faunas contain more small *Dyris* (15.5% *vs* 6.5%), and fewer *Tryonia* (2.2% *vs* 6.2%) and tall species of *Dyris* (3.3% *vs* 9.4%, see Table 5). Terrestrial and strictly freshwater taxa are almost entirely lacking in the maximum flooding intervals (0.2% *vs* 3.0%). Samples from maximum flooding intervals are completely dominated by Pebasian endemics (99.0%), even more than in the samples at the base of the parasequences.

	wave revinement	maximum flooding	upper shoreface
n	14	40	5
Neritina ortoni group	0,4	0,9	0,7
Neritina roxoi group	0,2	0,0	0,0
Ampulariidae	0,1	0,0	0,0
Tall *Dyris* group	9,4	3,3	21,2
Small *Dyris* group	6,5	15,5	16,3
Tryonia group	6,2	2,2	6,4
Sioliella group	2,0	3,4	2,3
Other Cochliopinae	0,7	1,5	1,9
Pachychilidae	0,9	0,1	0,1
Thiaridae	0,2	0,0	1,4
Pulmonata	0,1	0,0	0,0
Dreissenidae	0,5	0,8	0,7
Hyriidae	0,5	0,1	0,0
Mycetopodidae	1,0	0,0	0,1
Pachydon obliquus	42,1	43,8	19,9
other *Pachydon* group	28,2	27,0	28,0
Pebasia group	0,4	0,6	0,4
Ostomya group	0,5	0,8	0,6

Table 5. Distribution of taxa in sedimentary facies. Numbers are estimated percentages.

Only five samples were available from upper shoreface intervals. These show the occurrence of some (1.4% of estimated abundance) *Neritina roxoi*-group + Thiaridae + Pachychilidae, are considerably enriched in cochliopine snails (44% *vs* 25-26% in the other assemblages, especially for the large *Dyris* group), and deprived in pachydontine bivalves (44% *vs* 70% for the other assemblages). The comparative low abundance of pachydontines is due only to the low abundance of *Pachydon obliquus*.

The bases of parasequences contain mainly samples assigned to the *Tryonia* assemblage, but also samples assigned to the small *Dyris* and *Pachydon obliquus* assemblages do occur. Maximum flooding intervals are dominated by samples assigned to the small *Dyris* assemblage and the *Pachydon obliquus* assemblage. Only five samples from upper shoreface intervals were available. Two of these belong to the small *Dyris* assemblage, one to the *Pachydon obliquus* assemblage and two to the tall *Dyris* assemblage. However, samples dominated by tall species of *Dyris* were commonly encountered in the upper portions of parasequences in Pebas Formation outcrops. The comparative rarity of molluscs in (upper) shoreface intervals, that make up a significant amount of the Pebas deposits, appears to be a feature characteristic of the entire Pebas Formation. Given the common preservation of sedimentary structures in these intervals, with only rare bioturbation traces, the lack of molluscs can be explained in terms of high sedimentation rates, physical disturbance of sediments, oxygen or salinity stress. The ichnofauna indicates elevated salinities as a possible reason for the lack of molluscs. However, salinity stress does not seem to be a good enough explanation, given the absence of molluscs with a wide range of salinity tolerances (including some 'marine' molluscs) in samples studied from other parts of the Pebas Formation. With common indications for physical reworking, neither does oxygen stress appear to be a reasonable explanation. Either high sedimentation rates, or common physical sediment disturbance (or both) should explain the relative paucity of molluscs in the upper parts of parasequences. Figure 9 summarises the distribution of assemblages in the different depositional environments of the Pebas system.

Geochemistry

During their life, molluscs record environmental information in the chemical composition of their shells. Shells yield information on the aquatic chemistry, provenance areas and climate during shell growth. The preservation of Pebasian molluscs is extraordinary (Vonhof *et al.*, 1998), rendering them especially suitable for this type of analysis. Sediment geochemistry provides additional clues for the interpretation of depositional settings, provenance areas and water chemistry.

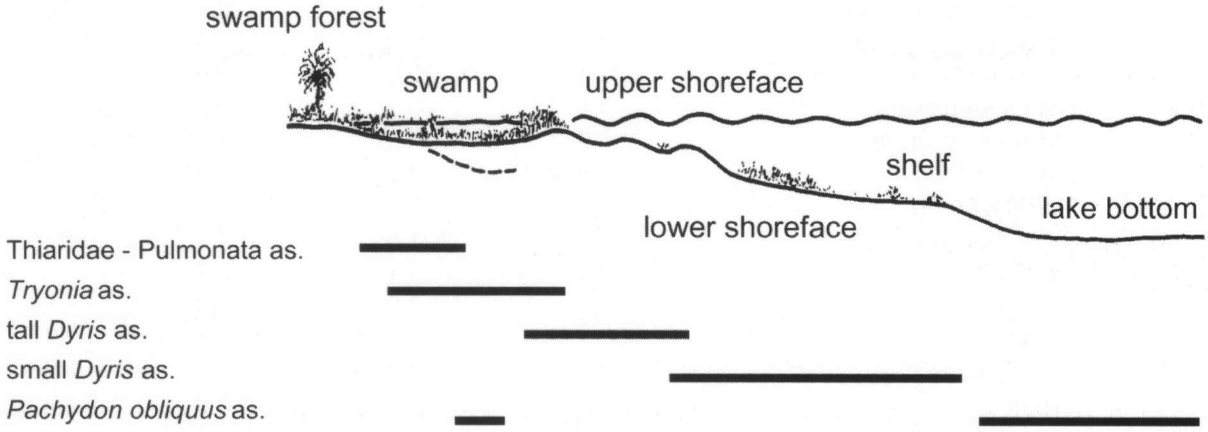

Figure 9. Inferred distribution of assemblages. Note that near-coastal dysoxic settings (*e.g.*, in channel scours, indicated by a dashed line) may contain the *Pachydon obliquus* assemblage, that otherwise dominates the deepest parts of the Pebas system. Shelf *c.* 5-10 m deep, lake bottom *c.* 10-?30m deep.

Isotope geochemistry

Strontium and stable isotope data published by Vonhof *et al.* (1998) indicate a freshwater depositional environment for the upper Pebas Formation (*Grimsdalea* Interval Zone of Hoorn, 1993), with the exception of incursion levels, where maximum salinities were calculated to range between 3 and 5 psu. Strontium isotope data from the middle and lower Pebas Formation (*Crassoretitriletes* Acme and *Psiladiporites/Crototricolpites* Concurrent Range zones of Hoorn, 1993, respectively) confirm the freshwater nature of the Pebas system. Pebas lake waters were, according to $^{86}/^{87}$Sr ratios, an admixture of predominantly Andean fluvial input (*c.* 70-80%) and shield-derived fluvial input (*c.* 20%). Based on end-member isotope water compositions inferred from strontium isotope compositions of upper Pebas Formation molluscs, Vonhof *et al.* (1998) calculated expected stable isotope compositions for the waters in the Pebas system. They interpreted a large positive excursion of observed δ^{13}C values in molluscan shells compared to the calculated water values as evidence for the lacustrine character of Pebasian depositional environments. δ^{18}O values were found to be very negative (usually in the range of –6 to –10 ‰), those of incursion levels were higher (in the range of –2 to –5 ‰). These very negative values of the Pebas shells agree well with a freshwater nature of the Pebas system as concluded from strontium analyses.

An additional 109 molluscs from seven samples were analysed for δ^{13}C and δ^{18}O. Data are shown in Appendix 4. As a whole, measurements (Figure 10) show some correlation between δ^{13}C and δ^{18}O (r^2 0.41; standard error of the estimate 1.55), and the isotope values are negative (typically between –4 and –10 ‰). The isotopic signature of molluscs from the seven measured levels broadly overlap. Specimens belonging to species that all samples have in common (*Pachydon obliquus* and *P. tenuis*) confirm the generalised isotopic signatures of samples as a whole (Figure 10).

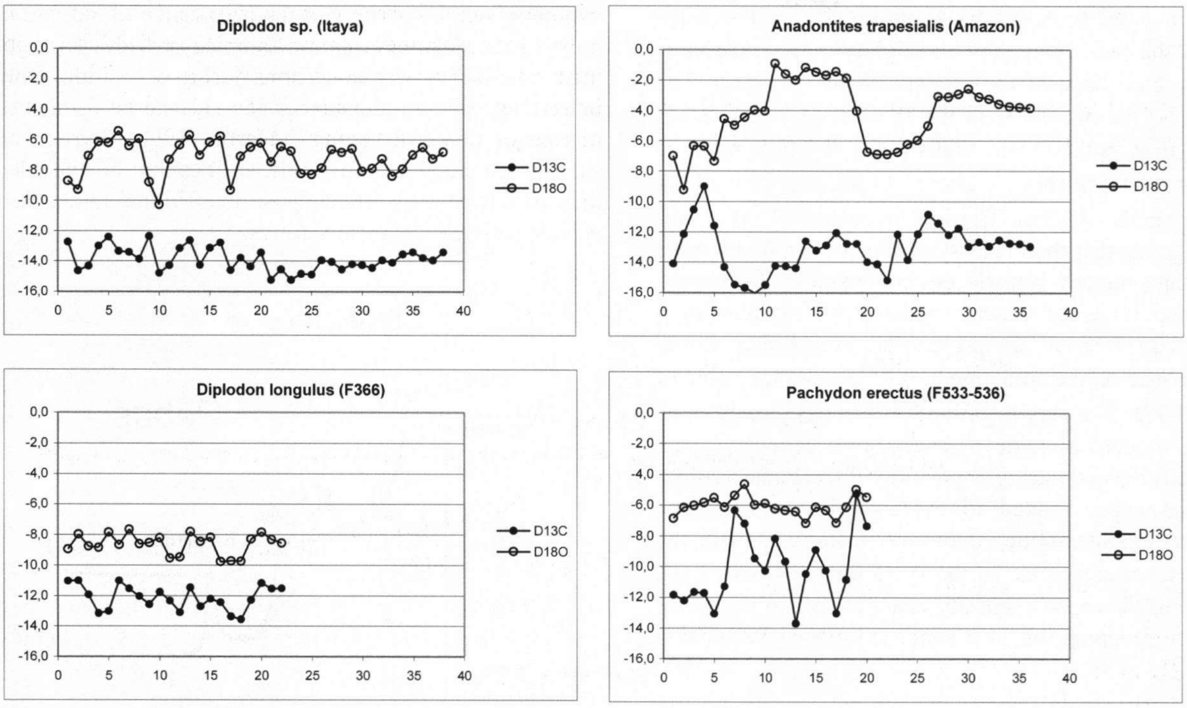

Figure 11. Stable isotope profiles through four shells. On the horizontal axis the growth increment number is indicated, going from juvenile to adult from left to right.

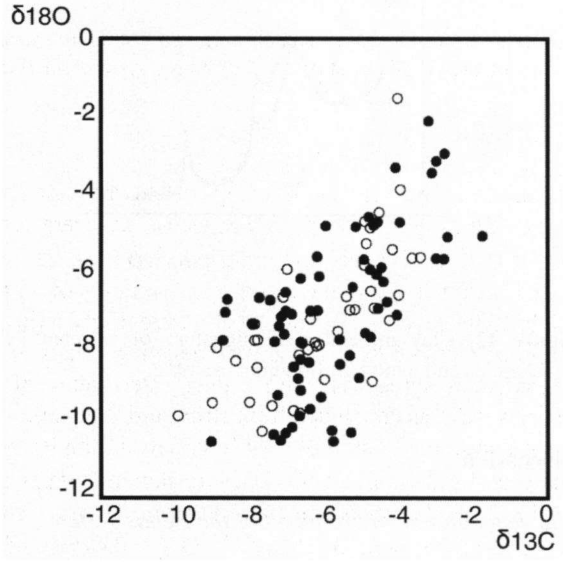

Figure 10. Stable isotope signature of species of *Pachydon* (*P. tenuis* and *P. obliquus* - filled circles) *vs* those of other species (open circles). No species-specific isotope signature differences can be observed. Both species of *Pachydon* occur in all assemblages measured.

Species-specific fractionation appears therefore subordinate as a source of isotopic variation between samples, although more measurements are needed to confirm this.

If the overall isotope signature of the Pebas shells points to freshwater settings, is it possible that we might have missed salinity changes on a seasonal or even finer scale? In order to address this question we have analysed isotope chemistry of shells along growth increments.

	mean D^{18}O	range D^{18}O	mean D^{13}C	range D^{13}C	n
Anodontites trapesialis	-4,2	8,3	-13,1	7,0	38
Diplodon sp.	-7,0	4,9	-13,9	2,9	36
Diplodon longulus	-8,6	2,1	-12,1	2,3	22
Pachydon erectus	-6,0	2,5	-10,1	8,4	20
various species (fossil)	-6,0		-7,2		110
all recent shells	-6,4		-8,3		74
all fossil shells	-5,6		-13,5		154

Table 6. Summary of stable isotope measurements.

For this pilot study, we have measured two fossil (Pebasian) and two modern (Amazonian) shells. Data are shown in Table 6, Appendix 4 and Figure 11. The mean $\delta^{18}O$ of the two fossil shells is slightly more negative (-7.3 ‰) than those of the modern shells (-5.6 ‰). The seasonal $\delta^{18}O$ amplitude of the fossils (2.0 – 2.5 ‰) is smaller than in the extant shells (4.9 – 8.3 ‰). Average $\delta^{13}C$ for the fossil shells is about –11 ‰, and those of the modern shells –13.5‰. The lower seasonal $\delta^{18}O$ amplitude suggests that the Pebas system was chemically more stable than modern aquatic environments in Amazonia. Residence times of waters in the Pebas system were longer than those of the present-day Amazonian floodplains, based on the enrichment of $\delta^{13}C$ isotopes (Vonhof *et al.*, 1998). The very negative $\delta^{18}O$ values clearly show that the modern climatic regime (the so-called Amazon hydrocell) existed during deposition of the Pebas Formation, and argue (added to evidence from Sr isotope analyses) against saline conditions. Combined with the low seasonal amplitude of the $\delta^{18}O$ for the fossil shells this excludes seasonal salinity changes due to excessive (seasonal) evaporation in a supposed closed Pebas system.

Sediment geochemistry

Twenty-seven samples from the Pebas Formation have been analysed for clay mineralogy (Figure 12). Pebas Formation clay mineral assemblages are dominated by low-charged smectite. Kaolinite is rare, and illite is very rarely encountered in Pebas Formation sediments. No differences in clay mineralogical composition have been found between samples from different stratigraphic levels of the Pebas Formation, or from different facies. Many of the smectite clays of the Pebas Formation contain *in situ* articulated valves of *Pachydon*. The co-occurrence of the smectite with these obligate aquatic taxa indicates that smectite is allochthonous to the Pebas Formation. Smectite can form as a result of weathering of a variety of source rocks (sediments) in poorly drained settings, such as floodplains. Rivers draining smectite-rich Neogene deposits in western Amazonia, such as the Jurua and Purus, yield a smectite- dominated clay mineral assemblage resembling that of the Pebas Formation (Figure 12). These modern river samples contain both high- and low-charged type of smectite. The latter thus probably originated in poorly drained Andean floodplains made up of comparatively immature sediments. Mineral assemblages (Kronberg *et al.*, 1989; Hoorn, 1994b) as well as the strontium isotope signature (Vonhof *et al.*, 1998) underline the Andes as a predominant source of sediments and water in the Pebas system. The fine-grained smectite clays are responsible for the unusual preservation of fossils in the Pebas Formation.

Pyrite does occur in some intervals in the upper Pebas Formation where marine incursions have been demonstrated. Otherwise pyrite is very rare or lacking. Siderite is abundant in the Pebas Formation. The scarcity or complete lack of pyrite and the abundance of siderite in most of the Pebas Formation samples provides an argument against brackish conditions during deposition. Only in very specific circumstances can siderite be formed in marine or brackish settings (Martin, 1999). Pyrite and siderite are diagenetic minerals, so it cannot be excluded that their formation reflects post-depositional rather than syndepositional chemical settings.

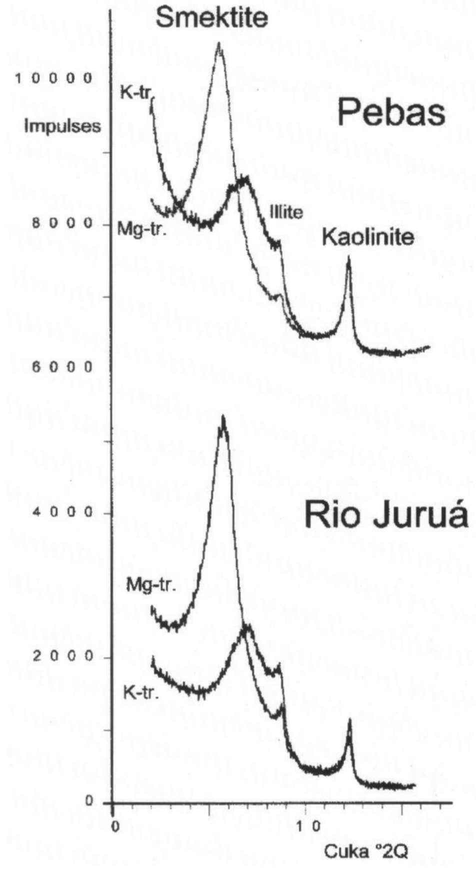

Figure 12. Clay mineralogical signature of selected Pebas samples and a modern floodplain sample.

Discussion

The depositional environment of the Pebas system

To start with, we shall summarise and discuss the palaeontological, geochemical and sedimentological characteristics of the Pebas Formation, as well as implications of these for the reconstruction of Miocene Amazonian palaeoenvironments. Secondly, we shall compare these data with several characteristics of modern environments to which the Pebas system has been compared in previous works. Finally, we shall synthesise the depositional system of the Pebas Formation, and link Miocene landscape evolution in western Amazonia to biotic evolution of the area.

A summary of characteristics for the Pebas system

* Molluscs

The extremely high endemicity and morphological diversity of the dominant hydrobiid snails and pachydontine bivalves is a clear indication of the evolutionary longevity of the Pebas system. The general signature of the fauna is similar to that of the modern Caspian Sea. The latter fauna is dominated by a highly diverse and endemic stock of (otherwise marine) limnocardiid bivalves and hydrobiid gastropods, and contains common dreissenids and neritids. The Caspian Sea is currently an inland sea, with salinities ranging between 0 and *c.* 16 psu. There is a balance between inflowing rivers and evaporation, and this maintains this salinity. The Caspian Sea is now not connected to the oceans, but in its Neogene-Quaternary history it used to be at various times. In 52% of the samples from the Pebas Formation stenotypic freshwater molluscs occur, often in life position. This contradicts a supposed brackish origin for much of the Pebas Formation that might be interpreted from the Caspian analogue. Furthermore, the few extant relics of taxa dominating the Pebas fauna (the pachydontine *Anticorbula*, and the cochliopines *Sioliella* and *Dyris*) all are freshwater forms (see *e.g.*, Wesselingh, 2000), illustrating the uncertainty of uniformitarian-based salinity inferences for long-lived environments.

There are no representatives of cosmopolitan marine and marginal marine molluscan taxa in the Pebas Formation, other than at incursion intervals in its upper part, where melongenid, nassariid and pyramidellid gastropods occur, as well as the bivalves *Macoma* (Vonhof *et al.*, 1998; van Aartsen & Wesselingh, 2000) and *Panamicorbula*. Even at the incursion intervals widespread marginal marine taxa such as oysters, mussels, arcids, and littorinids are wanting. In modern settings, such a pattern is explainable in terms of salinity regimes: the marginal marine taxa that do occur in the Pebas Formation have been reported from salinities around 3 psu and higher (*e.g.*, Rodriguez, 1963). This agrees very well with inferred maximum salinities of 3-5 psu for the incursion intervals using Sr isotopes (see below).

The predominance of pachydontine corbulids and the paucity of corbiculid bivalves, a group widely distributed in modern and Cainozoic freshwater environments of South America, may be explained by widespread dysoxia in the Pebas system. Many extant corbulid taxa are well adapted to low-oxygen conditions (Beesley *et al.*, 1998; Lewy & Samtleben, 1979). Intervals dominated by *in situ Pachydon obliquus* are often composed of black organic-rich clays. The other dominant group, cochliopine gastropods, is not known for its tolerance of low-oxygen conditions. It is possible that low-oxygen conditions were confined to lake-bottom sediments, as a result of high organic input and decomposition, and affected the water column only marginally. Cochliopine snails might have avoided unfavourable conditions by clinging onto erect or floating vegetation.

The molluscan fauna of present-day Amazonian aquatic environments is notably poor in species. The seasonally flooded parts of the floodplains are characterised by an abundance of ampullariid and pulmonate snails and sphaeriid bivalves (Irmler, 1975; pers. obs.). Floodplain lakes that do not suffer periodic anoxia, as well as smaller channels, harbour mainly unionoid bivalves. These faunas are markedly different from the Pebas fauna which is characterised by the predominance of pachydontines and cochliopines, and the (near-) absence of ampullariids, freshwater pulmonates and sphaeriids. Based on the molluscan faunas alone it is possible to exclude widespread floodplain conditions in the Pebas system, with the exception of depositional intervals containing the Thiaridae-Pulmonata assemblage faunas.

A comparatively high diversity and endemicity of the Pebasian molluscan faunas is at odds with a saline inland sea, apart from an evolutionary long-lived inland sea, or an estuarine origin. These two environments are characterised by low to very low faunal diversity, and by the dominance of widely distributed taxa.

* Ostracods and other invertebrate fossils

Muñoz-Torres *et al.* (1998) recorded a fauna of thirty-one species of ostracods from the Pebas Formation, all of them endemic to the Miocene of western Amazonia. *Cyprideis* is represented by a flock of seventeen species, making up over 90% of the individuals. Species of *Cyprideis* occur in athalassic, brackish and hyper-saline environments worldwide. According to Whatley *et al.* (1996, p. 233) the Pebasian ostracod fauna is comparable only to faunas known from 'brackish marginal marine or athalassic environments of low energy'. Strictly freshwater ostracods are rare in the Pebas Formation, as well as species reflecting marine settings. The high diversity of the genus *Cyprideis* in the Pebas is attributed to 'evolution in a stable, isolated body of saline water throughout the Miocene' (Whatley *et al.*, 1996, p. 233). Both ostracods and molluscs show high levels of endemicity, and are dominated by groups whose extant members live in a range of salinities. The abundance of Cyprideidae has been used to argue for brackish palaeoenvironments. However, comparison with the marine-like Pachydontinae which have a single descendant widespread in freshwater ecosystems, serve as a clear warning against using the highly endemic and extinct ostracods in a uniformitarian way to assess palaeosalinities, a fact that has been acknowledged by Whatley *et al.* (2000). Sr isotope ratios measured on a few of the Pebasian cypridid ostracods (H. Vonhof, unpubl. data) show a freshwater signature for them.

Foraminifera (mostly *Ammonia* spp.) are commonly found in incursion intervals, but have not been recognised in other samples so far. Barnacles were found in two samples. Rodriguez (1963) reported barnacles in Lake Maracaibo to occur in salinities as low as 2 psu.

* Plants and pollen

Based on composition of the pollen flora as well as on sedimentary structures, Hoorn (1993, 1994a, b) concluded that the Pebas Formation had been deposited in a fluvio-lacustrine system comparable to modern white-water Amazonian floodplains, with some marine influence. Most of the pollen taxa from the Pebas samples are also present in slightly older fluvial deposits to the north, the Mariñame Sand Unit. Both pollen floras are dominated by the same groups, but the Pebasian pollen flora is considerably enriched in spores compared to the Mariñame flora (*e.g.*, *Verrucatosporites usmensis* (van der Hammen, 1956) and *Psilamonoletes tibui* van der Hammen, 1956) make up an average of *c.* 40% in the Pebas flora compared to only *c.* 10% in the Mariñame flora). Such a difference may well result from prolonged transport in rivers that emptied into a lake environment. Robust spores survive transport better than less robust pollen (G. Sarmiento, pers. comm.). Hoorn (1993) found mangrove pollen, indicative of perimarine settings, in two intervals in the Pebas Formation, *viz.* in the Early–early Middle Miocene *Psiladiporites-Crototricolporites* Concurrent Range Zone (*c.* 20-17 Ma), and in the late Middle–early Late Miocene *Grimsdalea* Interval Zone (*c.* 12-10 Ma). The latter interval contains incursion levels that have been corroborated by isotope data and the occurrence of perimarine molluscs, foraminifera and barnacles (Hoorn, 1994a; Vonhof *et al.*, 1998). Other indicators of marine influence do not accompany the occurrence of mangrove pollen in the lower Pebas Formation. Mangroves occur along the southern shores of Lake Maracaibo (Wesselingh & Räsänen, pers. obs.), where salinities are close to 0 psu. Connection to marine habitats may thus be more important for the appearance of mangrove taxa than salinity. Furthermore, mangroves have been reported along riverbanks far inland, out of reach of marine influence (Morley, 2000). Hoorn (1993) used the occurrence of the fern *Acrostichum* in the Middle Miocene *Crassoretitriletes* Acme Zone of the Pebas Formation (*c.* 17-12 Ma) to infer coastal plain settings. There are no marine molluscan species, isotope data or mangrove pollen to support such an interpretation. *Acrostichum* have also been observed along freshwater lakes in Indonesia (B. Morley, pers. comm). Remains of plants and trees are not uncommon in the Pebas Formation. In a few cases shallow-rooting stumps of trees were found, indicating the presence of (swamp-) forests. Pollen of *Mauritia*-like palms are common in the Pebas flora. These palms are typical of parts of floodplains which experience prolonged flooding. All these data point to the presence of swamp forests rather than Terra Firme rainforest within the Pebas system.

Charophyte oogenia are common in the Pebas Formation, indicating the common presence of shallow, low-energy waters.

* Fishes

The fish remains of the Pebas Formation show a mixed ecological picture. Strictly freshwater inhabitants, such as cichliids (P. Gaemers, pers. comm.) and piranhas (Monsch, 1998) occur. Extant relatives of the most abundant Pebas fish taxa (*e.g.*, Sciaenidae, catfish) occur both in modern Amazonian freshwater and coastal South American ecosystems. The presence of both myliobatid and dasyatid teeth throughout Pebas Formation deposits (Monsch, 1998; J. Lundberg, pers. comm.) suggests marine influence. Freshwater rays (potamotrygonoids) are abundant in present-day Amazonia, but only very few remains from the Pebas Formation could be attributed with certainty to this family (J. Lundberg, pers. comm.).

The combination of obligate freshwater and marine rays is known from *e.g.* Lake Maracaibo (Venezuela). Marine rays are abundant, and are found up into the deltas surrounding the lake. The occurrence of marine rays in the Pebas Formation therefore does not indicate brackish settings during deposition *per se* but also may be explained as a result of a restricted connection of the Pebas system to the sea.

* Sedimentology

The predominance of coarsening-up parasequences in the Pebas Formation is at odds with a supposed fluvial origin of these deposits as proposed by Hoorn (1993, 1994a, b). Fluvial cycles are usually fining-up, see *e.g.* Räsänen *et al.* (1998). Tidal deposits have been recognised in various parts of the Pebas Formation (Räsänen *et al.*, in prep.). Although large inland basins may experience microtidal regimes, the widespread tidal deposits in the Pebas Formation suggest a common connection to marine environments. The marine signature of the ichnofacies supports such an interpretation, but contradicts indications excluding widespread brackish conditions in the Pebas Formation from molluscs and isotope geochemistry. The blueish-turquoise clays of the Pebas Formation with common organic material are indicative of widespread bottom dysoxia.

* Sediment geochemistry

Clay composition in the Pebas Formation is completely dominated by low-charged smectite that presumably resulted from weathering of volcanic source material in poorly drained floodplains of rivers draining the Andes. A predominantly Andean sediment source in the Pebas system is also shown by heavy mineral assemblages (Kronberg *et al.*, 1989; Hoorn, 1994b), as well as the strontium isotope signature (Vonhof *et al.*, 1998). The almost complete lack of kaolinite in the Pebas indicates the absence of Terra Firme habitats. The scarcity of pyrite (apart from incursion levels) and the abundance of siderite in Pebas Formation deposits point to freshwater settings, although it cannot be excluded that these reflect post-depositional conditions.

* Isotope geochemistry

The strontium signature of Pebasian shells reflects, apart from times when marine incursions did reach the area, a predominantly Andean freshwater component and a minor shield freshwater component (Vonhof *et al.*, 1998). The incursion level published in Vonhof *et al.* (1998) was deduced to be a mixture of shield freshwater and marine waters, with maximum salinities not exceeding 5 psu. Biogeographic evidence (Nuttall, 1990a; Vonhof *et al.*, 1998) points to a northerly (Caribbean) origin of marine influence. Based on the Sr isotope signature of the shells, the incursions found in the upper Pebas Formation must have entered through shield areas. Vonhof *et al.* (1998) concluded that the Apoporis region in Colombia (Hoorn, 1994b) was the most likely pathway of marine invasions in the Pebas system from the Llanos Basin.

Vonhof *et al.* proposed that a marked enrichment of $\delta^{13}C$ compared to expected values (those of modern Amazonian rivers) is an indication of a lacustrine palaeoenvironment. This is furthermore supported by the lower amplitude of (seasonal) $\delta^{18}O$ variation in the fossil shells compared to the modern shells. In general, Pebasian $\delta^{18}O$ values are negative (typically between –4 and –8 ‰ PDB). These values resemble the low $\delta^{18}O$ values found in modern western Amazonian freshwater bodies as a result of extensive recycling of rainwater ('the Amazon hydrocell'). These very low $\delta^{18}O$ values argue for similar wet climatic regimes in the Pebas, and exclude an inland sea setting whose salinities were maintained by evaporation (Kaandorp *et al.*, 2000).

A comparison of the Pebas system with modern systems

In the literature (*e.g.*, Nuttall, 1990a; Hoorn, 1993, 1994a, b; Räsänen *et al.*, 1998; Whatley *et al.*, 1998; Vonhof *et al.*, 1998), the Pebas system has been compared to a variety of modern depositional environments. Here, we briefly characterise these depositional systems, and list similarities and dissimilarities between them and the Pebas system.

* Long-lived lakes

Examples of modern long-lived lakes include giant lakes, such as Lake Baikal (Russia) and Lake Tanganyika (Africa), and small ones such as Lake Ohrid (Balkan). Long-lived lakes are located in (semi)enclosed drainage basins, often in tectonically active areas. These lakes are usually deep and chemically stable: water residence times are long. They usually contain freshwater, but the geochemical composition may vary depending on evaporation regimes in, and influx of dissolved salts from, the catchment area. Many of the long-lived lakes experience stratification, commonly depriving deeper parts from oxygen (Lake Baikal being a notable exception). No visible tides have been reported from these lakes. Longevity is typically in the order of magnitude of 10^6-10^7 years. The invertebrate fauna of long-lived lakes is largely endemic and diverse (both in numbers of species and adaptive traits) and has originated from freshwater ancestors (Michel, 1994, 2000). The presence of species flocks is a typical feature of these lakes.

Long-lived lakes and the Pebas system share their (taxonomically and morphologically) diverse, endemic flocks of hydrobiid species. The high diversity of endemic bivalves and ostracods of marine/brackish origin in the Pebas system (Pachydontinae and Cyprididae) is at odds with a long-lived lake environment, as are other marine indicators such as marine rays, mangroves and marine ichnofossils.

* Caspian Sea

The Caspian Sea is a unique system: it is evolutionarily long-lived and brackish. The Caspian Sea is located in an isolated drainage system, but was occasionally connected in its geological past to the oceans. Salinities range from 0 psu in the northern part and near river entrances to *c.* 16 psu in the southern parts of the sea. Hypersalinity is common in lagoons surrounding the sea. A balance of influx of river waters with low concentrations of dissolved salts and an overall evaporative climatic setting maintain the salinity. No oxygen stratification appears in the Caspian Sea. Microtides have been demonstrated. The Caspian Sea has existed at least for some 10 million years. The invertebrate fauna of the Caspian Sea is completely dominated by systematically and morphologically diverse endemic clades that have originated from both freshwater and marine ancestors (Dumont, 2000). The latter group sets the Caspian Sea fauna apart from long-lived lake faunas. Only in (the vicinity of) delta areas do more widely distributed, stenotypic freshwater taxa abound. The Caspian Sea and the Pebas system share their overall molluscan compositions dominated by hydrobiid snails and endemic bivalves of marine origin (Limnocardiidae *vs* Pachydontinae). Furthermore, both systems commonly contain dreissenids and neritids. The ostracod fauna is similarly endemic and diverse.

However, stenotypic freshwater molluscan species, commonly found *in situ* in the Pebas Formation, are restricted to marginal (deltaic) environments in the Caspian Sea. The very negative ^{18}O signature of many of the Pebas shells is incompatible with salinities maintained by evaporation; this should have led to considerably higher oxygen isotope ratios.

* Saline inland lakes or playa lakes

Examples of these are found in (semi-)desert areas worldwide. Saline inland lakes are located in isolated drainage basins. Many of these lakes dry up entirely during the dry season. Salinity varies, from freshwater (in times of massive influx of runoff), to saline and hypersaline. Tides are absent. Stratification leading to oxygen depletion in the lake does occur, despite their shallow nature. Sediments deposited in these systems often contain abundant evaporitic minerals. Saline inland lakes are usually geologically short-lived (10^3-10^5 years), and many exist only on a seasonal scale. The invertebrate faunas of these lakes are typically very low in species numbers. These taxa are morphologically conservative, and often widespread in other, similar systems. Occasionally marine indicators, such as foraminifera, occur even very far inland in this type of environment (Gasse *et al.*, 1987; Patterson et al., 1997).

Whatley *et al.* (1998) suggested that the delicate preservation of Pebasian ostracod shells could be attributed to deposition in an inland saline lake. The foraminifer *Ammonia* and 'marine' bivalves and gastropods have been reported from Saharan salt lakes (Gasse *et al.*, 1987), making them a potential analogue to the Pebas system. However, the general signature of the fauna of saline lakes and the Pebas system is very different. No highly diversified endemic faunas are known from saline inland lakes (apart from the Caspian Sea, discussed above). Furthermore, saline conditions in the Pebas system are defined by the highly negative $\delta^{18}O$ signature of the shells and the common presence of *in situ* stenotypic freshwater taxa. Apart from possibly secondary gypsum at a few levels, evaporites are not found in Pebas Formation deposits, and the tidal deposits known from the Pebas Formation are unknown from saline lake environments.

* Estuaries

Estuaries are zones of constant mixing of river- and seawater. Often, mixing occurs along predictable gradients from riverwater to seawater (Eisma *et al.*, 1976). The water residence time varies, depending on size and configuration, from days to weeks. Many estuaries experience strong to very strong tidal regimes. They are usually well oxygenated. For the last 2 Myr, estuaries are short-lived geological phenomena (10^3-10^4years), linked to short periods of sea level rise. The invertebrate faunas of estuaries are characterised as specimen rich, but species poor. Typically, non-endemic taxa of widespread genera dominate.

The Pebas system and (tropical) estuaries have abundant hydrobiids in common, as well as the presence of euryhaline fish taxa, mangroves, marine ichnofossils and tidal deposits. These two systems differ, however, in the molluscan faunal signature (taxonomic and morphological diversity, high endemicity in the Pebas). Furthermore, the *in situ* occurrence of stenotypic freshwater molluscs is only known from the uppermost (freshwater) reaches of estuaries, but common in Pebas Formation deposits. The Sr signature and the commonly highly negative $\delta^{18}O$ signature in the Pebas are at odds with brackish conditions. Enrichment of $\delta^{13}C$ in Pebas molluscs indicates residence times longer than those in estuaries. Estuarine indicators such as oysters, mussels, arcids and littorinids are lacking in the Pebas. Pyrite is commonly formed in estuarine settings, but is very scarce in the Pebas Formation.

* Lake Maracaibo

Lake Maracaibo in western Venezuela is a large lake (14,344 km^2) located at sea level, and connected to the sea through the Maracaibo straits (Rodriguez, 1963). Another, similar coastal system is the Cienega Grande of northern Colombia (von Cosel, 1986). Lake Maracaibo is located in a tectonically active (subsiding) area. The waters in the lake are mainly derived from the catchment area. Some direct precipitation and some influx of marine waters also occur, resulting in a freshwater to oligohaline lake (Holmden *et al.*, 1997). The lake is not very deep (only some 35 m) and appears to be rather well oxygenated. With 10 years (Holmden *et al.*, 1997), water residence times are higher than in fluvial or estuarine environments, but much lower than in long-lived lake environments. Microtides are present in the lake, which came into existence only some 10,000 years ago, with the rising sea level of the last deglaciation. The molluscan fauna of Lake Maracaibo is dominated by a few widely distributed species of generalist groups, occurring worldwide in tropical marginal marine and freshwater environments, viz. *Polymesoda* spp., *Neritina* spp. and the gastropod *Melanoides tuberculatus* (Müller, 1774) (Rodriguez, 1963; pers. obs.). Rodriguez (1963) documented faunal clines in the Maracaibo straits related to salinity regimes. For instance, he found that common marine indicators, such as thaiid and littorinid snails as well as mussels and oysters, occurred in salinities typically exceeding 5 psu. Maracaibo Lake and the Pebas system share the presence of mangroves, the combination of freshwater and marine stingrays and their tidal signature. Both systems are predominantly composed of waters received from their catchment areas but Lake Maracaibo experiences some marine influence as shown by low salinities (*e.g.*, Rodriguez, 1963).

The species-poor, cosmopolitan nature of the Maracaibo molluscan fauna is in sharp contrast to the diverse endemic Pebas fauna. No strictly freshwater taxa, such as unionoids, have been recognised during brief visits by the senior author to the lake in 1996 and 1997. Sulphur is very common in reductive deltaic sediments in the Maracaibo system, which should translate in the formation of pyrite. Pyrite is very rare in the Pebas Formation, where siderite dominates.

* White-water floodplains of the Amazon system ('varzea')

The floodplains of the main Amazon River (known as varzea) are mainly aquatic depositional environments. The active floodplains are usually tens of kilometres wide, and experience almost total inundation during the wet season. During the dry season (difference between highest and lowest water levels are in the order of 10 m in many places) the rivers become well defined by their levees. The major part of the varzea in the dry season is occupied by floodplain lakes and by seasonally flooded forests. Varzeas have been extensively documented by Sioli (1984) and Junk (1997). Residence times of waters are short. Rivers and inundated floodplains are well oxygenated. In floodplain lakes seasonal anoxia is common (Junk, 1997). The chemical composition of the water is entirely dominated by the Amazon River. Like Lake Maracaibo, the present-day varzeas originated at the beginning of the Holocene some 10,000 yrs ago (Irion *et al.*, 1995). The molluscan fauna of the varzea is dominated by obligate freshwater and terrestrial taxa, such as pearly freshwater mussels, sphaeriids, ampullariids and pulmonates (Irmler, 1975; Wesselingh, pers. obs.). The fauna is not diverse, and composed of widespread species.

The Pebas system and the varzea share their highly negative $\delta^{18}O$ signature, the Andean-dominated geochemical signature of the waters, and the common occurrence of *Mauritia*-like palms. The molluscan faunas of these two systems are very different. Morphologically and taxonomically diverse endemic groups dominate the Pebas fauna, whereas the varzea fauna is species-poor, and entirely dominated by obligate freshwater taxa. No mangroves, marine rays, marine ichnofauna or tidal deposits are known from the central and upper Amazon varzeas.

None of the above-mentioned modern environments is similar to the Pebas system. The Pebas system contains evidence of marine influence (marine ichnofauna, tidal deposits, mangrove pollen, marine rays), while on the other hand there is evidence of the (ecologically) prolonged isolated nature of the Pebas system: the highly diverse and endemic nature of molluscan and ostracod faunas. Strontium and oxygen isotopes and the common occurrence of obligate freshwater taxa point to predominantly freshwater settings. These conflicting indications occur together in the same beds, so they are not explained in terms of successive facies changes.

Synthesis: landscapes and landscape evolution in Miocene western Amazonia

The Pebas system may be characterised as a geologically long-lived aquatic system of huge size. Continuous, tectonically induced accommodation and rapid sediment infill drove the depositional system. The aquatic system was driven by precipitation in the catchment area and the lake itself, though there must have been connection to marine settings. The Pebas system contained shoals and swamps but lacked extensive emerged environments. At times, marine incursions invaded this lake.

Andean rivers, loaded with sediments from the emerging hinterland, likely formed an extensive swamp-delta fringe on the western and southern margins of the lake system. From the east, rivers draining shield areas and low-lying tropical forests entered Lake Pebas. This type of rivers carry little sediment. Nevertheless, Räsänen *et al.* (in prep.) record some deltaic structures of an easterly origin in the Pebas system. Outflow of freshwater and marine incursions were towards and from areas north of the Pebas system (Hoorn *et al.*, 1995; Vonhof *et al.*, 1998; Lundberg *et al.*, 1998). It cannot be excluded that some marine connection with the Pacific existed at that time through south-central Ecuador (Steinmann *et al.*, 1999). Very little is known about the stability of the Pebas system in terms of water-level fluctuations. Water-depth fluctuations recorded in the parasequences are interpreted to reflect local drowning, as a result of tectonic subsidence, and shoaling as a result of progradation (Räsänen *et al.*, 1998), lake-level variation or even eustacy (Hoorn, 1993; Räsänen *et al.*, 2000).

Lake Maracaibo is a good modern example of a precipitation-driven system connected to the sea. Lake Pebas was far larger than Lake Maracaibo, and may have been separated from the sea by two sills instead of one; one between Lake Pebas and the Llanos area, and a temporary one between the Llanos area and the Maracaibo or eastern Venezuela Basin. Tectonics rather than eustatic sea level change controlled the influx of saline waters into the Llanos Basin (Villamil, 1999), and also may have controlled overflow of the (episodic) marine Llanos into the Pebas system (L.G. Marshall & Lundberg, 1996).

Various terms have been applied to describe the setting in which the Pebas Formation was deposited. The use of poorly defined terms has caused considerable confusion amongst geologists and biogeographers, and therefore we discuss some of the names applied to the Pebas system here.

Floodplain environments (Hoorn, 1993, 1994a; Hoorn *et al.*, 1995) hardly seem an appropriate term for the Pebas system which was permanently aquatic with minor swamps and fluvial influence, and was connected to marine environments. To illustrate this: only 8 of 285 studied samples contained fauna comparable to (but not identical with) modern floodplain faunas.

The use of the term seaway (Räsänen *et al.*, 1995; Webb, 1995), despite the occurrence of marine influences, also appears inappropriate to describe the Pebas system, and has caused a lot of confusion (Hoorn, 1996; L.G. Marshall & Lundberg, 1996; Paxton *et al.*, 1996).

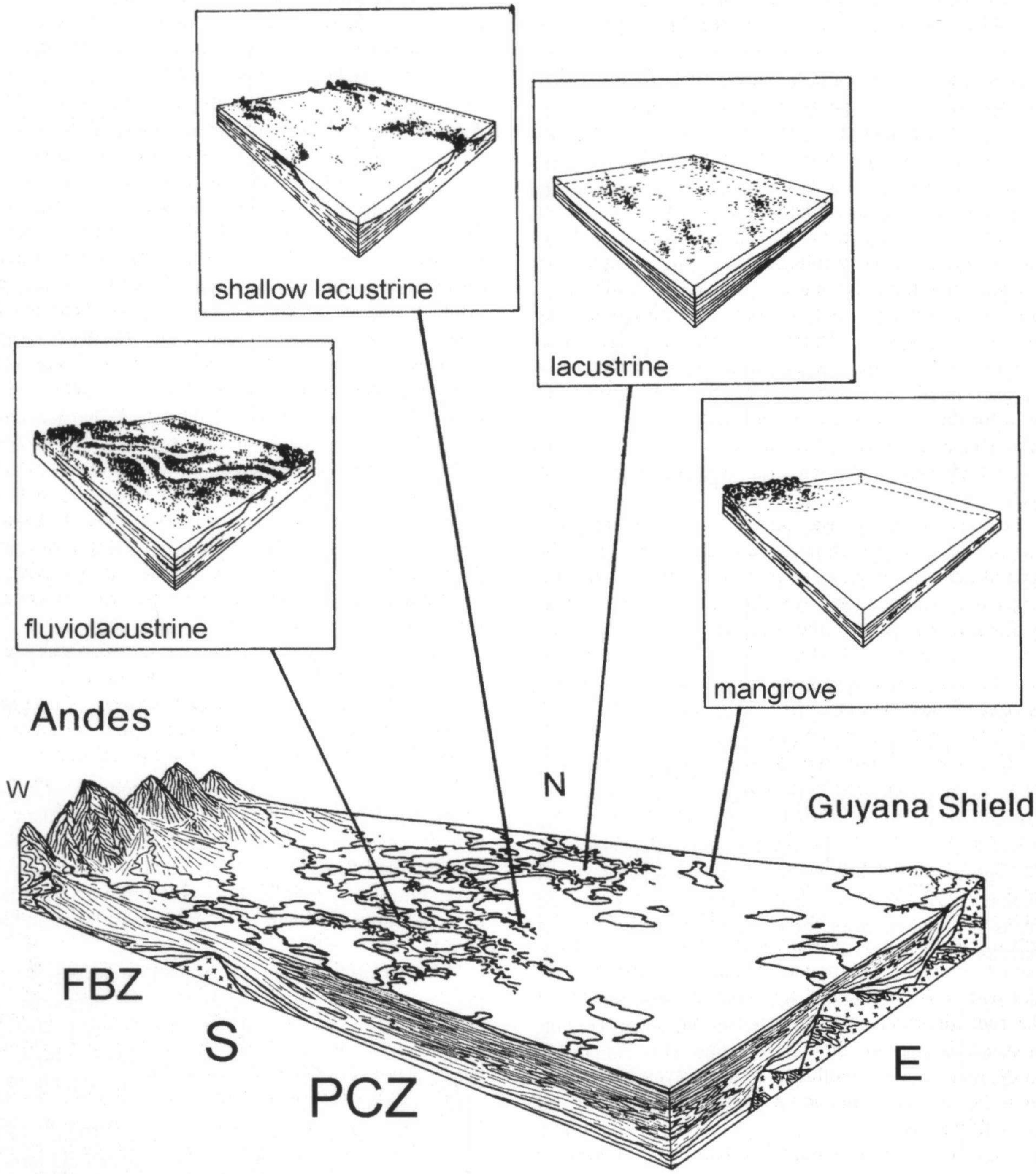

Figure 13. A palaeoenvironmental impression of Lake Pebas. The Andes to the left, the Guyana shield in the upper right-hand corner. The width of the block diagram is *c.* 1,500 km. Abbreviations: FBZ - Foreland Basin Zone, PCZ - Pericratonic Zone.

The notion proclaimed by Webb (1995) that Miocene western Amazonia was a marine area, with sea arms stretching south, east, west and north, is not supported by data at all.

Whatley *et al.* (1996) referred to an 'inland sea' to suggest a hydrologically closed saline lake, whose salinity was maintained by inflow of salts with rivers and evaporation in the lake itself. This was not the case in the

Pebas system as evidenced by *e.g.* the occurrence of mangroves and the highly negative $\delta^{18}O$ signature.

Neither is 'coastal plain environment' a suitable term to use for the entire Pebas system. The Pebas system was merely a large body of water with islands, swamps and shores. These areas might be classified as (non-marine!) coastal plain environments. Estuaries are orders of magnitudes smaller than the Pebas system. They are geologically short-lived and do not have large bodies of water with comparatively long residence times as in the Pebas. They also lack highly endemic faunas. We have chosen to name the system Lake Pebas. However, use of this term is not free from problems either. A lake suggests no connection to the sea (but see *e.g.*, Lake Maracaibo), and does not describe perfectly the episodic brackish settings in the Pebas system. There is no modern depositional setting similar to the Pebas system, so arguably a new environmental term might be considered. An appropriate term for the Pebas system would be 'para-marine megalake' ('marine-like megalake'). This lake happened to be located adjacent to the sea, and was thus perimarine as well.

The Pebas system was located in a series of active foreland basins and adjacent pericratonic regions. This type of huge geographic systems, occupied by long-lived water bodies of 'abnormal' salinities is known from the geological record, *e.g.*, the Neogene Paratethys of central/eastern Europe (of which the Caspian Sea is a relic) and the Late Cretaceous Clearwater Seaway of northern America. Thus, on a large (subcontinental) tectonic scale the Pebas system is not unique.

How then is it possible that a system with some connection to marine environments is not invaded by cosmopolitan, marginally marine taxa? The combination of the freshwater nature of the system with widespread dysoxia would have induced 'ecological' isolation. This isolation was insufficient to prevent some marine organisms (rays, ichnofauna, mangroves) to invade and establish in the area, but apparently prevented the successful establishment of widespread marginally marine molluscs and ostracods that should be competitively superior to the endemic species of the Pebas in any ordinary, marginal marine environment. This issue deserves further study, and Miocene molluscan, ostracod and fish faunas from the Llanos Basin should provide excellent material to elucidate this.

The Pebas system attained a huge size (Figure 1). Pebasian molluscs assigned to the Middle Miocene *Crassoretitriletes* Acme Zone have been found in boreholes as far west as the Pastaza region in Peru (*c.* 75°30'W) and as far east as Fonte Boa, Brazil (*c.* 66°°W). An even more easterly extension cannot be ruled out. Faunas from this interval are known from outcrops as far north as the lower Caqueta region in Colombia (*c.* 1°S), and as far south as the lower Urubamba valley in Peru (*c.* 11°S). The maximum size of the system during the Middle Miocene is in the order of magnitude of 1.1 million km^2. An irregular form of the system may downsize this estimate somewhat; on the other hand, the possibility that the system extended during the Middle Miocene more easterly than at present acknowledged may put the figure somewhat higher. A size of 1.1 million km^2 is roughly three times the size of the Caspian Sea. It is likely that Lake Pebas originated much earlier than the late Early Miocene. Rather low-diverse, yet typical pachydontine/cochliopine faunas are known from the Late Oligocene–earliest Miocene La Cira fauna of the Magdalena and Llanos basins in Colombia (Pilsbry & Olsson, 1935; Nuttall, 1990a; Guerrero, 1997). The Early Miocene La Tagua fauna of southern Colombia is a stratigraphically intermediate fauna between the La Cira and Pebas faunas *sensu stricto*. The La Cira and La Tagua faunas are characterised by the occurrence of *Pachydon hettneri* (Anderson, 1928), the Pebas fauna by the occurrence of *Pachydon obliquus* (Nuttall, 1990a). The La Tagua fauna was also found in cores from the Pastaza-Maranon foreland basin below intervals containing Pebasian molluscan fauna *s. str.* (Wesselingh, unpubl. data). This implies that the Pebas, La Tagua and La Cira faunas occurred during different time intervals in the same system that must have spanned at least 17 million years. The system was probably continuously (to some extent) lacustrine: the (intermittent) establishment of fluvial or marine palaeoenvironments would have eradicated the endemic *Pachydon*-dominated faunas.

The earliest lake (containing the La Cira fauna) occupied a narrow foreland basin zone east of the North Andean thrust front during the latest Oligocene, the deposits of which became later incorporated into intramontane basins. This lake gradually expanded (south)east onto the edge of the South American craton (*e.g.*, Cooper *et al.*, 1995; Villamil, 1999). It split into the Llanos Lake/embayment in the north and Lake Pebas in the south during the Early Miocene (Figure 14). During this time, the region experienced at least two periods of extensive marine ingressions, one during the late Middle Miocene (*c.* 12 Ma: Vonhof *et al.*, 1998) and the other during the late Early Miocene (contemporary with marine incursions in the Mariñame Sand Unit of Colombian Amazonia; see Hoorn, 1994b). More periods of extensive marine influence could have occurred in this system, but have not been demonstrated so far.

The Pebas-Llanos system may well have played a role in the adaptation of marine biota to freshwater Amazonian ecosystems. Lovejoy *et al.* (1998) calculated that potamotrygonoid rays evolved from marine ancestors in the Amazon system during the Early-Middle Miocene, as based on molecular-genetic divergence rates calibrated with a geological vicariance event of known age. This would comply with the age of the Pebas system. However, new fossil finds of potamotrygonoid rays in the Pebas Formation cast doubts on the age estimates of Lovejoy *et al.* (J. Lundberg, pers. comm.). The oldest fossils of some 'marine-like' Amazonian taxa (iniid dolphins, manatees, potamotrygonoid rays and the pachydontine *Anticorbula*) appear to be of Miocene age

(Lovejoy *et al.*, 1998; Lundberg, pers. comm.). Rainforest biota, apart from those of swamp forests, cannot have flourished in western Amazonia during the existence of Lake Pebas. The large size of the system, as well as its longevity, must have created a formidable barrier to dispersal of terrestrial biota, and have promoted separate evolution on the west and east sides of the lake. Possibly, divergence patterns within terrestrial groups, such as *e.g.* snakes (Zamudio & Greene, 1997) and poison frogs (Clough & Summers, 2000), may (in part) be attributable to Lake Pebas, and should not solely be attributed to the Andean montane or Panamanian seaway dispersal barriers. Lake Pebas is thought not to have continued into the Parana-Plate river basins (Lundberg *et al.*, 1998), allowing interchange of terrestrial biota along its southern shores. A possible southerly connection, however, is still subject of debate. The modern rainforest biota could only start to develop in western Amazonia after fluvial Amazonian ecosystems had replaced Lake Pebas, somewhere between 9 and 8 Myr ago (Lundberg *et al.*, 1998).

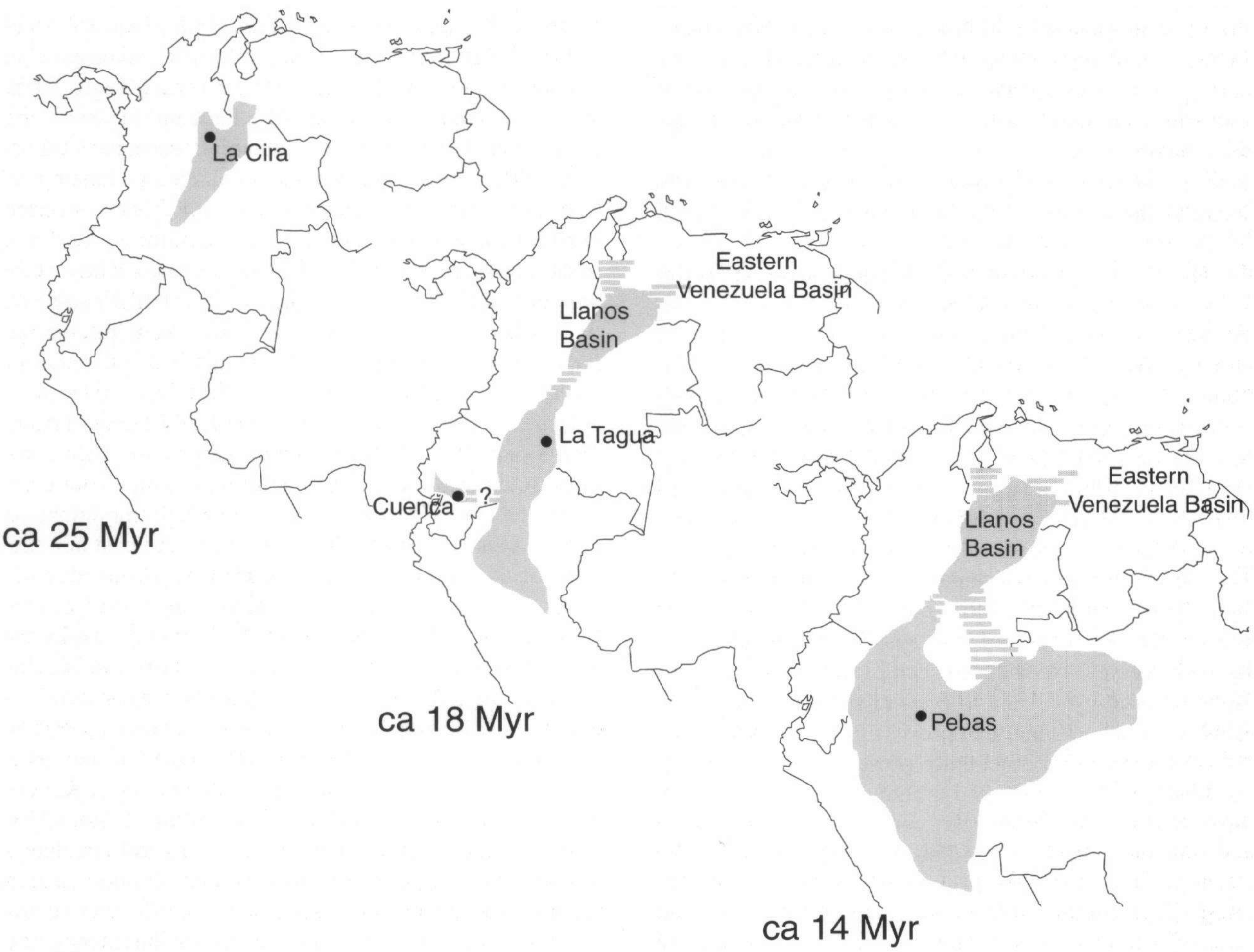

Figure 14. Evolution of Lake Pebas.

Conclusions

Molluscan faunas from the Miocene Pebas Formation of Peruvian Amazonia are characterised as almost entirely aquatic, endemic and extinct. The fauna is dominated by pachydontine bivalves and cochliopine gastropods in numbers of species and specimens.

Five assemblages are described from the Pebas fauna. One of these resembles modern Amazonian floodplain assemblages, but it makes up only 3% of the samples studied. Endemic pachydontine bivalves and cochliopine gastropods dominate the other four assemblages, which are assumed to represent evolutionarily long-lived endemic molluscan communities.

The taxonomic composition of the molluscan fauna and shell isotope geochemistry indicate that (open) aquatic settings dominated the Pebas system. Sedimentological and isotope data, as well as specific fossil plant and animal groups, point to widespread shallow conditions. Swamps were not uncommon in Lake Pebas. Due to the largely endemic and extinct character of the molluscan (as well as the ostracod) fauna it is difficult to assess palaeosalinities in the Pebas system based on the uniformitarian approach. Isotope data from the shells show that, apart from brief periods when marine incursions reached western Amazonia and conditions were oligo-mesohaline, Lake Pebas was composed of (mainly Andean-derived) freshwater. The occurrence of (rare) strictly freshwater taxa in more than half of the samples supports a predominantly freshwater signature. Bottom dysoxia was widespread, explaining the abundance of pachydontine corbulids and the near-absence of corbiculid bivalves.

The molluscan and ostracod faunas and isotope data both indicate a long-lived lake depositional environment for the Pebas Formation. The term lake does fully cover the system, but is more appropriate than other terms. Lake Pebas was neither deposited in an interior seaway nor in floodplain settings nor in an inland (hydrologically closed) lake setting. Based on the presence of marine organisms (rays, mangroves) and the occurrence of tidal deposits throughout the Pebas Formation, a connection to marine environments is proposed. Lake Pebas was located in a freshwater tidal basin with only occasional marine incursions. It is best described as a paramarine megalake, which happened to be perimarine as well.

The ichnofauna includes common brackish assemblages, also in intervals where isotope and faunal data indicate strictly freshwater settings. The use of documented salinity preferences of extant marginal marine taxa in reconstructing palaeosalinities in evolutionary long-lived lake systems is not straightforward, as is shown *e.g.* for the Pebasian Corbulidae and the Caspian Limnocardiidae.

The maximum size of Lake Pebas is estimated to have been *c.* 1.1 million km^2. Tectonic accommodation and precipitation in its hinterland mainly drove its persistence. The initial lake presumably formed during the latest Oligocene in the Colombian east Andean foreland basins (including the Magdalena Basin at that time), and expanded gradually eastward, separating into a Llanos-Sea/Lake in the north and Lake Pebas in the south. The system persisted for *c.* 17 million years, although few data on the early and the latest parts of its history are available. The Pebas-Llanos system may have played some role in the evolution of marine taxa in Amazonian freshwater ecosystems. It may also have played a significant, hitherto unrecognised, role as a dispersal barrier of terrestrial biota on the east and west sides of the lake.

Acknowledgements

For all their help we thank Jose Arimuya (Bellavista Nanay, Peru), Charles Barnard (Nationaal Natuurhistorisch Museum, Leiden, the Netherlands); Rafael Bunimuya (INRENA, San Roque, Peru), Gerhard Cadée (Nederlands Instituut voor Onderzoek der Zee, Den Burg, the Netherlands), Alejandro Chalco (formerly OXI, Lima, Peru), Pieter Gaemers (Leiden, the Netherlands), Gerald Ganssen (Vrije Universiteit, Amsterdam, the Netherlands), Edi Gittenberger (Nationaal Natuurhistorisch Museum, Leiden, the Netherlands), Javier Guerrero (UN, Bogotá, Colombia), Henry Hooghiemstra (Universiteit van Amsterdam, the Netherlands), Hugo the boatsman (Iquitos, Peru), John W.M. Jagt (Natuurhistorisch Museum Maastricht, the Netherlands), Arie W. Janssen (Nationaal Natuurhistorisch Museum, Leiden, the Netherlands), Salomon Kroonenberg (Tech-nische Universiteit Delft, the Netherlands); Henri Laurent (formerly OXI, Lima, Peru), John Lundberg (Academy of Natural Sciences of Philadelphia, USA), Kenny Monsch (Bristol University, UK), Bob Morley (Cambridge, UK), Fernando Muñoz-Torres (Ecopetrol, Bucaramanga, Colombia), Luisa Rebata (UTU, Turku, Finland), Kalle Ruokolainen (UTU, Turku, Finland), Juan Saldarriaga (Tropenbos-Colombia, Bogotá, Colombia), Jukka Salo (UTU, Turku, Finland), Gustavo Sarmiento (UN, Bogota, Colombia), Pepe Torres (UNAP, Peru), Hanna Tuomisto (UTU, Turku, Finland), Geerat Vermeij (University of California, Davis, USA), Antonio Villa (formerly INDERENA, Leticia, Colombia), Jaana Vormisto (UTU, Turku, Finland), John de Vos (Nationaal Natuurhistorisch Museum, Leiden, the Netherlands), Kitty Vijverberg (formerly Universiteit van Amsterdam, the Netherlands), Rob van Weezel (formerly Nationaal Natuurhistorisch Museum, Leiden, the Netherlands), Cor Winkler Prins (Nationaal Natuurhistorisch Museum, Leiden, the Netherlands) and Francisco Zavaleta (formerly OXI, Lima, Peru). Maaike Wickardt performed the tedious task of putting in order stratigraphic data in Appendix 1. Patrick Nuttall (formerly The Natural History Museum, London, UK) not only provided an absolutely brilliant starting point for this taxonomy-based research (*i.e.* his 1990 paper), but also greatly contributed to clarifying systematic matters through discussions during the early stages of the present work. In particular, we wish to thank Carina Hoorn (formerly UVA, Amsterdam, the Netherlands), who initiated the palaeontological research on the Pebas Formation, introduced the first author to the Pebas faunas and facilitated initial fieldwork in Colombia and Peru, and, last but not least, contributed enormously to our knowledge of the geological history of northwest Amazonia.

References

Aartsen, J.J. van & Wesselingh, F.P. 2000. New *Odostomia* species (Gastropoda, Heterobranchia, Pyramidellidae) from the Miocene Pebas Formation of Western Amazonia (Peru, Colombia). *Basteria* 64, 163-168.

Adams, H. 1860. Description of a new genus of freshwater bivalve Mollusca, belonging to the family Corbulidae, from the collection of Hugh Cuming, Esq. *Proceedings of the Zoological Society of London* 28, 203.

Anderson, F.M. 1928. Notes on Lower Tertiary deposits of Colombia and their molluscan and foraminiferal fauna. *Proceedings of the California Academy of Sciences* 17, 1-28.

Anderson, L. 1996. Neogene paleontology in the northern Dominican Republic, 16. The family Corbulidae (Mollusca, Bivalvia). *Bulletins of American Paleontology* 110, 6-34.

Baker, F.C. 1945. *The molluscan family Planorbidae*, 530 pp. Urbana (Illinois Press).

Baldock, J.W. 1982. Geology of Ecuador: explanatory bulletin of the National geological map of the Republic of Ecuador scale 1:1,000,000. MRNE, Quito.

Beesley, P.L., Ross, G.J.B. & Wells, A. (eds), 1998. *Mollusca: the Southern Synthesis. Fauna of Australia* 5, 1234 pp. Melbourne (CSIRO Publishing).

Berggren, W.A., Kent, D.V., Aubrey, M.-P. & Hardenbol, J. (eds), 1995. Geochronology, time scales and global stratigraphic correlation. *Society of Economic and Petroleum Mineralogists, Special Publication* 54.

Bernardi, A.C. 1856. Description des coquilles nouvelles. *Journal de Conchiology* 5, 82-84.

Boettger, O. 1878. Die Tertiarfauna von Pebas am oberen Marañon. Jahrbuch der Königlichen-Kaiserlichen Geologische Reichsanstalt Wien 28, 485-540.

Boss, K.J. 1978. On the evolution of gastropods in ancient lakes. *In*: Fretter, V. & Peake, J. (eds). *Pulmonates, 2a: Systematics, evolution and ecology*, 385-428. London (Academic Press).

Cadée, G.C. 1984. 'Opportunistic feeding', a serious pitfall in trophic structure analysis of (palaeo)faunas. *Lethaia* 17, 289-292.

Cernohorsky, W.O. 1984. Systematics of the family Nassariidae (Mollusca: Gastropoda). *Bulletin of the Auckland Institute and Museum* 14, 1-357.

Clough, M. & Summers, K. 2000. Phylogenetic systematics and biogeography of the poison frogs: evidence from mitochondrial DNA sequences. *Biological Journal of the Linnean Society* 70, 515-540.

Conrad, T.A. 1871. Descriptions of new fossil shells of the upper Amazon. *American Journal of Conchology* 6, 192-198.

Conrad, T.A. 1874. Remarks on the Tertiary clay of the Upper Amazon with descriptions of new shells. *Proceedings of the Academy of natural Sciences Philadelphia* 1874, 25-32.

Cooper, M.A., Addison, F.T., Alvarez, R., Coral, M., Graham, R.H., Hayward, A.B., Howe, S., Martinez, J., Naar, J., Peñas, R., Pulhma, A.J. & Taborda, A. 1995. Basin development and tectonic history of the Llanos Basin, Eastern Cordillera, and Middle Magdalena Valley, Colombia. *American Association of Petroleum Geologists Bulletin* 79, 1421-1443.

Cosel, R. von 1978. Die Gattung *Polymesoda* Rafinesque, 1820 an der Nordküste Südamerikas (Bivalvia: Corbiculidae). *Archiv für Molluskenkunde* 108, 201-213.

Cosel, R. von 1986. Moluscos de la region de la Cienaga Grande de Santa Marta (Costa del Caribe de Colombia). *Anales Instituto Investigaciones del Mar, Punta de Betin* 15/16, 79-370.

Costa, E.V. 1981. Revisão gastropodes fosseis da localidade do Tres Unidos, Formacao Pebas, Plioceno do Alto Amazonas, Brasil. *Anais II Congresso Latino-Americano Palaeontologia*, Porto Alegre, Abril 1981, 635-649.

Crosse, H. 1872. Diagnosis molluscorum Novae Caledoniae incolarum. Journal de Conchyliogie 20, 69-75.

Darrigan, G.A. 1992. Variación temporal y espacial de la distribucion de las especies de *Corbicula* Megerle, 1811 (Bivalvia, Corbiculidae), en el estuario del Rio de La Plata, Republica Argentina. *Neotropica* 38, 59-63.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345-366. Dumont, H.J. 2000. Endemism in the Ponto-Caspian fauna, with special emphasis on the Onychopoda (Crustacea). *Advances in Ecological Research* 31, 181-196.

Eisma, D., Mook, W.G. & Das, H.A. 1976. Shell characteristics, isotopic composition and trace-element contents of some euryhaline molluscs as indicators of salinity. *Palaeogeography, Palaeoclimatology, Palaeoecology* 19, 39-62.

Etheridge, R. 1879. Notes on Mollusca collected by C. Barrington Brown, Esq., A.R.S.M., from the Tertiary deposits of Solimoes and Javary Rivers, Brazil. *Quarterly Journal of the Geological Society of London* 35, 82-88.

Figueiredo Alvarenga, L.C. de & Ricci, C.N. 1989. Especie nova de *Mytilopsis* Conrad, 1857, do Rio Tocantins, Tucurui, Para, Brasil (Mollusca, Bivalvia, Dreissenidae). *Memorias do Instituto Oswaldo Cruz* 84, 27-33.

Furch, K. & Junk, W.J. 1997. Physicochemical conditions in the floodplains. *In*: Junk, W.J. (ed.). The central Amazon floodplain: Ecology of a pulsing system. *Ecological Studies* 126, 69-108.

Gabb, W.M. 1869. Descriptions of fossils from the clay deposits of the Upper Amazon. *American Journal of Conchology* 4, 197-200.

Gasse, F., Fontes, J.C., Plaziat, J.C., Carbonel, P., Kaczmarska, I., de Deckker, P., Soulié-Marsche, I., Callot, Y. & Dupeuble, P.A. 1987. Biological remains, geochemistry and stable isotopes for the reconstruction of environmental and hydrological changes in the Holocene lakes from North Sahara. *Palaeogeography, Palaeoclimatology, Palaeoecology* 60, 1-46.

Gittenberger, E. & Janssen, A.W. (eds), 1998. De Nederlandse zoetwatermollusken. Recente en fossiele weekdieren uit zoet en brak water. *Nederlandse Fauna* 2, 1-288.

Glaubrecht, M. 1996. Evolutionsökologie und Systematik am Beispiel von Süss- und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): Ontogenese-Strategien, paläontologische Befunde und historische Zoogeographie, 499 pp. Leiden (Backhuys Publishers).

Gorthner, A. 1992. Bau, Funktion und Evolution komplexer Gastropodenschalen in Langzeit-Seen mit einem Beitrag zur Paläobiologie von *Gyraulus 'multiformis'* im Steinheimer Becken. *Stuttgarter Beiträge zur Naturkunde* (B)190, 1-173.

Greve, L. de 1938. Eine Molluskenfauna aus dem Neogen von Iquitos am Oberen Amazonas in Peru. *Abhandlungen der Schweizerischen paläontologischen Gesellschaft* 61, 1-133.

Guerrero, J. 1997. Stratigraphy, sedimentary environments, and the Miocene uplift of the Colombian Andes. *In*: Kay, R.F., Madden, R.H., Cifelli, R.L. & Flynn, J.J. (eds). *Vertebrate paleontology in the Neotropics, the Miocene fauna of La Venta, Colombia,* 15-43. Washington D.C. (Smithsonian Press).

Haas, F. 1949. On fresh water mollusks from the Amazonian region. *Anales Instituto Biologico del Universidad de Mexico* 20, 301-314.

Haase, M. & Bouchet, P. 1998. Radiation of crenobiontic gastropods on an ancient continental island: the *Hemistomia*-clade in New Caledonia (Gastropoda: Hydrobiidae). *Hydrobiologia* 367, 43-129.

Hammen, T. van der 1956. A palynological systematic nomenclature. *Boletino Geologico* 4, 63-101.

Hedberg, H.D. 1936. Stratigraphy of the Rio Querecual section of northeastern Venezuela. *Bulletin of the Geological Society of America* 48, 1971-2024.

Hershler, R. & Thompson, F.G. 1992. A review of the aquatic subfamily Cochliopinae (Prosobranchia: Hydrobiidae). *Malacological Review*, Suppl. 5, 1-140.

Holmden, C., Creaser, R.A. & Muehlenbachs, K. 1997. Paleosalinities in ancient brackish water systems determined by ^{87}Sr/^{86}Sr ratios in carbonate fossils: A case study from the Western Canada sedimentary basin. *Geochimica Cosmochimica Acta* 61, 2105-2118.

Hoorn, C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105, 267-309.

Hoorn, C. 1994a. An environmental reconstruction of the paleo-Amazon River system (Middle to Late Miocene, NW Amazonia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 112, 187-238.

Hoorn, C. 1994b. *Miocene palynostratigraphy and paleoenvironments of northwestern Amazonia: evidence for marine incursions and the influence of Andean tectonics,* 156 pp. Amsterdam (University of Amsterdam) (unpubl. PhD thesis).

Hoorn, C. 1996. Technical comments: Miocene deposits in the Amazonian Foreland Basin. *Science* 273, 122, 123.

Hoorn, C., Guerrero, J., Sarmiento, G.A. & Lorente, M.A. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* 23, 237-240.

IFG, 1984. Mapa planimetrico de imagenes de satelite, 1:250.000. Neu Isenburg (IFG).

Irion, G., Müller, J., Nunes de Mello, J. & Junk, W.J. 1995. Quaternary geology of the Amazonian lowland. *Geo-Marine Letters* 15, 172-178.

Irmler, U. 1975. Ecological studies of the aquatic soil invertebrates in three inundation forests of Central Amazonia. *Amazoniana* 3, 337-409.

Junk, W.J. (ed.) 1997. The Central Amazon floodplain. Ecology of a pulsing system. *Ecological Studies* 126, 1-525.

Kaandorp, R.J.G., Vonhof, H.B., Wesselingh, F.P. & Ganssen, G.M. 2000. Stable isotope records of climate variation in growth increments of Amazonian fresh water bivalves. *European Union of Geological Sciences, 25th Annual Meeting,* Nice, Abstracts, 1 pp.

Kelleher, B., van der Velde, G. & bij de Vaate, A. 1999. Nu ook levende *Mytilopsis leucophaeata* (Dreissenidae) in de Waal. *Correspondentieblad van de Nederlandse Malacologische Vereniging* 307, 26-28.

Kronberg, B.I., Franco, J.R., Benchimol, R.E., Hazenberg, G., Doherty, W. & VanderVoet, A. 1989. Geochemical variations in Solimoes Formation sediments (Acre Basin, western Amazonia). *Acta Amazonica* 19, 319-333.

Kuiper, W. 2000. De weekdieren van de Nederlandse brakwatergebieden (Mollusca). *Faunistische Mededelingen* 12, 41-120.

Lamarck, J.B.A.P. M. de, 1819. *Histoire naturelle des animaux sans vertèbres.* Bivalvia 6, 1-233. Paris (Déterville & Verdière).

Lange de Morretes, F. 1949. Ensaio de Catalogo dos Moluscos do Brasil. *Arquivos do Museu Paranaense* 7, 1-194.

Leistikow, A. & Janssen, R. 1997. A record of the bivalve *Guianadesma sinuosum* Morrison from the central Amazon basin (Bivalvia: Corbulidae). *Basteria* 61, 17-22.

Lewy, Z. & Samtleben, C. 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia* 12, 341-351.

Lovejoy, N.R., Bermingham, E. & Martin, A.P. 1998. Marine incursion into South America. *Nature* 396, 421, 422.

Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L. & Wesselingh, F. 1998. The stage for Neotropical fish diversification: A history of tropical South American rivers. *In*: Malabarba, L.R. *et al.* (eds). Phylogeny and classification of neotropical fishes, 13-48. Porto Alegre (Edipurcs).

Maia, R.G., Godoy, H.K., Yamaguti, H.S., de Moura, P.A., Da Costa, F.S., de Holanda, A.M. & Costa, J. 1977. *Projeto de Carvao no Alto Solimoes. Relatorio Final,* 137 pp. Rio de Janeiro(CPRM-DNPM).

Marshall, L.G. & Lundberg, J.G. 1996. Technical comments: Miocene deposits in the Amazonian Foreland Basin. *Science* 273, 123, 124.

Marshall, W.B. 1927. New Uruguayan mollusks of the genus *Corbicula.* Proceedings of the United States National Museum 66, 1-12.

Martin, R.E. 1999. *Taphonomy: a process approach,* 508 pp. Cambridge (Cambridge University Press).

McCune, B. & Mefford, M.J. 1999. *PC-ORD. Multivariate analysis of ecological data, version 4.* Gleneden Beach (MjM Software Design).

Michel, E. 1994. Why snails radiate: a review of gastropod evolution in long-lived lakes, both recent and fossil. *Archiv für Hydrobiologie* (Beiheft Ergebnisse der Limnologie) 44, 285-317.

Michel, E. 2000. Phylogeny of a gastropod species flock: exploring speciation in Lake Tanganyika in a molecular framework. *Advances in Ecological Research* 31, 275-302.

Monsch, K.A. 1998. Miocene fish faunas from the northwestern Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143, 31-50.

Morley, R.J. 2000. *Origin and evolution of tropical rain forests,* 362 pp. Chichester (John Wiley & Sons).

Müller, O.F. 1774. *Vermium terretrium et fluviatilium, seu animalium Infusoriorum, Helminthicorum, et Testaceorum, non marinorum succincta historia* 2, 1-214.

Müller, P., Geary, D.H. & Magyar, I. 1999. The endemic molluscs of the late Miocene Lake Pannon: their origin, evolution, and family-level taxonomy. *Lethaia* 32, 47-60.

Muñoz-Torres, F., Whatley, R. & van Harten, D. 1998. The endemic non-marine Miocene ostracod fauna of the Upper Amazon Basin. *Revista española de Micropaleontologia* 30, 89-105.

Nuttall, C.P. 1990a. A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. *Bulletin of the British Museum of Natural History* (Geology) 45, 165-371.

Nuttall, C.P. 1990b. Review of the Caenozoic heterodont bivalve superfamily Dreissenacea. *Palaeontology* 33, 707-737.

Olsson, A.A. 1961. *Panamic-Pacific Pelecypoda*, 574 pp Ithaca (Paleontological Research Institution).

Patterson, R.T., McKillop, W.B., Kroker, S., Nielsen, E. & Reinhardt, E.G. 1997. Evidence for rapid avian-mediated foraminiferal colonization of Lake Winnepegosis, Manitoba, during the Holocene Hypsithermal. *Journal of Paleolimnology* 18, 131-143.

Paxton, C.G.M., Crampton, W.G.R. & Burgess, P. 1996. Technical comments: Miocene deposits in the Amazonian Foreland Basin. *Science* 273, 123.

Petri, S. & Fulfaro, V.J. 1983. *In*: Queiroz, T.A. (ed.). *Geologia do Brasil* (Fanerozoico), 408-412. Sao Paulo (Universidade de Sao Paulo).

Pilsbry, H.A. & Olsson, A.A. 1935. Tertiary fresh-water mollusks of the Magdalena embayment, Colombia. *Proceedings of the Academy of Natural Sciences of Philadelphia* 87, 7-39.

Räsänen, M., Gingras, M.K., Wesselingh, F. & Pemberton, G. 2000. Sequence stratigraphy of the marginal marine Miocene Pebas/Solimoes Formation in Amazonian Foreland Basin, Peru. *II Latin-American Sedimentological Congress/ VIII Argentinian Meeting of Sedimentology*, Mar del Plata, March 2000, Abstracts, 1 p.

Räsänen, M.E., Linna, A.M., Santos, J.C.R. & Negri, F.R. 1995. Miocene deposits in the Amazonian Foreland Basin. *Science* 269, 386-389.

Räsänen, M., Linna, A., Irion, G., Rebata Hernani, L., Vargas Huaman, R. & Wesselingh, F. 1998. Geología y geoformas de la zona de Iquitos. *In*: Kalliola, R. & Flores Paitán, S. (eds). Geoecología y desarollo Amazónico: estudio integrado en la zona de Iquito, Peru. *Annales Turkuensis* (AII)114, 59-137.

Räsänen, M.E., Gingras, M.K., Wesselingh, F.P., Vonhof, H.B., Romero Pittman, L., Räsänen, P. & Siiro, P. in preparation. Seasonal and tidal brackish and freshwater sedimentation of transgressive-regressive parasequences of the lower Pebas formation (Middle Miocene) Amazonian foreland basin, Peru.

Rebata, L. Hernani 1997. *Description of Neogene-Quaternary tide and wave-influenced estuary-sediments along Nauta Iquitos road, km 0-15, Loreto-Peru, NW Amazonia*, 93 pp. Turku (University of Turku) (unpubl. MSc thesis).

Recluz, C.A. 1849. Description de quelques nouvelles espèces de coquilles. *Revue et Magasin de Zoologie Paris* 2, 64-71.

Rodriguez, G. 1963. The intertidal estuarine communities of Lake Maracaibo, Venezuela. *Bulletin of Marine Science of the Gulf and Caribbean* 13, 194-218.

Romero-Pittman, L. 1997. Relaciones bioestratigraficas y paleoambientales de la fauna de la formación Pebas – Area de Iquitos (Dpto. De Loreto, Peru). IX Congreso Peruano de Geologia. Resúmenes extendidos. *Sociedad Geologico del Peru, Volumen Especial* 1, 609-614.

Roxo, M.G. de Oliveira 1924. Breve noticea sobre os fosseis terciario do Alto Amazonas. *Boletim do Servicio geologico-mineralogico Brasil* 11, 41-52.

Russell, H.D. 1941. The recent mollusks of the family Neritidae of the Western Atlantic. *Bulletin of the Museum of Comparative Zoology* 88, 347-404.

Savazzi, E. & Yao Peiyi 1992. Some morphological adaptations in freshwater bivalves. *Lethaia* 25, 195-209.

Simone, L.R.L. 1999. Anatomy and systematics of *Anticorbula fluviatilis* (H. Adams, 1860) (Bivalvia: Lyonsiidae) from the Amazon Basin, Brazil and Peru. *The Nautilus* 113, 48-55.

Sioli, H. (ed.) 1984. *The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin*, 763 pp. Dordrecht (Junk).

Smith, J. 1999. Multivariate techniques in palynofacies analysis. *In*: Harper, D.A.T. (ed.). *Numerical palaeobiology*, 361-393. London (John Wiley and Sons Ltd.).

Steinmann, M., Hungerbühler, D., Seward, D. & Winkler, W. 1999. Neogene tectonic evolution and exhumation of the southern Andes: a combined stratigraphy and fission-track approach. *Tectonophysics* 307, 255-276.

Tschopp, H.J. 1953. Oil explorations in the Oriente of Ecuador, 1938-1950. *Bulletin of the American Association of Petroleum Geologists* 37, 2303-2347.

Vermeij, G.J. & Wesselingh, F.P. 2002. Neogastropod molluscs from the Miocene of Western Amazonia, with comments on marine to freshwater transitions in molluscs. *Journal of Paleontology* 76, 265-270.

Villamil, T. 1999. Campanian–Miocene tectonostratigraphy, depocenter evolution and basin development of Colombia and western Venezuela. *Palaeogeography, Palaeoclimatology, Palaeoecology* 153, 239-275.

Vonhof, H.B. 1998. *The strontium isotope stratigraphic record of selected geologic events*, 138 pp. Amsterdam (Vrije Universiteit) (unpubl. PhD thesis).

Vonhof, H.B., Wesselingh, F.P. & Ganssen, G.M. 1998. Reconstruction of the Miocene western Amazonian aquatic system using molluscan isotopic signatures. *Palaeogeography, Palaeoclimatology, Palaeoecology* 141, 85-93.

Way, C.M., Hornbach, D.J., Miller-Way, C.A., Payne, B.S. & Miller, A.C. 1990. Dynamics of filter feeding in *Corbicula fluminea* (Bivalvia: Corbiculidae). *Canadian Journal of Zoology* 68, 115-120.

Webb, S.D. 1995. Biological implications of the Middle Miocene Amazon seaway. *Science* 269, 361, 362.

Wesselingh, F.P. 1993. *On the systematics of Miocene aquatic mollusks from Los Chorros (dept. Amazonas, Colombia) and Nuevo Horizonte (dept. Loreto, Peru), with comments on palaeoenvironments and palaeogeography*, 215 pp. Amsterdam (Vrije Universiteit) (unpubl. MSc thesis).

Wesselingh, F.P. 1998. Over het onderscheid tussen *Dreissena* van Beneden, 1835 en *Mytilopsis* Conrad, 1858. *Correspondentieblad van de Nederlandse Malacologische Vereniging* 302, 52-54.

Wesselingh, F.P. & Gittenberger, E. 1999. The Giant Amazonian Snail (Pulmonata: Acavidae) beats them all. *Veliger* 42, 67-71.

Wesselingh, F.P. 2000. On relict hydrobiid species in Brazilian Amazonia (Gastropoda, Prosobranchia, Hydrobiidae). *Basteria* 64, 129-136.

Whatley, R., Muñoz- Torres, F. & van Harten, D. 1996. Des ostracodes d'un lac salé Néogène à l'ouest du bassin Amazonien. *Proceedings of the Third European Symposium on Ostracoda* (Bierville), 25 pp.

Whatley, R., Muñoz-Torres, F. & van Harten, D. 2000. *Skopaeocythere*: a minute new limnocytherid (Crustacea, Ostracoda) from the Neogene of the Amazon Basin. *Ameghiniana* 37, 163-167.

Zamudio, K.R. & Greene, H.W. 1997. Phylogeography of the bushmaster (*Lachesis muta*: Viperidae): implications for neotropical biogeography, systematics, and conservation. *Biological Journal of the Linnean Society* 62, 421-442.

Appendix 1. Locality data

Figure 15. Fieldwork area.

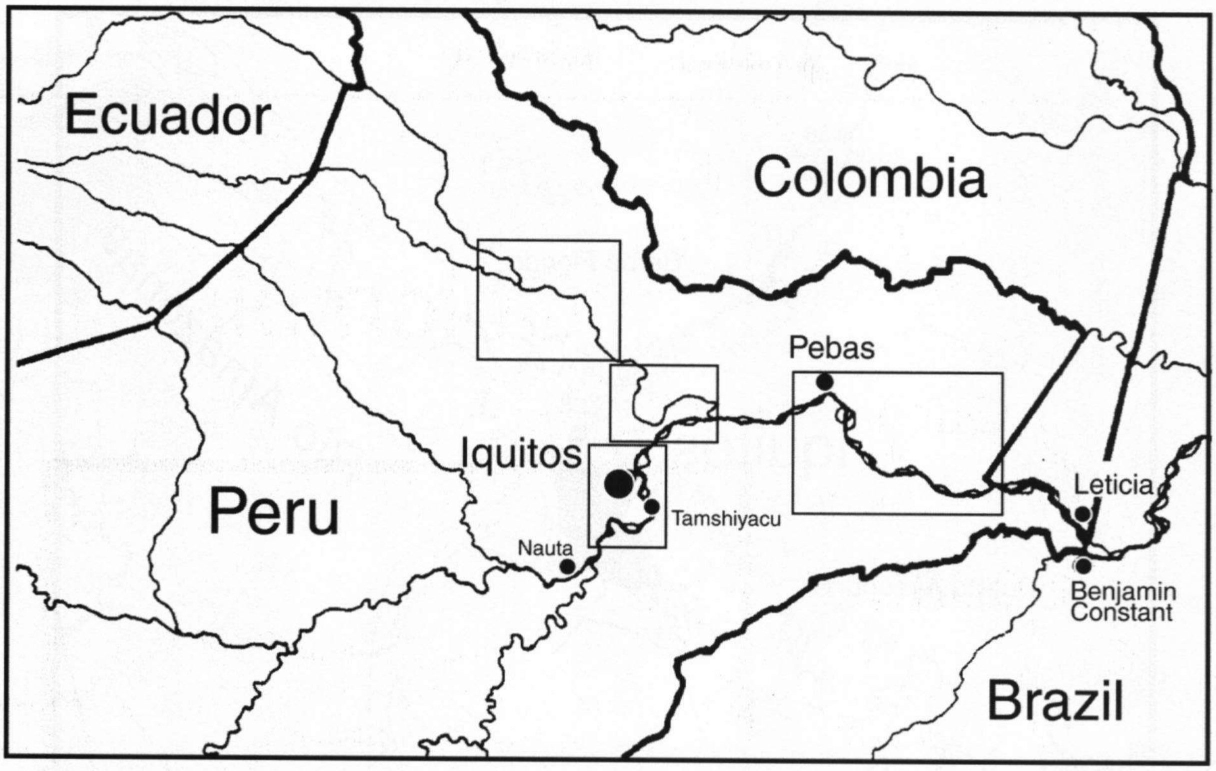

Figure 16. Fieldwork area.

The first author collected all samples from outcrops situated mainly along riverbanks in the Peruvian department of Loreto. River courses in the accompanying maps are redrawn from the Mapa Planimetrico (IFG, 1984). Co-ordinates are estimates from the Mapa Planimetrico and found to be slightly inaccurate when compared with GPS co-ordinates (for a few localities) in later years. LB- left bank, RB- right bank.

1. Porvenir: LB (W-bank) Amazon River, exact location unknown (73°23'W, 4°14'S), sample 688 (2-9-96).
2. Porvenir II: LB (W-bank) Amazon River, 50 m N of Porvenir IV, sample 702 (5-9-96).
3. Porvenir IV: LB (W-bank) Amazon River, 250 m N of Porvenir II, samples 703-705,707 (6-9-96).
4. Porvenir VI: LB (W-bank) Amazon River, 50 m N of Porvenir IV, sample 715 (5-9-96).
5. Porvenir VIII: LB (W-bank) Amazon River, 200 m N of Porvenir VI, samples 716, 206 (5-9-96).
6. Porvenir IX: LB (W-bank) Amazon River, 100 m N of Porvenir VIII, samples 207, 718-722 (5-9-96).
7. Porvenir X: LB (W-bank) Amazon River, 50 m N of Porvenir IX, samples 724-726 (6-9-96).
8. Porvenir XIV: LB (W-bank) Amazon River, 120 m N of Porvenir IX, northern tip of village (73°23'W, 4°14'S), sample 687 (2-9-96).
9. Barradero de Omagua I: RB (E-bank) Itaya River, below village (73°23'W, 4°10'S), sample 800 (13-9-96).
10. Barradero de Omagua II: stream bank, 50 m above confluence with Itaya River, in village (73°23'W, 4°10'S), sample 801 (13-9-96).
11. Itaya I: RB (E-bank) Itaya River (73°23'W, 4°08'S), samples 802-803 (13-9-96).
12. Itaya II: RB (E-bank) Itaya River (73°23'W, 4°07'S), sample 804 (13-9-96).
13. Itaya III: RB (E-bank) Itaya River (73°23'W, 4°05'S), samples 805-806 (13-9-96).
14. Nuevo Horizonte II: road cutting (E- side) Iquitos-Nauta road, km 40, 200 m S of village (73°25'W, 4°05'S), samples 365-366, 836 (16-9-96).
15. Nuevo Horizonte III: road cutting (W- side) Iquitos-Nauta road, km 38, c. 2 km N of village (73°26'W, 4°02'S), samples 202-203, 837 (16-9-96).
16. Nuevo Horizonte IV: road cutting (W- side) Iquitos-Nauta road, ca. 400 m N of Nuevo Horizonte III, sample 368 (16-9-96).
17. Paraiso: LB (W-bank) Itaya River, below village (73°23'W, 4°03'S), samples 807-808 (13-9-96).
18. San Antonio I: LB (W-bank) Itaya River, at S side of village (73°23'W, 4°01'S), samples 809-810 (13-9-96).
19. San Antonio II: LB (W-bank) Itaya River, at N side village, c. 200 m N of San Antonio I (73°23'W, 4°01'S), samples 811-815 (13-9-96).
20. San Antonio III: LB (W-bank) Itaya River, below school, c. 250 m N of San Antonio/ Itaya I (73°23'W, 4°01'S), samples 816-819 (13-9-96).

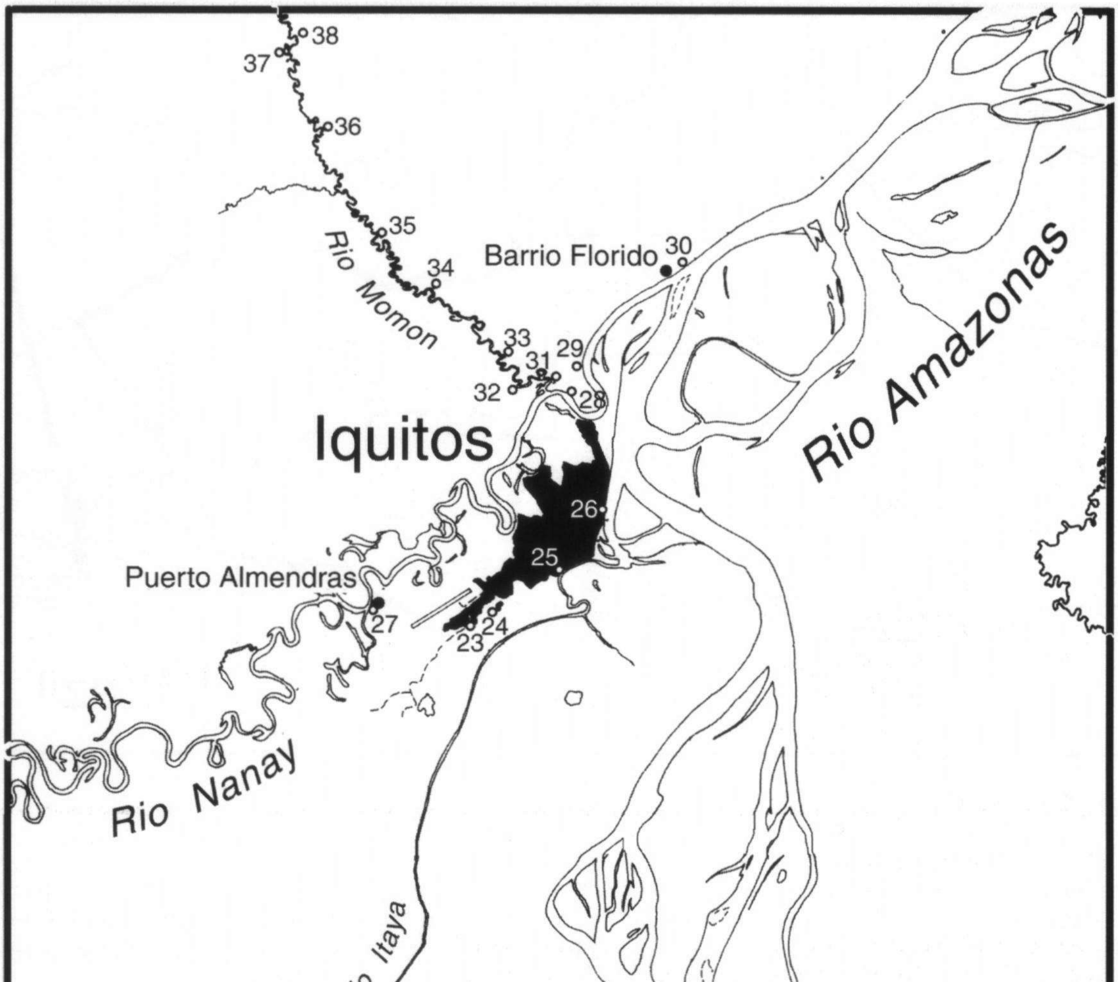

Figure 17. Iquitos area.

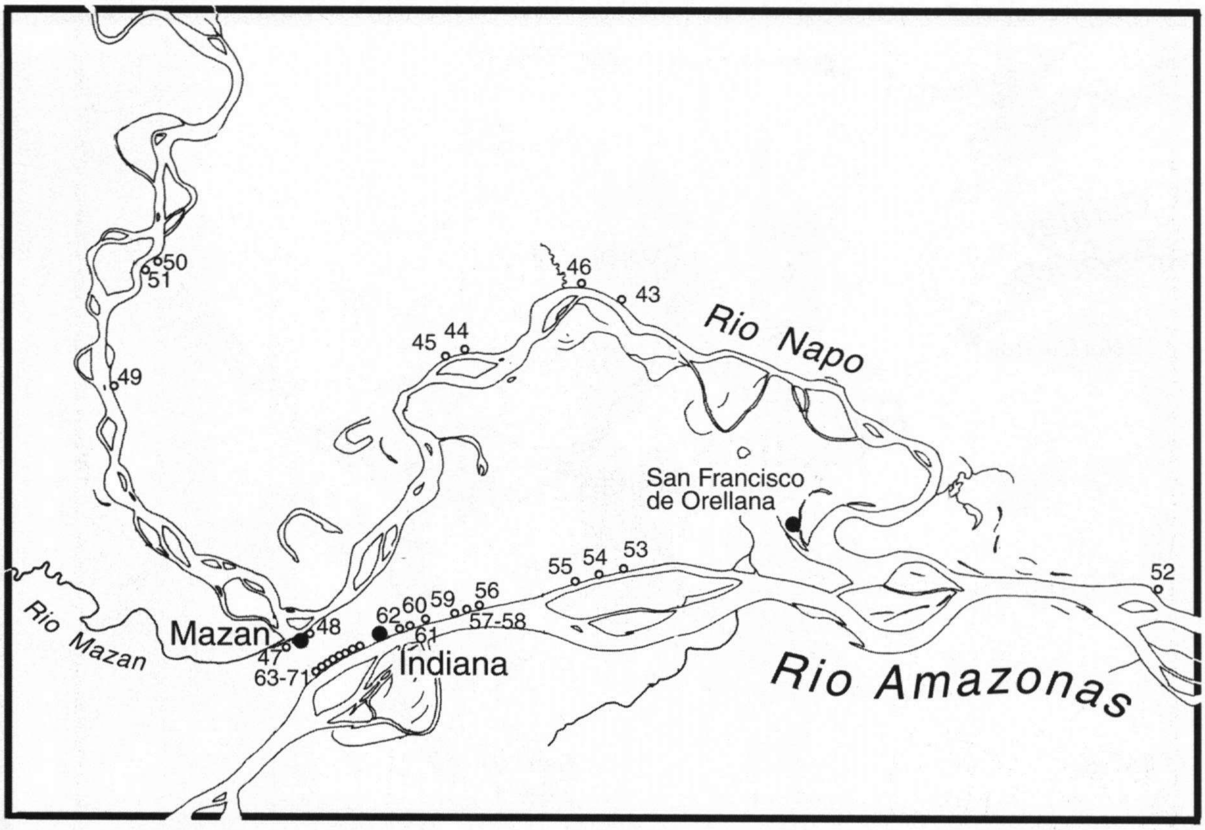

Figure 18. Lower Napo River and Amazon River, north of Iquitos.

21. Palo Seco: LB (W-bank) Itaya River (73°22'W, 4°00'S), sample 820 (13-9-96).
22. Soledad: LB (W-bank) Itaya River at S-side village (73°21'W, 3°59'S), sample 821(13-9-96).
23. Santo Tomas: rill at W-side of road Iquitos-Nauta, km 1 (73°18'W, 3°48'S), sample 360 (13-8-96).
24. San Roque: artificial INIA-research station, c. 1 km SE of airport Iquitos (73°16'W, 3°47'S), sample 913 (3-10-96).
25. Iquitos-Itaya: LB (W-bank) Itaya, 500 m S of port of Belem, at factory (73°15'W, 3°46'S), samples 361-364 (13-8-96).
26. Iquitos Puerto Ganso-Azul: outcrop in harbour, below market, at grifos (73°14'W, 3°45'S).
27. Puerto Almendras: RB (E-bank) Nanay River, 25 m N (downstream) of port (73°22'W, 3°49'S), sample 835 (15-9-96).
28. Santo Tomas: LB (W-bank) Nanay River, c. 1km W/NW of port of Bellavista (73°15'W, 3°41'S), samples 302-304 (3-8-96).
29. Santa Maria: LB (W-bank) Nanay River, 300 m S of naval base (73°15'W, 3°40'S), samples 200, 350, 353 (12-8-96).
30. Barrio Florido: outcrop on W-bank of confluence Nanay and Amazon rivers, below refinery, 200 m N of village (73°12'W, 3°37'S), samples 305-306, 308-310 (3-8-96).
31. Boca Momon: LB (N-bank) Momon River, 300 m upstream from confluence with Nanay River (73°15'W, 3°41'S), samples 356-358 (12-8-96).
32. Momon V: RB (S-bank) Momon River, c. 1.5 km W of confluence with Nanay River, below Fundo de Dueño Donaire (73°16'W, 3°41'S), sample 355 (12-8-96).
33. Momon IV: LB (N-bank) Momon River, c. 4 km NW of confluence with Nanay River, below house (73°16'W, 3°40'S), sample 354 (12-8-96).
34. Porvenir-Momon: LB (E-bank) Momon River (73°20'W, 3°36'S), samples 832-834 (14-9-96).
35. Santo Tomas-Momon: LB (E-bank) Momon River (73°21'W, 3°33'S), samples 370 (date unknown), 827-828 (14-9-96).
36. Momon III: LB (E-bank) Momon River (73°20'W, 3°36'S), samples 829-831 (14-9-96).
37. Momon II: RB (W-bank) Momon River (73°23'W, 3°32'S), sample 826 (14-9-96).
38. Momon I: RB and LB (W and E-bank) Momon River (73°22'W, 3°31'S), samples 823-825 (14-9-96).
39. Tamshiyacu: RB (E-bank) Amazon River, 500 m E of port (73°09'W, 4°01'S), samples 684-686 (2-9-96), samples 754-758 (8-9-96)
40. Quebrada Tamshiyacu: LB (N-bank) of Quebrada Tamshiyacu, c. 50 m above confluence with Amazon River (73°08'W, 4°01'S), sample 851 (22-9-96).
41. Nuevo Tarapaca: LB (N-bank) of Quebrada Tamshiyacu, under tourist lodge (73°07'W, 4°02'S), sample 850 (22-9-96).
42. Santa Elena-Tamshiyacu: RB (S-bank) of Quebrada Tamshiyacu (73°05'W, 4°04'S), samples 848-849 (2-9-96).
43. Boca Napo I: RB (N-bank) of Napo River, c. 2 km E of confluence with Socosani River, c. 100 m W of church on hill (72°53'W, 3°17'S), sample 855 (23-9-96).

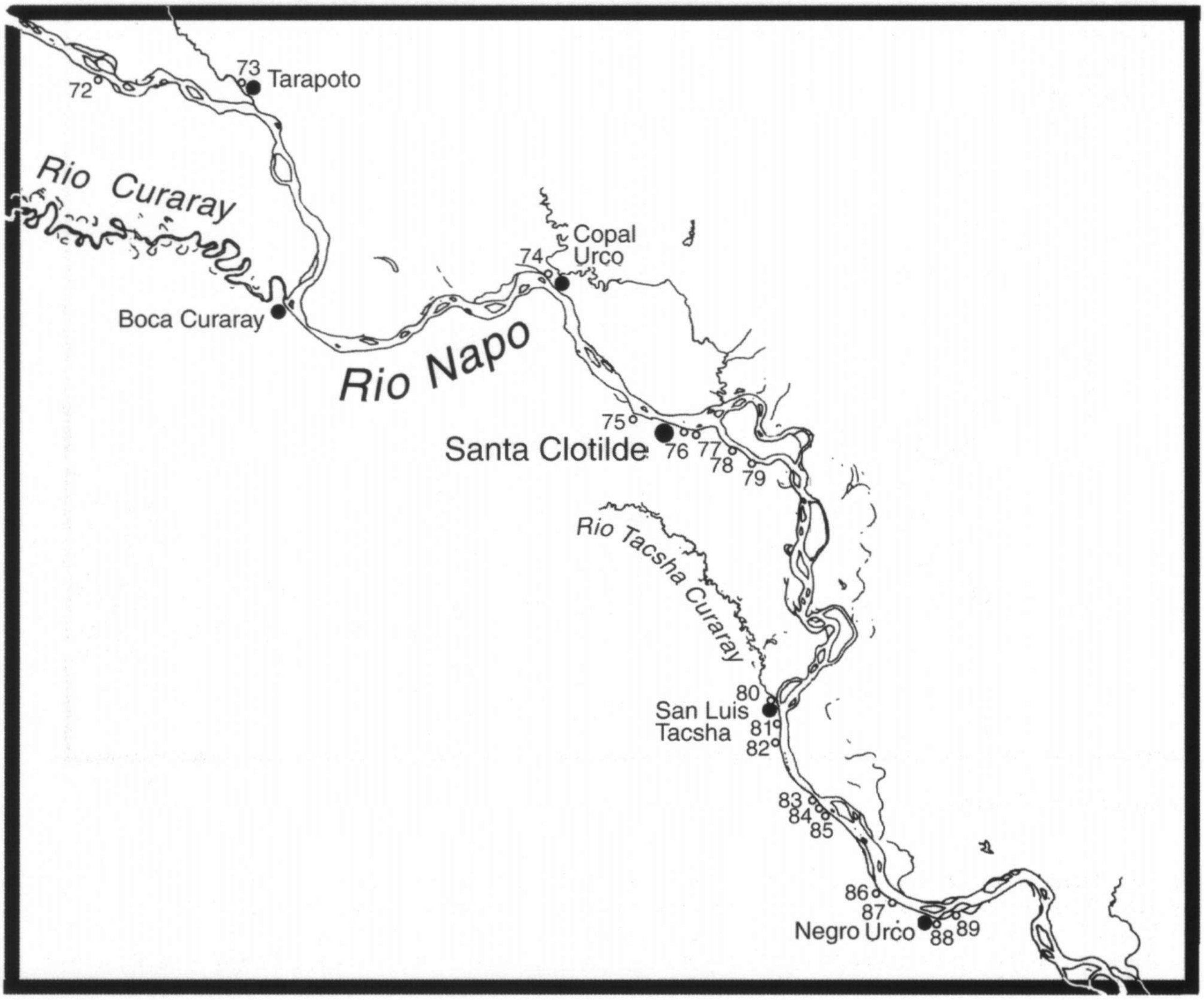

Figure 19. Napo River.

44. Boca Napo II: LB (N-bank) Napo River, c. 5 km W of Socosani (73°00'W, 3°18'S), samples 906, 210 (1-10-96).
45. Boca Napo IV: LB (N-bank) Napo River, c. 7 km W of Socosani, sample 905 (1-10-96).
46. Socosani II: LB (N-bank) Napo River, 500 m E of confluence with Socosani River (72°55'W, 3°16'S), sample 911 (1-10-96).
47. Mazan I: LB (E-bank) Napo River, 900 m S of port (73°06'W, 3°30'S), sample 856 (23-9-96), sample 902 (1-10-96).
48. Mazan IV: RB (E-bank) Napo River, 300 m N of port (73°06'W, 3°30'S), sample 903 (1-10-96).
49. Santa Marta: LB (E-bank) Napo River, N-end of exposure (73°13'W, 3°20'S), samples 900-901 (30-9-96).
50. Buen Pasa I: LB (E-bank) Napo River, c. 1 km E of village, near confluence with brook (73°11'W, 3°15'S), sample 898 (30-9-96).
51. Buen Pasa II: LB (E-bank) Napo River, 800 m E of village (73°11'W, 3°15'S), sample 899 (30-9-96).
52. Oran: outcrop LB (N-bank) Amazon River, 1 km W of village, 400 m NW of cape (72°31'W, 3°28'S), sample 640 (1-9-96).
53. Yanamono III: outcrop LB (W-bank) Amazon River, 4 km N of S-tip Isla Yanamono (72°52'W, 3°27'S), samples 204-205 (1-9-96).
54. Yanamono I: brook, 20 m above confluence with Amazon River (W-bank), c. 3 km N of S-tip Isla 13. Yanamono (72°54'W, 3°28'S), sample 311 (6-8-96).
55. Yanamono II: LB (W-bank) Amazon River, c. 1 km S of Yanamono I, c. 2 km N of S-tip Isla Yanamono (72°55'W, 3°28'S), samples 312-313 (6-8-96).
56. Santa Teresa III: LB (W-bank) Amazon River, 500 m N of village, on cape (72°59'W, 3°29'S), sample 314 (7-8-96).
57. Santa Teresa II a: LB (W-bank) Amazon River, 200 m N of village, at brook (73°00'W, 3°29'S), samples 318, 320-322 (7-8-96).
58. Santa Teresa II b: LB (W-bank) Amazon River, 230 m N of village (73°00'W, 3°29'S), samples 323-324 (7-8-96).
59. Santa Teresa I: outcrop LB (W bank) Amazon River below village (73°00'W, 3°29'S), samples 649, 653, 659, 668-669 (1-9-96), samples 325-328 (7-8-96).

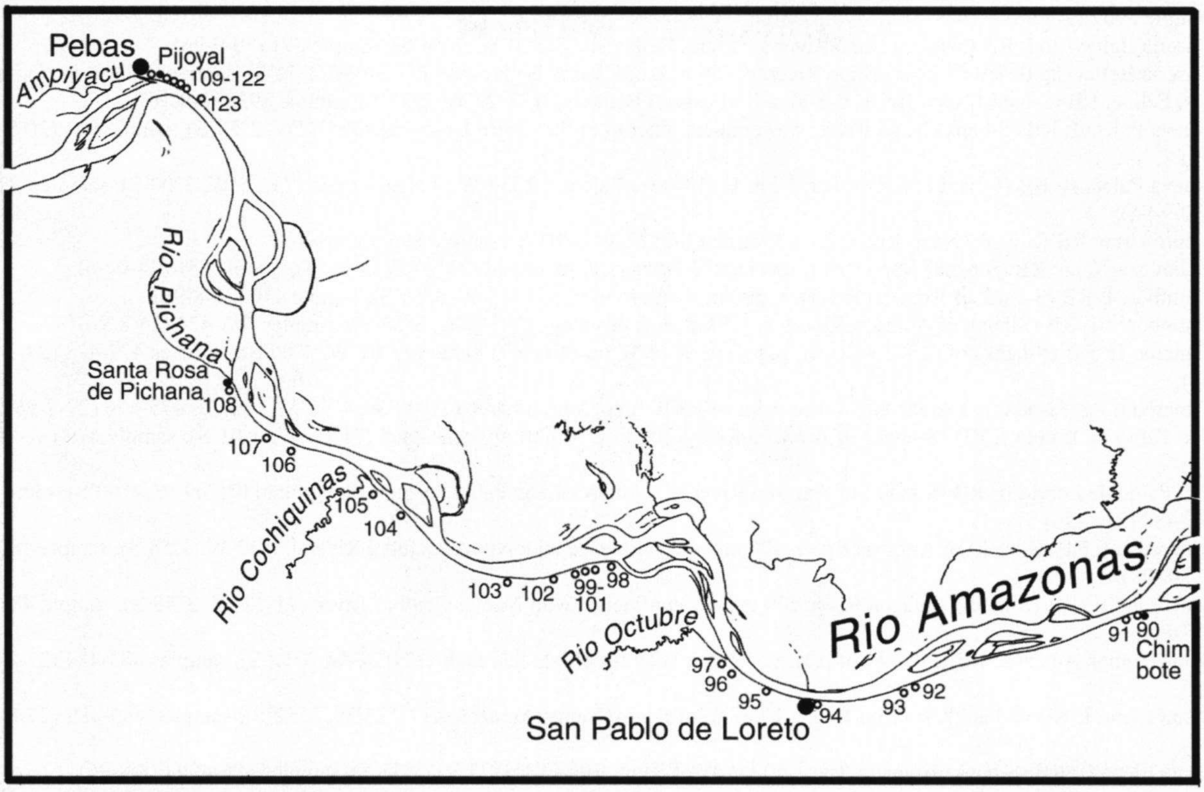

Figure 20. Pebas-Chimbote.

60 Santa Teresa IV: LB (W-bank) Amazon River, 1 km S of village (73°01'W, 3°29'S), sample 329 (7-8-96).
61. Santa Teresa V: LB (W-bank) Amazon River, 3 km S of village (73°01'W, 3°29'S), samples 382, 383 (17-8-96).
62. Indiana I: LB (W-bank) Amazon River, 200 m N of port (73°02'W, 3°29'S), samples 330-332 (7-8-96).
63. Indiana II: LB (W-bank) Amazon River, 3.1 km S of village, 150 m N of Barradero de Mazan (73°05'W, 3°31'S), samples 333, 335-336, 353 (8-8-96), samples 371, 383 (15-8-96).
64. Indiana III: LB (W-bank) Amazon River, 1.2 km S of port (73°03'W, 3°30'S), sample 338 (8-8-96).
65. Indiana IV: LB (W-bank) Amazon River, 1.4 km S of port, 200 m S of Indiana III, samples 340 (8-8-96), 370 (16-8-96), samples 681-682 (1-9-96).
66. Indiana V: LB (W-bank) Amazon River, 1.65 km S of port, 250 m S of Indiana IV, at stair to tourist lodge, samples 342-343, 345. Level 345 was taken 50 m S of outcrop (8-8-96).
67. Indiana VI: LB (W-bank) Amazon River, 1.9 km S of port, 250 m S of Indiana V, samples 346-350 (8-8-96).
68. Indiana VII: LB (W-bank) Amazon River, 2.3 km S of port, 400 m S of Indiana VI, at brook, samples 351, 201 (100 m N of large channel incision) (8-8-96). Sample 379 was taken 150 m N of Indiana VII (16-8-96).
69. Indiana VIII: LB (W-bank) Amazon River, 2.95 km S of port, 650 m S of Indiana VII, 300 m N of Barradero de Mazan, samples 373-377 (16-8-96).
70. Indiana X: LB (W-bank) Amazon River, 2.15 km S of village, sample 372 (16-8-96).
71. Indiana, unknown section: LB (W-bank) Amazon River S of village, samples 213-214 (unknown date).
72 Napo I: RB (S-bank) Napo River (74°17'W, 2°07'S), samples 208-209 (25-9-96).
73. Tarapoto I: LB (E-bank) Rio Tarapoto, under the village (74°08'W, 2°07'S), sample 859 (25-9-96).
74. Copal Urco I: LB (E-bank) Napo River, 500 m S of confluence with Rio Urco (23.47'W, 2°20'S), samples 869-871 (26-9-96).
75. Santa Clotilde I: RB (S-bank) Napo River, c. 1 km E of village (73°38'W, 2°30'S), sample 882 (29-9-96).
76. Santa Clotilde II: RB (S-bank) Napo River, c. 1.5 km E of village (73°37'W, 2°30'S), sample 881 (29-9-96).
77. Santa Clotilde III: RB (S-bank) Napo River, c. 2 km E of village (73°37'W, 2°30'S), sample 880 (29-9-96).
78. Fortaleza: RB (S-bank) Napo River, W-end of exposure (73°36'W, 2°31'S), sample 885 (29-6-96).
79. San Lorenzo: RB (S-bank) Napo River, at cape 100 m W of village at E-end of exposure, c. 1 km E of Fortaleza (73°35'W, 2°32'S), sample 886 (29-9-96).
80. San Luis Tacsha: RB (W-bank) Napo River, at confluence with Tacsha Curaray River (73°33'W, 2°48'S), sample 888 (29-9-96).
81. Santa Maria Tacsha: RB (W-bank) Napo River, c. 1 km S (downstream) from confluence with Tacsha Curaray River (73°33'W, 2°49'S), sample 889 (29-9-96).

82. Santa Teresa Tacsha: RB (W-bank) Napo River, c. 2 km below confluence with Tacsha Curaray River (73°33'W, 2°50'S), sample 890 (29-9-96).
83. Caseria Bellavista I: RB (S-bank) Napo River at caseria Bellavista (73°30'W, 2°54'S), sample 891 (30-9-96).
84. Caseria Bellavista II: RB (S-bank) Napo River, c. 500 m E of Caseria Bellavista I (73°30'W, 2°54'S), sample 892 (30-9-96).
85. San Felipe: RB (S-bank) Napo River, c. 800 m E of caseria Bellavista (73°29'W, 2°55'S), sample 893 (30-9-96).
86. Nueva Paleta I: RB (S-bank) Napo River, westernmost outcrop of the Negro Urco area (73°26'W, 2°59'S), sample 894 (30-9-96).
87. Nueva Paleta II: RB (S-bank) Napo River, 1 km E of Nueva Paleta I, 2 km W of Negro Urco (73°25'W, 3°00'S), sample 895 (30-9-96).
88. Negro Urco: RB (S-bank) Napo River, 50 m E of port (73°22'W, 3°02'S), sample 896 (30-9-96).
89. Bellavista-Napo: RB (S-bank) Napo River, few hundred meters W of school (73°20'W, 3°01'S), sample 857 (24-9-96).
90. Chimbote I: RB (S-bank of Amazon River), c. 500 m west of village (70°45'W, 3°55'S), sample 470 (26-8-96).
91. Chimbote III: RB (S-bank of Amazon River), c. 1.5 km west of village (70°46'W, 3°55'S), samples 473-474 (26-8-96).
92. Timareo II: RB (S-bank) of Amazon River, c. 500 m W of W tip of Isla Timareo (71°01'W, 4°00'S), samples 477-478 (27-8-96).
93. Timareo I: RB (S-bank) of Amazon River, c. 1 km W of W tip of Isla Timareo (71°02'W, 4°00'S), samples 475-476 (27-8-96).
94. San Pablo de Loreto I: RB (S-bank) of Amazon River, 200 m E of port at water level (71°06'W, 4°01'S), sample 479 (27-8-96).
95. San Pablo de Loreto II: RB (S-bank) of Amazon River, c. 4 km W of San Pablo, at sport playground (71°09'W, 4°00'S), sample 480 (27-8-96).
96. Mayoruna I: RB (S-bank) of Amazon River, 400 m S of confluence with Nuevo Octubre River (71°12'W, 3°58'S), sample 481 (27-8-96).
97. Mayoruna II: RB (S-bank) Amazon River 200 m S of confluence with Nuevo Octubre River (71°12'W, 3°58'S), sample 482 (27-8-96).
98. Santo Tomas-Amazon: RB (S-bank) of Amazon River, at W tip of Isla San Isidro (71°22'W, 3°52'S), samples 483-484 (27-8-96).
99. Santa Elena I: RB (S-bank) Amazon River, 1 km W of Santo Tomas Amazonas (71°23'W, 3°52'S), samples 485-489 (27-8-96).
100. Santa Elena II: RB (S-bank) Amazon River, 500 m W of Santa Elena I (71°23'W, 3°52'S), samples 496-499 (28-8-96).
101. Santa Elena III: 150 m long outcrop. Outcrop A located 300 m W of woodmill, and 600 m W of outcrop 102. Santa Elena II (71°24'W, 3°53'S), samples 500-509 (28-8-96).
103. Beiruth: RB (S-bank) Amazon River (71°28'W, 3°53'S), samples 490-492 from outcrop at river bank ('isleta') (27-8-96).
104. San Antonio de Mateo I: RB (W-bank) Amazon River, c. 1 km N of S-tip Isla (71°34'W 3°49'S), sample 493 (27-8-96).
105. San Miguel de Cochiquinas: RB (S-bank) Amazon River, c. 1.5 km E of confluence with Cochiquinas River (71°36'W, 3°47'S), samples 494, 495 (28-8-96).
106. Condor: outcrop RB (S-bank) Amazon River, lower part 300 m W of village, upper part 150 m W of village (71°41'W, 3°44'S), samples 510-515 (29-8-96).
107. San Francisco: outcrop RB (S-bank) Amazon River, lower part at SE tip of Isla Pichana, upper part 50 m to the E (71°43'W, 3°43'S), samples 530-531 (29-8-96).
108. Santa Rosa de Pichana: outcrop RB (W bank) Amazon River, c. 200 m S of confluence with Pichana River (71°46'W, 3°40'S), samples 211-212, 532-537, 539-542 (30-8-96).
109. Pebas I (Pijoyal IV): LB (N-bank) Ampiyacu River, 150 m W of naval base Pijoyal (71°50'W, 3°20'S), samples 435-437 (25-8-96).
110. Pebas II (Pijoyal I): LB (N-bank) Amazon River, 150 m E of naval base Pijoyal, sample 433 (24-8-96).
111. Pebas III (Quebrada Pijoyal): LB (N-bank) Amazon River, 300 E of naval base Pijoyal, at brook (waterfall), samples 560-561 (31-8-96), sample 429 (20-8-96).
112. Pebas IV (Pijoyal II): LB (N-bank) Amazon River, 350 m E of naval base Pijoyal, samples 427-428 (24-8-96).
113. Pebas V (Pijoyal III): LB (N-bank) Amazon River, 450 m E of naval base Pijoyal, samples 430-431 (24-8-96).
114. Pebas VI (Ave Maria III): LB (N-bank) Amazon River, 900 m E of naval base Pijoyal, samples 576-578 (31-8-96).
115. Pebas VII (Ave Maria IV): LB (N-bank) Amazon River, 1050 m E of naval base Pijoyal, sample 404 (22-8-96).
116. Pebas VIII (Ave Maria I): LB (N-bank) Amazon River, 1150 m E of naval base Pijoyal, samples 401-402 (21-8-96).
117. Pebas IX (Ave Maria II): LB (N-bank) Amazon River, 1350 m E of naval base Pijoyal, sample 400 (21-8-96).
118. Pebas XI (Santa Julia II): LB (N-bank) Amazon River, 1650 m E of naval base Pijoyal, sample 588 (31-8-96), samples 405-408 (22-8-96).
119. Pebas XIII (Santa Julia IV): LB (N-bank) Amazon River, 2250 m E of naval base Pijoyal, samples 415, 417-420 (23-8-96).
120. Santa Julia: LB (N-bank) Amazon River, 2650 m E of naval base Pijoyal, published in Hoorn, 1993: samples 625-626, 628-629, 631, 635-636 (31-8-96).
121. Pebas XV (Santa Julia V): LB (N-bank) Amazon River, 3000 m E of naval base Pijoyal, sample 424 (23-8-96).
122. Pebas XVI (Santa Julia VI): LB (N-bank) Amazon River, 3200 m E of naval base Pijoyal, samples 421-423 (23-8-96).
123. Pebas XVII (Tarma): LB (N-bank) Amazon River, 6500 m E of naval base Pijoyal (71°47'W, 3°22'S), samples 425-426 (23-8-96).

Appendix 2. Sampling categories and faunal indices

Classification

The following taxonomic groups have been used (with references to illustrated specimens):

Neritina ortoni group – Nuttall (1990a) recognised one species of *Neritina* in the Pebas Formation (*Neritina ortoni* Conrad, 1871). The very abundant new material shows that at least four species are represented. Two of these, viz. *Neritina ortoni* (Nuttall, 1990a, figs 9-22) + *Neritina* sp.1 (Nuttall, 1990a, fig. 16a, b, and Figure 7.6 in the present paper) make up the *Neritina ortoni* group.
Neritina roxoi group – This group is composed of *Neritina roxoi* de Greve, 1938 (Nuttall, 1990a, figs 23, 24) + *Neritina puncta* Etheridge, 1879 (Nuttall, 1990a, figs 7, 8)
Ampullariidae – *Ampullarius* s.l. sp. indet.
Large *Dyris* group – This category contains *Dyris ortoni* Gabb, 1869 (Nuttall, 1990a, figs 104-108), *Dyris lintea* (Conrad, 1871) (Nuttall, 1990a, figs 49-53, *not* figs 54-58) and *Dyris* sp. Wesselingh (1993, fig. 37).
Small *Dyris* group –All other *Dyris* species (e.g. *Dyris gracilis* Conrad, 1871, *D. tricarinatus* (Boettger, 1878), *Dyris hauxwelli* Nuttall, 1990, various undescribed *Dyris* spp. figured in Wesselingh (1993) and in Figure 3 of the present paper).
Tryonia group – Includes all species referred to in Nuttall (1990a) as *Liris*. Tentatively attributed are the species listed by Nuttall as *Dyris tuberculatus* (de Greve, 1938) and *D. semituberculatus* Nuttall, 1990 (whose generic assignment needs clarification) as well as a species of a presumably new genus, a shell of which Nuttall (1990a, fig. 43) classified as a juvenile of *Dyris gracilis* Conrad, 1871.
Sioliella group – All species formerly referred to as *Ebora* or *Eubora* are here assigned to *Sioliella* following Wesselingh (2000). Furthermore, species belonging to the genera *Tropidobora*, *Toxosoma* and ?*Littoridina* listed by Nuttall (1990a) are included in this group. Also *Liosoma curta* Conrad, 1874 was recognised valid (contra Nuttall, 1990a) and is included in this group, as well as the species listed by Nuttall as *Vitrinella hauxwelli* Nuttall, 1990 and *V. degrevei* Nuttall, 1990 (which both should be transferred to *Nanivitrea*). In addition, species tentatively attributed to *Lithococcus* are included in this group.
Other Cochliopinae – Include undescribed species assigned by Wesselingh (1993) to ?*Heleobia*, ?*Lyrodes* (now tentatively transferred to *Onobops*, see Figure 3*)*, *Pyrgophorus* and ?*Cochliopina*. Apart from *Pyrgophorus*, generic assignment is very uncertain in this group.
Pachychilidae – All species of *Sheppardiconcha* and *Doryssa* are included in the Pachychilidae. *Sheppardiconcha* is assigned to the Pachychilidae because of the lack of embryonal shells that are well known from *Aylacostoma* and *Hemisinus*, and the occurrence of a subsutural micro-ornament also known in the pachychilid genus *Paleoanculosa*.
Thiaridae – Include two species of *Aylacostoma* listed by Nuttall (1990a) as *Verena browni* (Etheridge, 1879) and *V. lataguensis* Nuttall, 1990, as well as *Hemisinus kochi* (Bernardi, 1856). *Charadreon* species (including *C. eucosmius* (Pilsbry & Olsson, 1935) were tentatively placed in this family (Wesselingh, 1996), but should possibly be included in the Pachychilidae.
Perimarine snails – Include *Melongena woodwardi* (Roxo, 1924), *Nassarius* sp. and three species of *Odostomia* (for the latter, see van Aartsen & Wesselingh, 2000).
Pulmonata – Include the terrestrial *Pebasiconcha immanis* Wesselingh & Gittenberger, 1999, *Orthalicus linteus* (Conrad, 1871) and an indeterminate species, as well as three species of the freshwater Planorbidae and a species of *Hebetancylus*.
Corbiculidae – *Corbicula* cf. *cojambitoensis* Palmer, 1941.
Sphaeriidae – Contains two, possibly unnamed, species, one of which has been assigned to *Eupera*, the other to *Pisidium*.
Dreissenidae – Includes *Mytilopsis sallei* (Récluz, 1849) and *M. scripta* (Conrad, 1874). Assignment to *Mytilopsis* following Kelleher *et al.* (1999) and not Wesselingh (1998).
Hyriidae – Includes *Diplodon longulus* Conrad, 1874, a possible undescribed *Diplodon* species and a *Castalia* species (Figure 8).
Mycetopodidae – Includes *Anadontites batesi* Woodward, 1871 and *A. capax* (Conrad, 1874).
Pachydon obliquus Gabb – includes only this species.
Other *Pachydon* group – This group includes *Pachydon tenuis* Gabb, 1869, *P. carinatus* Conrad, 1871, *P. amazonensis* (Gabb, 1869), *P. trigonalis* Nuttall, 1990, *P. erectus* Conrad, 1871, *P. ledaeformis* (Dall, 1871) and *Pachydon* sp. Wesselingh (1993, figs 142, 143).
Pebasia group – This group includes *Pebasia dispar* (Conrad, 1874) and *Pebasia* indet.

Ostomya group – *Ostomya papyria* Conrad, 1874, *Ostomya* sp. indet.(listed in Wesselingh (1993, figs 158, 159) as ?*Cryptomya* sp., Gen. et sp. indet.1 (listed in Wesselingh (1993, figs 152-154) as aff. *Raetomya*, Gen. et sp. indet.2 (listed in Wesselingh 1993 as aff. *Bushia*: fig. 163) and *Anticorbula* sp. (listed in Wesselingh (1993, figs 155, 156) as *Guianadesma* sp.). *Anticorbula* is considered a corbulid (following Nuttall, 1990) and not a lyonsiid (Simone, 1999).

Endemicity

The endemic/non-endemic status of Pebasian taxa is inferred on the basis of a number of criteria. Pebasian taxa known from deposits from intramontane basins in Ecuador, or from Venezuela, are not considered endemics (*Mytilopsis scripta* (Conrad, 1874), *Corbicula* cf. *cojambitoensis* Palmer, 1941, *Panamicorbula* sp., *Sheppardiconcha tuberculifera* (Conrad, 1874), and *Neritina roxoi* de Greve, 1938). The two extant members of the Pebas fauna (*Mytilopsis sallei* (Récluz, 1849) and *Hemisinus kochi* (Bernardi, 1856)) are not endemic either. Furthermore, groups that are characteristic of 'normal' fluvial (Ampullariidae, Mycetopodidae, Hyriidae, Pachychilidae, Thiaridae, Sphaeriidae) or perimarine settings (*Melongena*, *Nassarius* and *Odostomia* spp.) that occur in the Pebas Formation are assumed to be non-endemics. Within some of the other groups listed as endemics below taxa possibly occur that were presumably not endemic (*Lithococcus* sp. in the *Sioliella* group and *Pyrgophorus* spp. in the 'Other Cochliopinae' group), but their numbers are subordinate. The *Tryonia* group poses a problem, since several *Tryonia* finds are known from Miocene deposits of Andean basins. Since none of the Pebasian species has been found outside western Amazonia so far, *Tryonia* is classified as endemic.
The endemicity ratio is the estimated abundance of endemics in samples.
Endemics: *Neritina ortoni* group, *Tryonia* group, small *Dyris* group, large *Dyris* group, *Sioliella* group, other Cochliopinae, *Pachydon obliquus*, other *Pachydon* group, *Pebasia* group and *Ostomya* group.
Non-endemics: *Neritina roxoi* group, Ampullariidae, Pachychilidae, Thiaridae, perimarine taxa, Pulmonata, *Corbicula*, Sphaeriidae, Dreissenidae and Tellinidae.

Freshwater indicators

The following groups are considered as freshwater inhabitants (see also remarks in text): *Neritina roxoi* group, Ampullariidae, Pachychilidae, Thiaridae, Pulmonata (although this group includes both freshwater and terrestrial snails), *Corbicula*, Sphaeriidae, Hyriidae, Mycetopodidiae.

Marine indicators

The following taxa are considered as indicators of marine or perimarine conditions (salinity >2 psu): the molluscs *Melongena woodwardi* (Roxo, 1924), *Nassarius* sp., *Odostomia nuttalli* van Aartsen & Wesselingh, 2000, *O. cotuhensis* van Aartsen & Wesselingh, 2000, *Odostomia* sp., *Macoma* sp., *Panamicorbula* sp., indeterminate barnacles and the Foraminifera *Ammonia* sp. and *Haplophragmoides* sp. (but see for the occurrence of foraminifers in non-marine environments Patterson *et al.*, 1997).

Appendix 3. Taxonomic composition and ecological characteristics of the Pebas fauna.

			SP	AB	FE	LSC	T	F	FB	B	HS
1	Neritidae			0,9%	brow (scav)	epf vag					
		Neritina	4 (3)					X	X	X	X
2	Ampullariidae			0,0%	leafs/lich	epf vag					
		Ampullarius s.l.	1 (0)				X	X			
3	Hydrobiidae			28,2%	depf	epf/inf vag					
	Cochliopinae										
		Tryonia	8 (4)					X	X		
		Gen. nov.	2 (0)					?			
		Dyris	25 (6)					X	?		
		Pyrgophorus	2 (0)					X			
		?Lyrodes	2 (0)					X			
		?Onobops	4 (0)						X	X	
		Nanivitrea	4 (3)					X			
		Sioliella	9 (5)					X	?		
		Lithococcus	3 (0)					X			
		Tropidobora	3 (1)					?			
		Littoridina	2 (1)					?	?		
		Toxosoma	7 (1)					?			
		Liosoma	2 (1)					?			
		?Heleobops	2 (0)					X			
4	Pachychilidae			0,6%	brow	epf vag					
		Sheppardiconcha	5 (4)					X			
		Doryssa	2 (0)					X			
5	Thiaridae			0,7%	brow	epf vag					
		Aylacostoma	2 (2)					X			
		Hemisinus	1 (1)					X	(X)		
		Charadreon	2 (1)					X			
Perimarine taxa (6-8)				0,1%							
6	Melongenidae				carn/scav	epf vag					
		Melongena	1 (1)							X	
7	Nassariidae				scav	epf vag					
		?Nassarius	1 (0)							X	
8	Pyramidellidae				carn/scav	epf vag					
		?Odostomia	3 (0)							X	
Pulmonata (9-12)				0,7%							
9	Planorbidae				depf (brow)	epf/inf vag					
		Helisoma	2 (0)					X			
		Drepanotrema	1 (0)					X			
10	Ferrissidae				depf (brow)	epf vag					
		Hebetancylus	1 (0)					X			
11	Acavidae				leafs/lich	epf vag					
		Amazoniconcha	1 (1)				X				
12	Bulimidae				leafs/lich	epf vag					
		Bulimus	1 (1)				X				
		pulmonate indet.	1 (0)				X				
13	Sphaeriidae			0,1%	susf	inf/epf ses					
		Eupera	1 (0)					X			
		Sphaerium	1 (0)					X			
14	Corbiculidae			0,1%	susf (depf)	inf ses					
		Corbicula	1 (1)					X	X		
15	Hyriidae			0,4%	susf	inf ses					
		Castalia	1 (0)					X			
		Diplodon	2 (1)					X			
16	Mycetopodidae			0,3%	susf	inf ses					
		Anodontites	2 (2)					X			
17	Dreissenidae			1,6%	susf	epf ses					
		Mytilopsis	2 (2)					X	X		X
18	Tellinidae			0,0%	susf (depf)	inf ses					
		Macoma	1 (0)						X	X	

19	Corbulidae			66,5%	susf	inf ses					
	Corbulinae										
		Panamicorbula	1 (0)						X		
	Pachydontinae										
		Pachydon	12 (10)					?	?		
		Pebasia	2 (1)					?	?		
		Ostomya	2 (1)					?	?		
		Gen. indet.1	2 (0)					?	?		
		Gen. indet.2	1 (0)								
		Anticorbula	1 (0)					X			
total			**136 (55)**								

SP	estimated number of species (with described species in brackets)
AB	estimated abundance corrected for 100% sum
FE	feeding ecology
	brow browsers
	carn carnivores
	depf deposit feeders
	leafs
	lich lichens
	scav scavengers
	susf suspension feeders
LSC	life site characteristics
T	terrestrial
FE	obligate freshwater
FB	fresh and/or brackish water
B	obligate brackish/marine
HS	hypersaline

Appendix 4. Stable isotope data

S.D. of replicate analyses < 0,05, S.D. > 0,05 in bold (max. 0,22)

level	species	d13C	d18O
686	*Pachydon obliquus*	-9,8	-6,8
686	*Pachydon obliquus*	-8,1	-6,3
686	*Pachydon tenuis*	-9,7	-6,9
686	*Pachydon carinatus*	-9,9	-6,8
686	*Pachydon obliquus*	-9,6	-7,5
686	*Pachydon cuneatus*	-6,1	-4,9
686	*Pachydon erectus*	-7,7	-5,0
686	*Pachydon obliquus*	-10,3	-7,8
686	*Mytilopsis cf. sallei*	-9,2	-6,7
686	*Pebasia dispar*	-9,4	-6,2
686	*Diplodon longulus*	-10,5	-5,9
686	*Tryonia tuberculata*	-6,4	-4,5
686	*Sioliella* cf. *crassilabra*	-7,9	**-5,7**
686	*Dyris sp.1*	-10,3	-5,4
686	*Littoridina* cf. *crassa*	**-6,2**	**-4,7**
686	*Dyris ortoni*	-6,0	-4,5
686	*Neritina roxoi*	-7,3	-7,3
686	*Neritina roxoi*	-5,8	-5,0
686	*Neritina ortoni*	-8,3	-5,4
686	*Shepp.* cf. *coronatum*	-7,1	-6,3
685	*Pachydon tenuis*	-7,1	-5,4
685	*Pachydon erectus*	-7,1	-4,6
685	*Neritina ortoni*	**-7,5**	**-7,3**
685	*Toxosoma eboreum*	-7,9	-7,4
685	*Dyris tricarinatus*	-4,9	-4,8
685	*Dyris* sp.1	-10,3	-5,9
685	*Neritina ortoni* juv.	-6,5	-5,3
685	*Toxosoma eboreum*	-7,1	-6,5
685	*Mytilopsis* cf. *sallei*	-10,4	-7,5
685	*Pebasia dispar*	-8,0	-6,7
685	*Dyris ortoni*	-6,9	-4,4
685	*Pachydon obliquus*	-6,7	-4,1
685	*Pachydon obliquus*	-5,8	-3,7
685	*Sioliella crassilabra*	-10,5	-9,2
685	*Pachydon amazonensis*	-7,2	-4,1
685	*Pachydon erectus*	-8,9	-5,2
533	*Pachydon obliquus*	-8,3	-6,8
533	*Pachydon obliquus*	-7,5	-8,0
533	*Pachydon obliquus*	-8,9	-6,1
533	*Pachydon obliquus*	-7,7	-5,7
533	*Pachydon obliquus*	-8,0	-6,3
533	*Pachydon obliquus*	-6,8	-5,5
533	*Pachydon obliquus*	-9,5	-8,1
533	*Mytilopsis scripta*	-10,3	-7,2
533	*Pachydon carinatus*	-8,5	-5,7
533	*Dyris tricarinatus*	-10,2	-7,0
533	*Toxosoma eboreum*	-9,3	-7,4
533	*Dyris hauxwelli*	-9,7	-6,5
533	*Dyris tricarinatus*	-8,5	-6,5
533	*Onobops* sp.1	-8,6	-6,9
533	*Mytilopsis scripta*	-10,5	-7,3
536	*Pachydon obliquus*	-7,3	-6,5
536	*Pachydon obliquus*	-6,8	-7,2

level	species	d13C	d18O
536	*Pachydon obliquus*	-8,6	-7,9
536	*Pachydon obliquus*	-6,0	-7,1
536	*Pachydon obliquus*	-9,9	-10,1
536	*Pachydon obliquus*	-8,4	-8,5
536	*Pachydon tenuis*	-8,0	-6,7
536	*Pachydon tenuis*	-8,0	-6,4
536	*Toxosoma eboreum*	-6,2	-6,3
536	*Toxosoma eboreum*	-6,6	-7,2
536	*Tryonia minuscula*	-7,2	-8,8
536	*Tryonia minuscula*	-6,3	-6,7
536	*Dyris ortoni*	-7,1	-7,2
536	*Dyris hauxwelli*	-7,2	-7,0
538	*Pachydon tenuis*	-5,0	-4,9
538	*Pachydon tenuis*	-6,6	-4,8
538	*Pachydon tenuis*	-4,8	-5,0
538	*Pachydon tenuis*	-9,0	-4,8
538	*Pachydon tenuis*	-4,6	-4,6
538	*Mytilopsis* cf. *sallei*	-4,9	-6,1
538	*Pachydon tenuis*	-1,6	-4,1
538	indet. *Pulmonata*	-4,8	-4,6
538	*Mytilopsis* cf. *sallei*	-5,8	-2,8
538	*Pachydon obliquus*	-4,0	-4,0
538	*Dyris lintea*	-5,2	-1,8
538	*Dyris lintea*	-3,5	-3,2
538	*Dyris lintea*	-3,2	-3,1
538	*Dyris lintea*	-4,8	-4,0
538	*Dyris lintea*	-5,0	-5,2
538	*Dyris lintea*	-2,2	-3,3
538	*Dyris lintea*	-3,0	-2,8
538	*Tryonia minuscula*	-3,4	-4,2
538	*Tryonia minuscula*	-4,7	-4,9
539	*Pachydon obliquus*	-8,1	-6,5
539	*Pachydon obliquus*	-5,4	-5,0
539	*Pachydon obliquus*	-5,9	-5,0
539	*Pachydon obliquus*	-5,7	-3,5
539	*Pachydon tenuis*	-5,5	-4,2
539	*Pachydon obliquus*	-7,1	-4,7
539	*Pachydon obliquus*	-7,1	-5,3
539	*Pachydon tenuis*	-7,4	-4,3
539	*Dyris tricarinatus*	-7,8	-4,8
539	*Dyris tricarinatus*	-5,7	-6,3
539	*Dyris tricarinatus*	-8,9	-6,8
539	*Tryonia minuscula*	-8,4	-6,7
539	*Tryonia minuscula*	-5,8	-3,1
539	*Tryonia minuscula*	-5,2	-2,7
542	*Pachydon obliquus*	-7,9	-8,0
542	*Pachydon obliquus*	-7,9	-7,9
542	*Pachydon obliquus*	-9,5	-9,1
542	*Pachydon obliquus*	-7,5	-8,0
542	*Pachydon obliquus*	-8,1	-9,0
542	*Toxosoma eboreum*	-6,9	-7,6
542	*Toxosoma eboreum*	-6,8	-7,9
542	*Pachydon erectus*	-7,9	-8,8
542	*Tryonia minuscula*	-7,5	-8,0
542	*Dyris hauxwelli*	-6,8	-8,7
542	*Sioliella* spec. indet.	-7,7	-7,2

Stable isotope data of growth increments

standard deviation of 5 replicate measurements < 0,05

	Diplodon sp. (Itaya River)		*Anadontites trapezialus* (Amazon River)		*Diplodon longulus* (Pebas Formation)		*Pachydon erectus* (Pebas Formation)	
growth-increment	D13C	D18O	D13C	D18O	D13C	D18O	D13C	D18O
1	-12,7	-8,7	-14,1	-7,0	-11,0	-8,9	-11,8	-6,9
2	-14,6	-9,3	-12,1	-9,2	-11,0	-8,0	-12,2	-6,1
3	-14,3	-7,1	-10,5	-6,3	-11,9	-8,8	-11,6	-6,0
4	-13,0	-6,1	-9,0	-6,4	-13,1	-8,9	-11,7	-5,8
5	-12,4	-6,2	-11,6	-7,3	-13,0	-7,8	-13,1	-5,5
6	-13,3	-5,4	-14,3	-4,6	-11,0	-8,7	-11,3	-6,1
7	-13,4	-6,4	-15,5	-5,0	-11,5	-7,7	-6,3	-5,4
8	-13,9	-5,9	-15,7	-4,5	-12,1	-8,6	-7,2	-4,6
9	-12,4	-8,8	-16,0	-4,0	-12,6	-8,5	-9,4	-6,0
10	-14,8	-10,3	-15,5	-4,0	-11,7	-8,2	-10,3	-5,9
11	-14,3	-7,3	-14,2	-0,9	-12,3	-9,5	-8,2	-6,2
12	-13,1	-6,4	-14,3	-1,6	-13,1	-9,5	-9,7	-6,3
13	-12,6	-5,7	-14,4	-2,0	-11,5	-7,8	-13,7	-6,4
14	-14,2	-7,0	-12,6	-1,2	-12,7	-8,4	-10,5	-7,2
15	-13,1	-6,2	-13,2	-1,5	-12,2	-8,2	-8,9	-6,1
16	-12,8	-5,8	-12,9	-1,7	-12,4	-9,8	-10,2	-6,3
17	-14,6	-9,3	-12,1	-1,4	-13,4	-9,7	-13,0	-7,2
18	-13,8	-7,1	-12,8	-1,9	-13,5	-9,7	-10,8	-6,1
19	-14,4	-6,5	-12,8	-4,0	-12,3	-8,3	-5,3	-5,0
20	-13,4	-6,2	-14,0	-6,7	-11,2	-7,8	-7,4	-5,5
21	-15,2	-7,5	-14,1	-6,9	-11,5	-8,3		
22	-14,5	-6,5	-15,2	-6,9	-11,5	-8,6		
23	-15,2	-6,8	-12,2	-6,8				
24	-14,8	-8,2	-13,8	-6,2				
25	-14,9	-8,3	-12,2	-6,0				
26	-13,9	-7,9	-10,9	-5,0				
27	-14,1	-6,7	-11,4	-3,1				
28	-14,5	-6,8	-12,2	-3,1				
29	-14,2	-6,6	-11,8	-2,9				
30	-14,3	-8,1	-13,0	-2,6				
31	-14,4	-7,9	-12,7	-3,1				
32	-13,9	-7,3	-12,9	-3,3				
33	-14,1	-8,4	-12,5	-3,6				
34	-13,5	-7,9	-12,7	-3,7				
35	-13,4	-7,0	-12,8	-3,8				
36	-13,8	-6,5	-13,0	-3,8				
37	-13,9	-7,3						
38	-13,4	-6,8						