

The nature of aquatic landscapes in the Miocene of western Amazonia: an integrated palaeontological and geochemical approach

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The Miocene Pebas Formation from the section Santa Rosa de Pichana (Loreto, Peru) was investigated using a combination of analyses of sedimentary facies, molluscan communities and taphonomy, and stable isotopes of both entire shells and growth bands in bivalves. Three sequences, comprising a succession of transgressive, maximum flooding and regressive/prograding intervals, are documented. Molluscs are most common in the transgressive/highstand intervals and are almost absent in regressive/prograding intervals. The fauna is dominated by endemic Pebasian species, such as *Pachydon* and *Dyris* spp. The nature of the deposits as well as the availability of oxygen varied in a predictable way within each of the sequences and determined the nature of the assemblages. Highest diversity was reached in the late transgressive phase before the development of dysoxia that was widespread during the late highstand and early regressive/prograding phase. The mollusc and isotope data show no indications of elevated salinities, in contrast to ichnofossils found in the section. This discrepancy is interpreted to result either from temporal separation of the ichnofossils and the mollusc fossils or from evolution beyond usual ecological tolerances of taxa that produced these ichnofossils into freshwater settings.

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Introduction

Ecological conditions during deposition of the Pebas Formation (Miocene, western Amazonia) have been the subject of scientific debate ever since the publication of the first fossil faunas from these strata by Gabb (1869). Interpreted depositional settings ranged from fluviolacustrine to long-lived lake to a seaway (see Wesselingh *et al.*, 2002 for references). Only recently two papers were published that interpreted the same successions very differently. Gingras *et al.* (2002) considered the common occurrence of mesohaline-polyhaline settings during deposition of the Pebas Formation based on ichnofossils and tidal sedimentary structures. In contrast, Wesselingh *et al.* (2002) argued for a long-lived system of predominantly freshwater lakes and swamps with only very limited marine influence, up to oligohaline at its maximum. These latter authors derived their conclusions from the molluscan faunas, and strontium and stable isotope signatures in the shells. The conflicting interpretations were partially based on the same sections. Subsequently, more information has become available about possible depositional settings in the Pebas Formation (Vanhof *et al.*, 2003; Wesselingh, 2006a, b; Kaandorp *et al.*, 2005, 2006), adding to rather than resolving the confusion.

The present paper aims to document environmental settings during deposition of Pebas Formation intervals in a single outcrop (Santa Rosa de Pichana, Loreto, Peru).

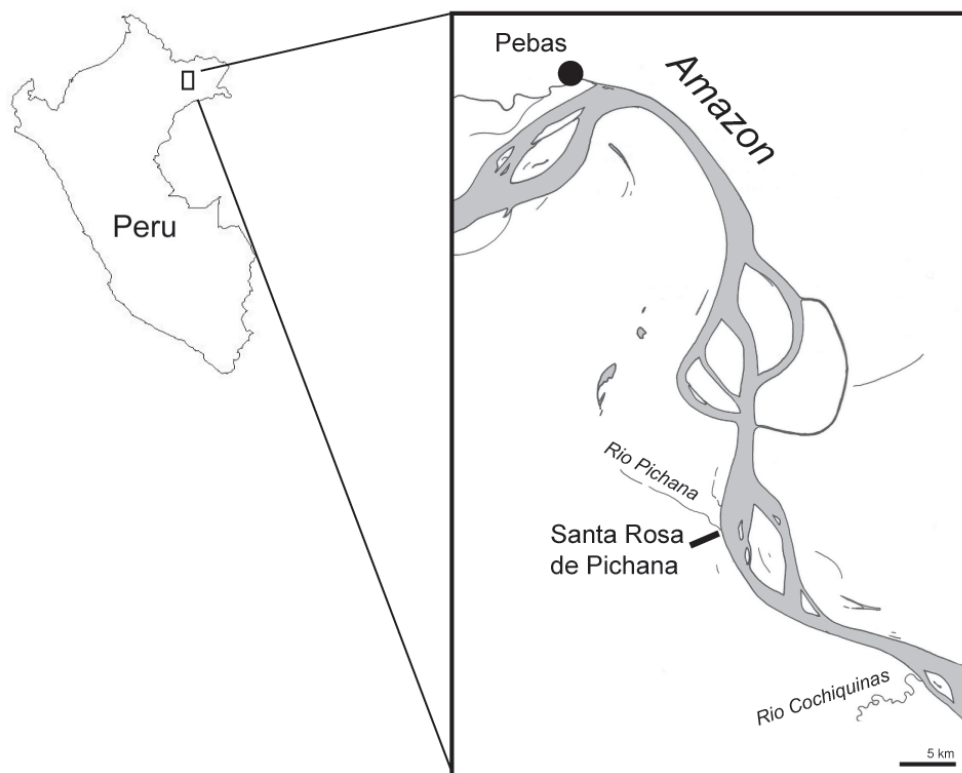


Fig. 1. Location of the section Santa Rosa de Pichana. Inset map shows the location of the study area in northeastern Peru.

Table 1. Taphonomic criteria.

Wear –
1. No traces of abrasion.
2. Few traces of abrasion at vulnerable parts such as the umbo and shell edges of bivalves and the apex of gastropods.
3. Umbones/edges worn; abrasion (corrugation or polishing) also apparent on other parts of the shell's surface.
4. Umbones/apex heavily worn or entirely eroded, surface worn to strongly worn (usually corrugate).
5. Only strongly worn fragments.
Fragmentation –
1. All or almost all shells entire (apart for shells obviously broken during sampling/washing).
2. Whole shells more common than damaged shells and fragments.
3. Whole shells about as common as damaged shells and fragments.
4. Damaged shells and fragments more common than whole shells.
5. Fragments/damaged shells only.
Dissolution marks –
1. No dissolution marks.
2. Superficial etching marks rare.
3. Surface (partially) etched, few, usually shallow dissolution holes.
4. Surface etched to strongly etched, dissolution holes common and of variable depth.
5. Surface strongly etched with common very deep dissolution holes.
Periostracum –
1. Common (>10% of shells).
2. Occur (5-10% of shells).
3. Rare (1-5% of shells).
4. Very rare (<1% of shells).
5. Absent.
Shell integrity –
1. Shell surface robust, commonly (partially) translucent.
2. Shell surface robust, but dull.
3. Shell surface dull, parts may be scratched.
4. Shell surface soft, easily scratchable.
5. Shells fall apart when touched.
Colour mixing –
1. All shells and fragments of the same colour.
2. One dominant colour, rarely additional colours.
3. One dominant colour, common additional colours or two colours common.
4. One or two common colours and several additional colours.
5. Various different colours, none predominant.
Mixed preservation –
1. All shells and fragments with about the same colour, shell integrity, wear and dissolution status.
2. Almost all shells and fragments with about the same colour, shell integrity, wear and dissolution status or slight variation in preservation characteristics only.
3. Some variation in colour, shell integrity, wear and/or dissolution status.
4. Common variation in colour, shell integrity, wear and/or dissolution status.
5. Strong variation in colour, shell integrity, wear and dissolution status.

This outcrop contains a succession of predominant characteristic fining-coarsening up sedimentary sequences (Fig. 1). It is almost certainly the locality known as 'Pichua' or 'Pichana' (see Nuttall, 1990) from which some of the oldest published faunas from the Pebas Formation originate (Woodward, 1871; Conrad, 1871, 1874). The section of Santa Rosa is located in the Middle Miocene *Crassoretitriletes* zone of Hoorn (1993) and in Molluscan Zone MZ7 of Wesselingh *et al.* (2006a), and is of similar age to the exposures near Pebas. The locality contains some of the most regularly developed fining-coarsening up stratigraphic sequences that are very common throughout the Pebas Formation. Therefore, it is considered to be a representative example of Pebas Formation deposits.

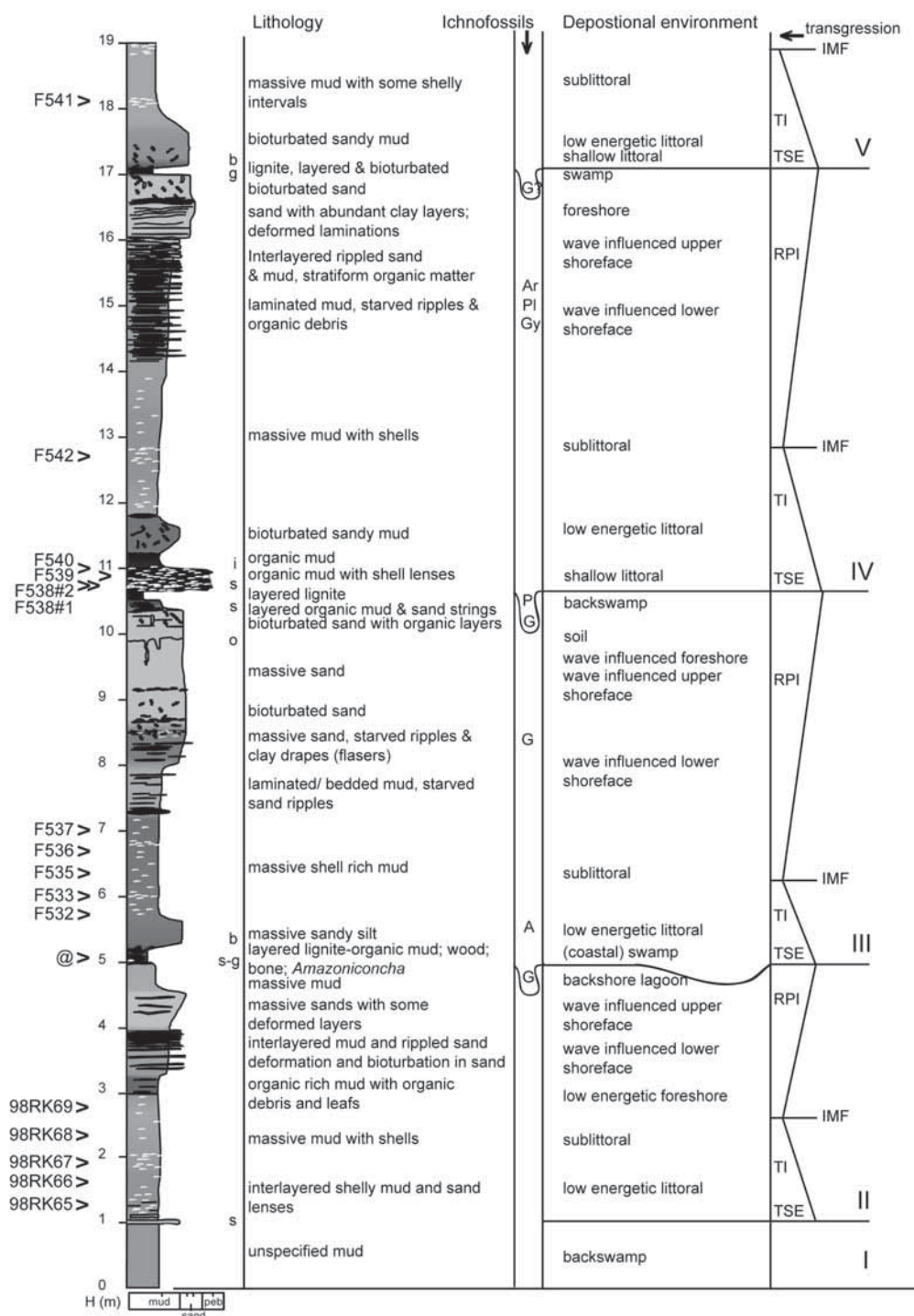
Material and methods

The exposure at Santa Rosa de Pichana is located on the west bank of the Amazon (3°40'.04"S, 71°45'.58"W; Fig. 1), south of the confluence of the Rio Pichana and the Amazon. Here, the Pebas Formation strata are exposed continuously over approximately 1 km length. The section was logged and sampled c. 200 m south of this confluence. We visited the outcrop on a number of occasions; Wesselingh and Räsänen (in 1996), Kaandorp and Vonhof (in 1998), and Räsänen and Gingras (in 1999). Räsänen performed sedimentary facies descriptions for the upper 16 m of the outcrop. Crude lithological descriptions of the lower 3 m taken c. 50 m to the south of the section of Räsänen were made by Vonhof and Kaandorp. We have applied the term 'sequence' throughout this paper, although the sequences described herein might also be termed 'parasequence', especially when comparing to the sequence terminology applied by Wesselingh *et al.* (2006b). A brief assessment of ichnological content was conducted only; it is likely that in some intervals ichnofossils may have been overlooked. Mollusc samples were collected by Wesselingh (indicated with F numbers), and Kaandorp and Vonhof (indicated by RK numbers).

Samples (usually taken at c. 20 cm intervals) typically contained 1 kg of sediment, but samples 98RK67-69 were smaller (about 200-300 grams). The samples that consisted of unconsolidated sedimentary rock were washed (minimum sieve mesh 1 mm), and the washing residues were qualitatively assessed for taphonomic parameters (Table 1). The scores were summed in a taphonomic index to provide a crude indication of the quality of preservation of samples; low scores indicate good preservation, high scores indicate poor preservation of faunas.

The species-sample matrix was subjected to a variety of analyses, using PC-ORD (McCune & Medford, 1999). The taxonomy follows Wesselingh (2006a). Simpson's diversity index, Shannon's diversity index and evenness (Etter, 1999) were computed. The sample-species matrix was subjected to cluster analysis (both the raw and log transformed ($y = \log(x+1)$) data, using Bray-Curtis similarity and flexible β clustering

Fig. 2. Stratigraphic log of the Santa Rosa de Pichana section with facies interpretations, depositional sequences and the location of mollusc samples. Key: peb = pebbles; b = bioturbated contact, g = gradual contact, i = interlayered contact, o = oxidized horizon, s = sharp contact, IMF = interval of maximum flooding, RPI = regressive/prograding interval, TI = transgressive interval, TSE = transgressive surface of erosion, G = *Glossifungites*, A = *Asterosoma*, P = *Psillichmus*, Ar = *Arenicolites*, Gy = *Gyrolithes*, Pl = *Planolites*, @ indicates level with *Amazoniconcha immanis*, roman numbers refer to sequences. ►



methods ($\beta = -0.75$). Indicator species analyses (Dufrêne & Legendre, 1997) were run using raw data and excluding rare species (species occurring only in a single sample). Non-metric multidimensional scaling (NMDS; Etter, 1999) was run using Bray-Curtis similarity index of the log-transformed data set in order to investigate the spatial dimensions of variation between samples and between species.

Two types of stable oxygen and carbon isotope analyses were performed: analyses of whole or substantial parts of whole shells (for methodology, see Vonhof *et al.*, 1998); and isotope analyses of successive growth bands within shells (for methodology, see Kaandorp *et al.*, 2003). Whole-shell analyses were performed on 133 shells. Two bivalves from level 98RK65 and two bivalves from the interval F532-F537 (indicated by 96FWSR) were cut, and isotopic analyses were performed along growth bands. The isotope data of the four bivalves have been published as part of an earlier study by Kaandorp *et al.* (2006) and are discussed below in the light of the present study. Also, trace element data on two of these four bivalves published in Kaandorp *et al.* (2006) are discussed below. Two additional $\text{Sr}^{87}/\text{Sr}^{86}$ ratios measured on shells from this section were available from Vonhof *et al.* (2003).

Description of the section and facies interpretation

The studied section is over 19 m thick (Fig. 2). Some metres of section exposed at the top could not be reached for study. The section yields three, 4.0-6.5 metre thick depositional sequences (II-IV), as well as the top of a fourth (I) and the base of a fifth (V). The lowest complete sequence (Sequence II in Fig. 2) starts at a transgressive surface of erosion (TSE) developed in probable backshore lagoonal muds of sequence I. The transgressive interval is predominantly composed of mudstone, but contains a thin basal sandstone layer, and further sand lenses, organic debris and shells. In the base (samples 98RK65 and 98RK66), strongly abraded shells and shell fragments as well as paired *Pachydon* bivalves were found, indicating that these basal layers contain both *in situ* and reworked specimens. The fine-grained maximum flooding interval (98RK69) contains paired *Pachydon obliquus* specimens and also dispersed organic debris. This interval turns gradually to a prograding low-energy wave-influenced bay/lake-margin sequence topped by backshore lagoonal mudstones with some rhizoliths.

Sequence III starts with an evident wave ravinement surface representing the TSE. From this level an assemblage assigned to the *Glossifungites* ichnofacies (composed of *Thalassinoides* burrows; Fig. 3a) is protruding into the underlying lagoonal mudstones of sequence II. The *Glossifungites* ichnofacies is an omission surface developed in hard or firm substrate (Bromley, 1990). The TSE is covered by transgressive deposits represented by reworked lignite grading laterally in the section into layered organic mudstone. The base of this layer has a lag of wood debris (including a tree trunk) and passes laterally into a c. 1 m deep channel. Also, the top of the lignite/organic mudstone is somewhat bioturbated and contains a thin mollusc lag deposit, made up of terrestrial snails and snail fragments (*Pebasiconcha immanis*). The lower part of the fining up transgressive interval contains the trace fossil *Asterosoma* (Fig. 3b) and *Planolites* reburrowed by *Chondrites* (Fig. 3c). The unit is topped by massive sandy siltstones. The maximum flooding interval contains massive mudstone with abundant shells (samples F532-F537) and some carbonate concretions. The fauna is very well preserved and

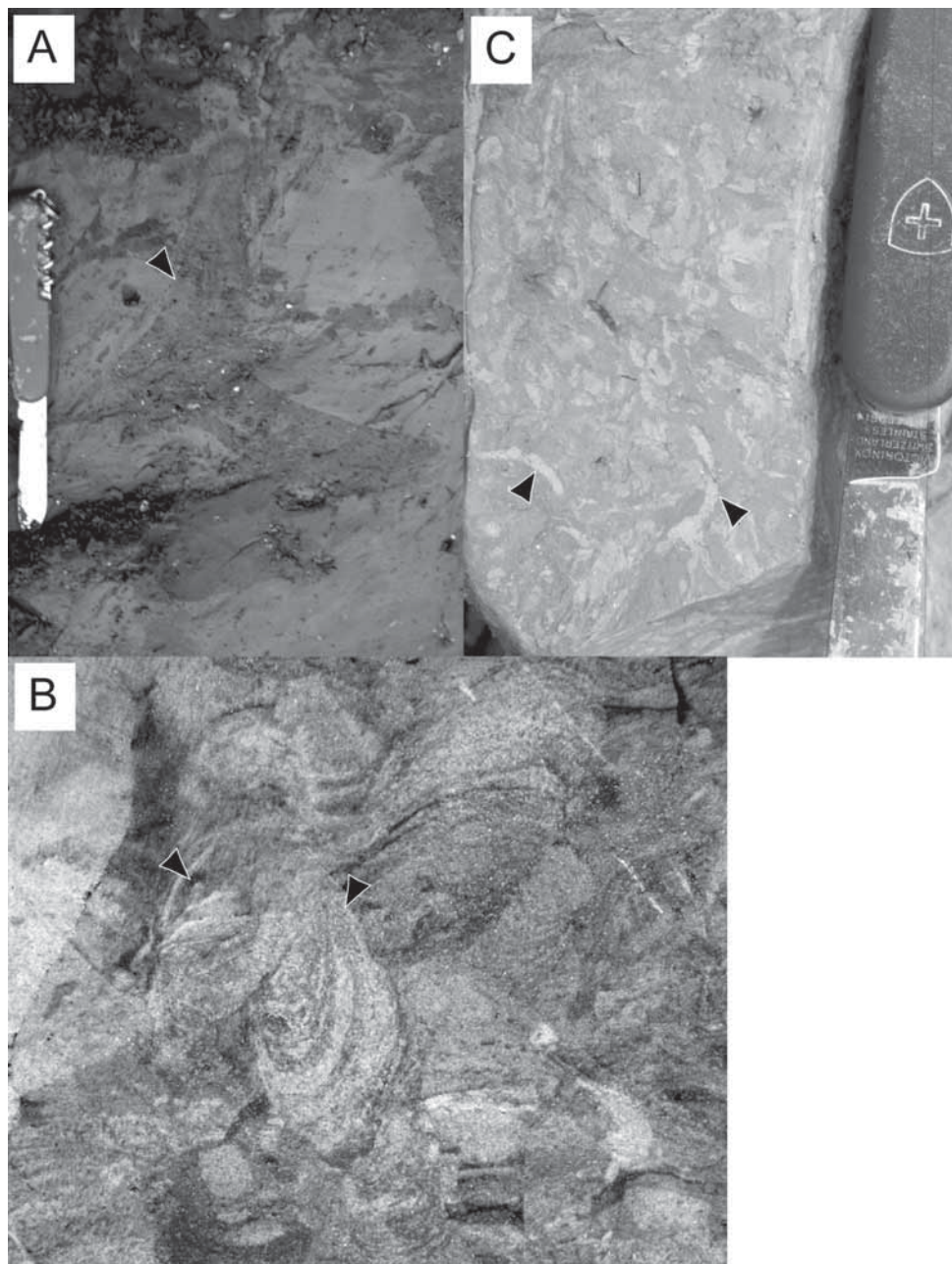


Fig. 3. Examples of ichnological characteristics of the Pebas Formation in the area of the Santa Rosa de Pichana section. (a) Sand-filled *Thalassinoides* (arrow) in sandy silt from the Santa Rosa de Pichana (from c. 11.5 m height in the section). (b) *Asterosoma* (indicated by arrows) from the lower part of the section displayed at Indiana (Loreto, Peru). Field of view 14 cm. (c) *Chondrites* reburrowing *Planolites* from Santa Rosa de Pichana (from c. 7.5 m height in the section). Arrows indicate parts of the image where small *Chondrites* in cross section are just visible as small dots within the *Planolites*.

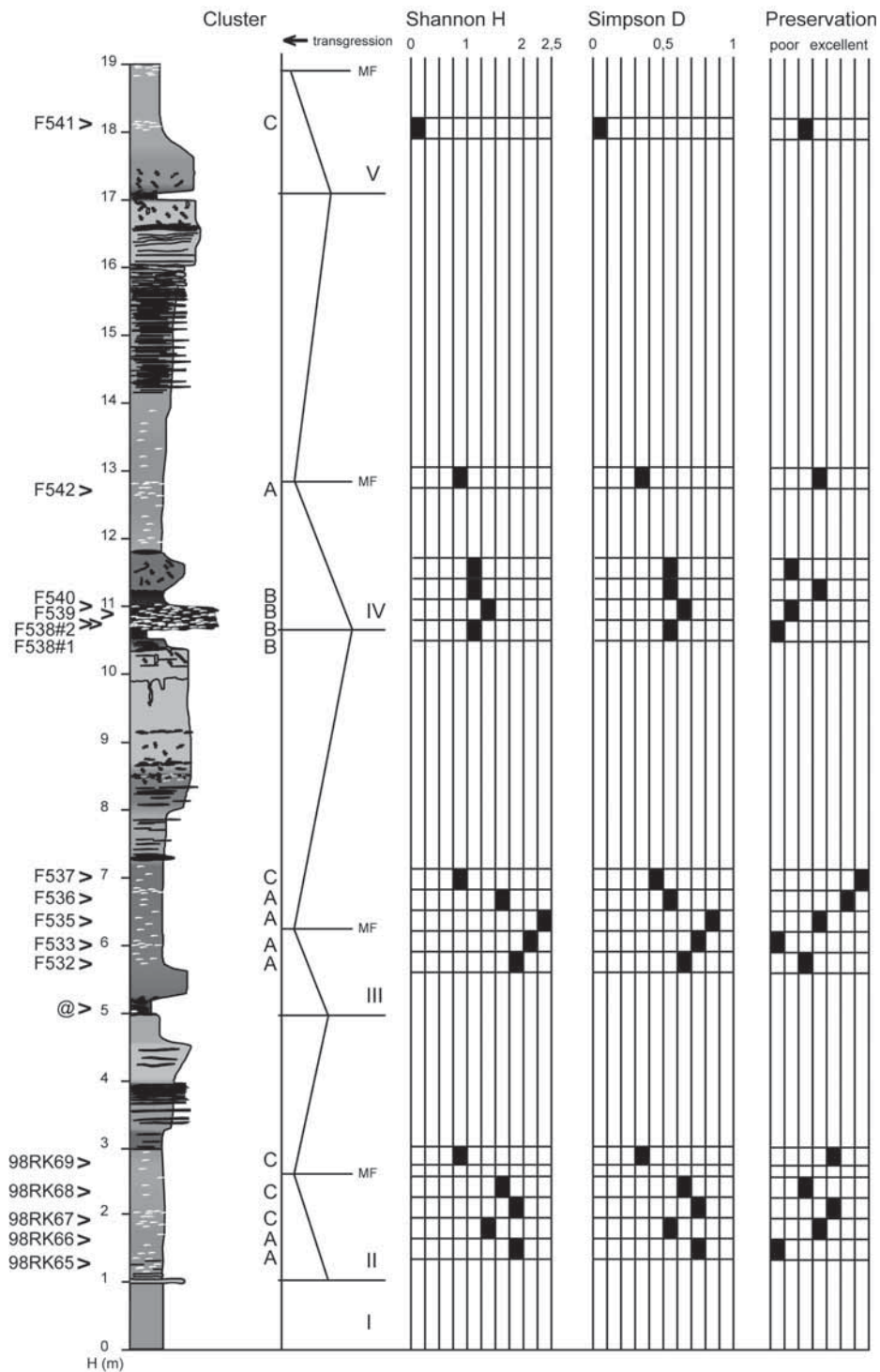
dominated by various *Pachydon* species that are often found *in situ* or with valves in close proximity, indicating some bioturbation, but no profound physical disturbance of the depositional environment. The maximum flooding interval grades upwards into a well developed, massive shoreface sand interval of almost 2 m thickness that is topped by a regressive backshore peat horizon. In the lower shoreface interval a thin organic layer penetrated by a minor *Glossifungites* ichnofacies with *Thalassinoides* was observed together with some thin shell strings. The shoreface is capped by one of the thickest, well-developed pedogenic horizons encountered in the Pebas Formation.

Sequence IV is initiated with a well-developed *Glossifungites* ichnofacies penetrating through the entire pedogenized horizon of sequence III. Also, a horizontally deposited large *Pylonichmus*, with rhythmical sediment infill, was observed penetrating the shoreface deposits. Similar burrows were previously interpreted to represent tubular tidalites, that is, open burrows that trapped tidal lamination (Gingras *et al.*, 2002). The wave ravinement surface is covered with a 40 cm thick, shell-bearing lag (F538-F539) topped by redeposited organic matter, which is also covered by a thin shell layer (F540). The shell layers in this interval are composed of lenses dominated by oriented gastropods (principally *Dyris hershleri* and *D. lintea*). In this transgressive interval the sandstones are clearly bioturbated, and grade upward into the massive mollusc-rich mudstones of the maximum flooding interval (F542), in which *in situ* specimens of *Pachydon obliquus* are common. The lower shoreface of the regressive interval is made up of interlayered mudstone and sandstone with abundant starved ripples and organic debris. *Gyrolithes*, *Arenicolites* and *Planolites* burrows are recorded in this interval. Within the upper shoreface, the sediments are mildly deformed and locally bioturbated at the top. These sands are ultimately capped by a terrestrial regressive peat horizon.

The erosional transgressive base of sequence V is initiated with bioturbated sandy siltstones, the lower contact of which is lightly burrowed. These transgressive deposits grade into the mudstones of the maximum flooding interval, which yielded two shell-bearing layers with *in situ* *Pachydon obliquus* (level F541).

The three complete sequences (II-IV), as well as the incomplete sequence V all have transgressive bases with reworked organic debris and shell bioclasts and are overlain by transgressive sandstones. The base of sequence III is interpreted to represent a channel cutting 1 m into the substrate. This channel contains reworked bone and teeth, as well as wood fragments and even logs. Laterally, the channel grades into reworked or winnowed lignite that contains giant terrestrial gastropods (*Pebasiconcha immanis*). The coarse-grained, shell-rich base of the cycles grade rapidly into mudstone intervals. These yield relatively high quantities of shells as well as dispersed organic matter. The shell content in the overlying mudstones is comparatively low. The mudstones grade upwards into a siltstone and fine-grained sandstone alternation that in turn grades into massive sandstones in cycles III and IV. A coarsening-up trend defines the major part of these cycles (apart for the very base and top).

Fig. 4. Diversity indices in the section of Santa Rosa de Pichana. Key: H = Shannon's diversity index; D = Simpson's diversity index; grain-size in lithological column as in Fig. 2. A, B, C refer to mollusc clusters (see text). ►



Molluscan composition and diversity

In total, 54 identifiable mollusc species were encountered (Appendix 1). In species numbers, the Cochliopidae (28 species, 51%) dominate, with the Pachydonatinae (17 species, 31%) as the second most abundant group. *Pachydon obliquus* is the dominant species (47% in abundance).

The fauna is dominated by endemic Pebas species (84% of species), even more so in terms of abundance (95%; for definition of endemicity, see Wesselingh, 2006a). Non-endemic freshwater species occur in low numbers (0.9% of the fauna). Even in the sample where these taxa are most common (98RK65), they make up only 6%. Fluvial (non-endemic) freshwater taxa are rare, but they do occur in eight of the 16 samples. Terrestrial taxa (two species) are very rare. Some juvenile shells of *Corbula cotuhensis*, a species that may represent saline (brackish) conditions, were found in two samples. The studied fauna can be characterised as predominantly endemic and freshwater. The variation of diversity indices in the section is shown in Figure 4.

The samples of Sequences II (98RK65-98RK69) and III (F532-F537) show a similar trend of successive increase in diversity, followed by a decrease (Fig. 4). The lowermost sample of Sequence II (98RK65) breaks with this trend, but it includes various taxa that are interpreted as being reworked from other assemblages, explaining its higher then expected diversity (see below). In general, diversity is intermediate in the lower transgressive part of sequences, peaks at the late transgressive interval and drops at the maximum flooding, when faunas become dominated by *Pachydon obliquus*.

Molluscan communities and taphonomic characteristics

Three clusters are defined based on the cluster analyses. Different analyses (using raw data and log transformed data, including or excluding rare species) produced very similar clusters with the exception of sample F542 that either falls in cluster A or in cluster C. In NMDS plots, the clusters do not show overlap in both the 2 and 3 dimen-

Table 2. Rank abundance of species that make up more 1% of the sum within the three clusters; abundance in %.

Cluster					
A		B		C	
56.9	<i>Pachydon obliquus</i>	32.2	<i>Dyris hershleri</i>	78.1	<i>Pachydon obliquus</i>
7.6	<i>Dyris tricarinata</i>	26.7	<i>Pachydon obliquus</i>	3.7	<i>Tryonia minuscula</i>
4.7	<i>Tryonia minuscula</i>	24.8	<i>Tryonia minuscula</i>	3.5	<i>Dyris tricarinata</i>
4.0	<i>Mytilopsis sallei</i>	4.8	<i>Dyris tricarinata</i>	2.8	<i>Mytilopsis sallei</i>
3.3	<i>Dyris hauxwelli</i>	3.5	<i>Dyris lintea</i>	2.1	<i>Pachydon amazonensis</i>
2.8	<i>Pachydon amazonensis</i>	2.7	<i>Pachydon tenuis</i>	1.4	<i>Pachydon tenuis</i>
2.6	<i>Toxosoma eboreum</i>	2.4	<i>Mytilopsis sallei</i>		
2.6	<i>Onobops communis</i>	1.4	<i>Pachydon amazonensis</i>		
2.1	<i>Dyris lintea</i>				
1.6	<i>Ostomya papyria</i>				
1.5	<i>Pachydon ledaeformis</i>				
1.2	<i>Sheppardiconcha tuberculifera</i>				

sional solution (residual stress = 0.09 and 0.05, respectively). Sample F542 plotted closer to cluster A samples than to cluster C samples. The three clusters described below result from analyses on raw data excluding rare species. Table 2 contains rank abundance data for the clusters, Table 3 summarizes the diversity indices of the clusters and taphonomic characteristics of the samples are provided in Table 4.

Cluster A – The seven samples from this cluster contain 57 species. The dominant species is *Pachydon obliquus* (57%: Table 2). Various delicate and small species of *Dyris* occur only in samples from cluster A. The cluster has the highest diversity and evenness (Table 3). Indicator species with very high indicator values are *Dyris microbispiralis* (Indicator Value of 100), *D. hauxwelli* (90), *D. gracilis* (85), *Onobops communis* (84) and *Cochliopina? hauxwelli* (86). Nineteen species have indicator values over 50. The mollusc composition of samples in cluster A are very similar to samples attributed to the Small-*Dyris* assemblage of Wesselingh *et al.* (2002), with the exception of assumed reworked taxa, such as *Sheppardiconcha tuberculifera*, *Anodontites capax*, *Tryonia scalarioides tuberculata* and *Dyris lintea* in sample 98RK65.

Table 3. Diversity indices for the clusters (standard deviation in brackets). Key: H = Shannon’s diversity index; D = Simpson’s diversity index; E = Evenness; n = number of samples; formulae in Table 2.

	H	D	E	n
Average Cluster A	1.71 (0.47)	0.62 (0.16)	0.50 (0.12)	7
Average Cluster B	1.22 (0.09)	0.58 (0.03)	0.49 (0.04)	4
Average Cluster C	1.11 (0.69)	0.43 (0.26)	0.42 (0.23)	5
Average all clusters	1.40 (0.55)	0.55 (0.19)	0.47 (0.15)	16

Table 4. Taphonomic parameters. Key: f = level of fragmentation in sample; dm = dissolution marks (holes); gd = generalised dissolution or shell integrity; cm = colour mixing; mp = mixed preservation styles; per = periostracum. Criteria outlined in Table 1.

Sample	cluster	wear	f	dm	gd	cm	mp	per	sum
F541	C	2	3	3	4	2	2	1	16
F542	A	2	2	3	3	2	2	1	14
F540	B	3	3	4	3	1	3	3	17
F539	B	3	2	2	3	2	2	2	14
F538#2	B	4	2	3	3	2	3	2	17
F538#1	B	5	2	4	4	1	3	2	19
F537	C	1	2	1	1	1	1	1	7
F536	A	2	1	1	2	1	2	2	9
F535	A	2	3	2	2	2	3	1	14
F533	A	3	3	3	4	1	5	2	19
F532	A	3	3	2	3	2	2	2	15
98RK69	C	2	2	3	2	1	2	3	12
98RK68	C	2	3	2	4	1	3	1	15
98RK67	C	2	3	2	2	1	2	2	12
98RK66	A	3	2	2	3	2	2	2	14
98RK65a	A	3	3	4	4	2	4	2	20

Shells in cluster A samples are generally well preserved. Wear, fragmentation and integrity of shells are intermediate. The presence of shells and shell fragments of different colour is rare. There are few dissolution marks and periostracum remains are relatively rare. The Small-*Dyris* assemblage, to which these samples are attributed, occurred in little agitated lake bottoms (Wesselingh *et al.*, 2002). Judging from the common occurrence of charophytic oogenia, these waters must have been clear. The (modest) variation in mixed preservation styles may, apart for reworking in the basal samples of lacustrine successions, indicate either depths between fair weather and storm wave base or relatively low deposition rates leaving shells exposed for prolonged periods near the lake floor.

Cluster B – The four samples in this cluster contain only 25 species. There are three common species, *Dyris hershleri* (32% of the specimens), *Pachydon obliquus* (27%) and *Tryonia minuscula* (25%). Indicative species are *Dyris hershleri* (indicator value of 100), *D. lintea* (75), *Tryonia minuscula* (59) and *Pachydon tenuis* (56). Shannon's diversity index is low, but Simpson's index is high, as is the measure of evenness. Samples from this cluster contain relatively few species, none of which is dominant. The mollusc content of the samples in this cluster resembles that of samples assigned to the *Tryonia* and the Tall-*Dyris* assemblages of Wesselingh *et al.* (2002).

Cluster B samples are moderately well preserved. Abrasion of the shells is prominent and dissolution pits are common. Furthermore, the integrity of the shell carbonate is often somewhat compromised; shells that are 'soft' and easily scratched are common. Periostracum remains are common. Possibly, periostracum was more prominently developed in order to withstand (episodic) lowered pH conditions, as indicated by the common dissolution holes in the shells. Tall-*Dyris*/*Tryonia* assemblages represent nearshore (foreshore, beach and back swamp) environments (Wesselingh *et al.*, 2002). These settings experienced the strongest physical disturbance (erosion and transport from waves, currents and rivers) in the Pebas system. The four samples attributed to this cluster are from an organic-rich interval with shell lenses and beds containing transported bioclasts (samples F538#1 and F538#2 represent two shell lenses at the same height in the section). In sample 98RK65, taxa typical of the Tall-*Dyris* and *Tryonia* assemblages (*Anodontites capax*, *Sheppardiconcha tuberculifera*) were found to have similar preservation characteristics (mostly fragments that are strongly worn, contain dissolution holes and whose carbonate is softened) as the samples attributed to cluster B. These shells and fragments have clearly been transported into cluster A faunas, as is also suggested by isotope evidence (see below). Apparently, fast deposition took place during deposition of cluster B faunas, enabling the preservation of the organic periostracum.

Cluster C – The four samples attributed to this cluster yield 33 species. Samples from this cluster are characterised by the dominance (78%) of *Pachydon obliquus*. There are no species indicative for this cluster; *P. obliquus* has the highest indicator value (IV = 29). Diversity and evenness are lowest of the three clusters; there are few rare species. The mollusc composition in Cluster C samples is very reminiscent to samples assigned to the *Pachydon obliquus* assemblage by Wesselingh *et al.* (2002). Shells in cluster C sam-

ples are in general well preserved. They are usually little worn and mixed preservation styles are rare, with the exception of carbonate integrity. Two samples (F541 and 98RK68) yield shells whose carbonate is softened, which are mixed with shells that are durable and well preserved. In general, the amount of fragmentation is slightly higher than in samples from the other associations.

The *Pachydon obliquus* assemblage represents dysoxic muds deposited below storm wave base on lake bottoms (Wesselingh *et al.*, 2002). Slightly elevated fragmentation levels may point to higher densities of predators and/or lower deposition rates leaving shells exposed longer to predation. Softening of shells may represent interstitial low pH values due to breakdown of organic matter within the clays. Mixtures of such soft shells, and shells that are well preserved and hard, may indicate commonly low sedimentation rates for these intervals.

The level containing solely *Pebasiconcha immanis* (base of sequence III at c. 5.00 m) should be attributed to the Thiariidae-Pulmonata assemblage of Wesselingh *et al.* (2002). The snail lived in terrestrial environments, presumably on forest floors (Wesselingh & Gittenberger, 1999).

Carbon and oxygen isotope geochemistry

Stable oxygen and carbon isotope data of entire shells or larger portions of shells are shown in Appendix 2 and Figure 5. A positive correlation exists between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (Fig. 5a) with the R^2 of 0.5217 ($n = 133$). Maximum values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are around 2 and 0 ‰, respectively; minimum values are slightly below -11‰. Average values are -6.8 and - 5.7‰, respectively. The isotope averages for the three clusters are given in Table 5 and shown in Fig. 5b-e. Clusters B and C have no overlap, but both overlap with cluster A.

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope ratios of one *Dyris lintea* specimen (respectively, +1.88 and -0.42, Appendix 2, Figs. 5 and 6) could be interpreted as indicative of seawater. However, the co-occurrence with pearly fresh water mussels that cannot withstand the slightest elevated salinity requires another explanation. Within the Pebas fauna, taxa attributed to Cluster B, including pearly freshwater mussels, are found halfway between riverine and marine values (Fig. 5). Therefore, we conclude that the stable isotope signatures of the Pebasian shells cannot be explained from mixing models involving a ma-

Table 5. Average isotope ratios for the three clusters. In sample 98RK65 an admixture of fauna elements attributable to cluster A (*Pachydon obliquus*) and to cluster B (the other measured species) was found (see below). Subtracting these latter species from cluster A resulted in cluster A-, and adding them to cluster B resulted in Cluster B+ (see also Fig. 4b-f). Key: n = number of analysed samples; Avg = average; SD = standard deviation.

Cluster	n	Avg $\delta^{13}\text{C}$	SD	Avg $\delta^{18}\text{O}$	SD
A	73	-6.86	2.11	-5.53	2.32
A-	60	-7.40	1.51	-6.13	2.01
B	33	-5.47	1.82	-4.46	1.23
B+	46	-5.16	2.14	-3.98	1.50
C	27	-8.35	1.42	-7.56	0.76

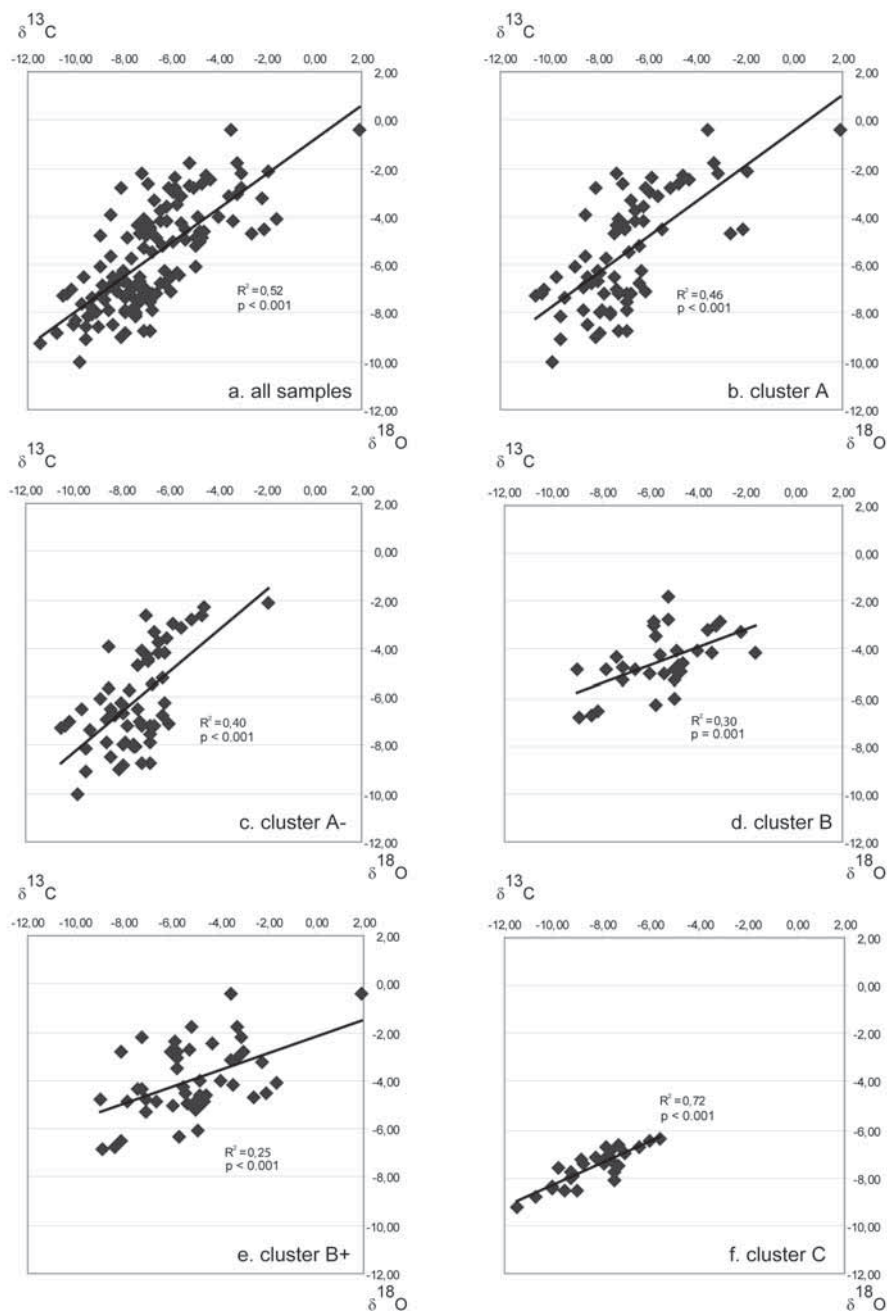


Fig. 5. (a) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of whole shell analyses from Santa Rosa de Pichana. (b) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for shells attributed to cluster A. (c) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for shells attributed to cluster A- (see Table 6). (d) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for shells attributed to cluster B. (e) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for shells attributed to cluster B+ (see Table 6). (f) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for shells attributed to cluster C. All correlations significant (Anova, $p \leq 0.001$).

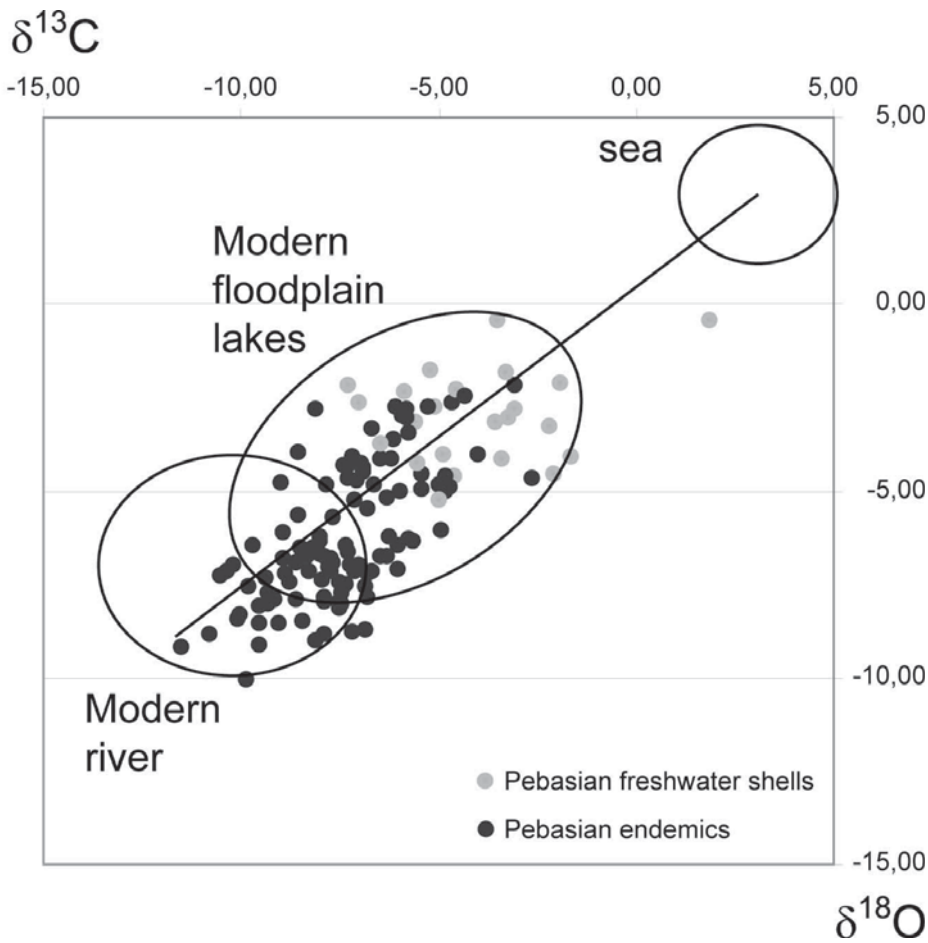


Fig. 6. Isotope ratios of the Pebasian shells and indications of typical isotope signatures of marine and Amazonian river shells. Pebasian shells from cluster B, which include typical freshwater taxa such as pearly fresh water mussels, have the highest values, whereas the endemics from the A and especially C clusters yield very low values. A strong enrichment of $\delta^{13}\text{C}$ isotope ratios and a slight elevation of $\delta^{18}\text{O}$ isotope ratios are explained by shallow, possibly seasonally isolated habitats, where outgassing, evaporation and plant growth modified the original river isotope signatures.

rine end member. The isotope ratios almost certainly reflect lake systems, where the original river water signals have been modified by, amongst others, outgassing, equilibration with atmospheric CO_2 and plant growth, leading to strongly elevated $\delta^{13}\text{C}$ signatures, evaporation and proximity to marine source water of precipitation, leading to elevated $\delta^{18}\text{O}$ signatures (Vanhof *et al.*, 1998, 2003; Kaandorp *et al.*, 2006). Isotope signatures from growth bands in modern Peruvian floodplain lake pearly fresh water mussels representing the dry season actually closely resemble the values found in the B-cluster shells from the Pebas Formation.

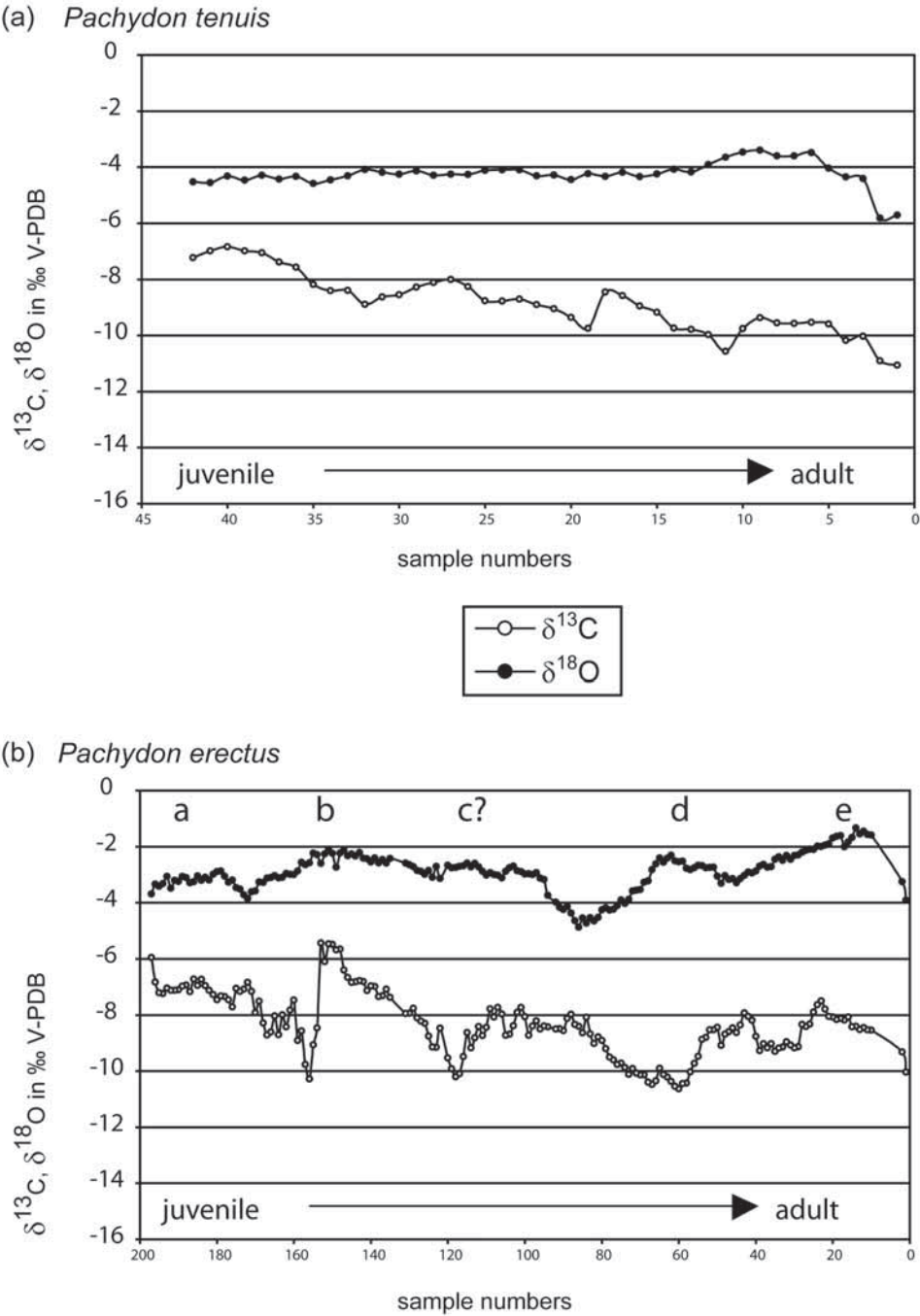
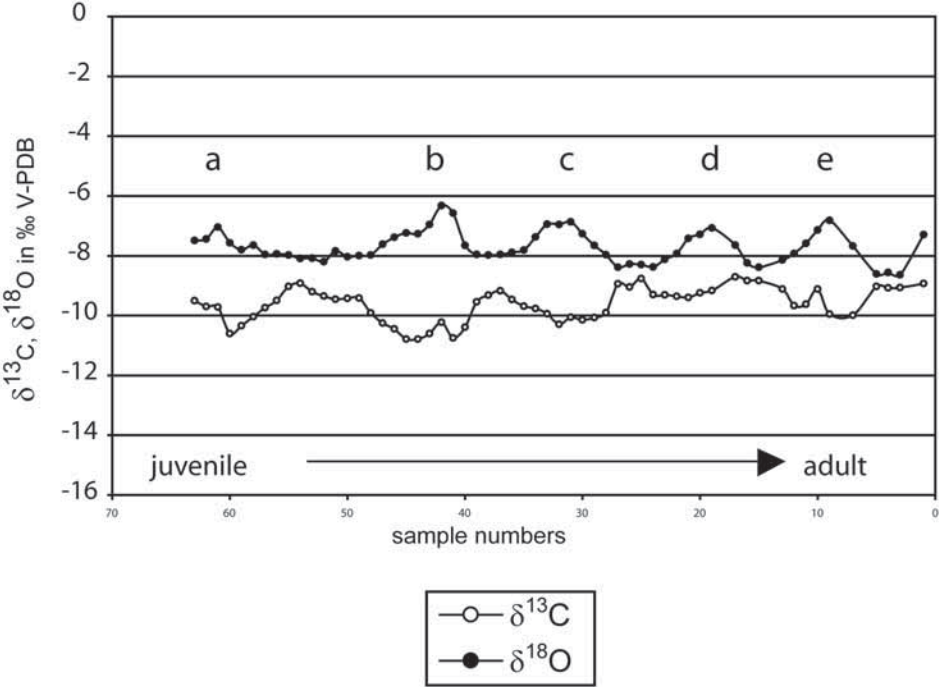
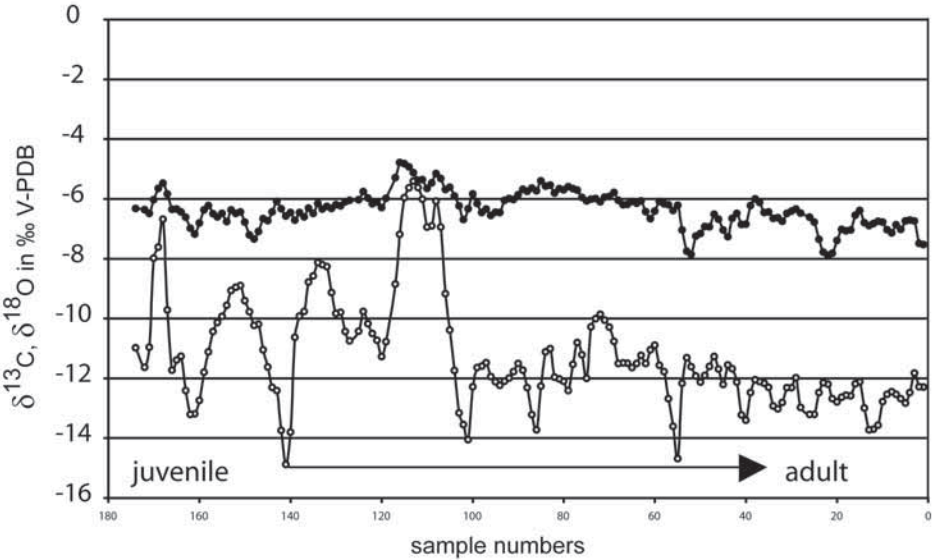


Fig. 7. Values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ along growth bands in four bivalves from Santa Rosa de Pichana (from Kaandorp *et al.*, 2006). (a) *Pachydon tenuis* and (b) *P. erectus* from level 98RK65, (c) *Diplodon longulus* and (d) *P. tenuis* from the interval in which samples F532-F537 were taken.

(c) *Diplodon longulus*



(d) *Pachydon tenuis*



Growth band chemistry

Two shells (*Pachydon tenuis* and *Diplodon longulus*) from the interval comprising levels F532-F536 have low isotope ratios ($\delta^{18}\text{O}$ average c. -7‰ , $\delta^{13}\text{C}$ below -10‰ ; Fig. 7). The two specimens from 98RK65 (*Pachydon tenuis* and *P. erectus*) yield slightly higher isotope values (average $\delta^{18}\text{O}$ c. 4‰ ; $\delta^{13}\text{C}$ at c. -9‰). Poorly developed cycles of $\delta^{18}\text{O}$ in *Pachydon* are irregular and of a low amplitude (typically 2-3‰). *Pachydon* specimens show an average decreasing amplitude during growth. Cyclicity of $\delta^{13}\text{C}$ is irregular. In the juvenile stages of two of the three specimens, variations are very large (up to 9‰). Kaandorp *et al.* (2006) concluded that the flat oxygen isotope profiles were consistent with freshwater biotopes in water bodies with prolonged residence times (lakes).

Low amplitude cyclicity in $\delta^{18}\text{O}$ that is well visible in the *Diplodon* specimen is in anti-phase with regular $\delta^{13}\text{C}$ cycles of low amplitude (c. 1-2‰). Kaandorp *et al.* (2006) explained the anti-phase $\delta^{13}\text{C}$ - $\delta^{18}\text{O}$ cycles in the *Diplodon* specimen as reflecting seasonal environmental change affecting the dissolved inorganic carbon (DIC) pool. Either increased stratification and remineralization of organic matter in bottom water during the dry season or seasonal switching of water sources between more local and more distal parts of the drainage basin with different C_3/C_4 plant distributions could explain the anti-phase signal in *Diplodon*. Additional trace-element analyses on the *Diplodon longulus* and *Pachydon tenuis* specimens from level F532-F537 confirmed seasonality interpretations from the oxygen record in *Diplodon*, but added no insights into the age of the *Pachydon* specimen (Kaandorp *et al.*, 2006). The irregular occurrence of iron spikes was interpreted as recurring episodic lowering of dissolved oxygen in the water column. High barium concentrations in *Pachydon tenuis* were suggested to relate to the tolerance of this species to low oxygen concentrations in the bottom waters (Kaandorp *et al.*, 2006; Wesselingh, 2006b).

The relative flat and irregular oxygen and carbon isotope profiles in the *Pachydon* specimens were explained to reflect little and unpredictable variation in the aquatic chemistry, indicating long residence times of the water. The low to very low $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were found to be incompatible with any substantial marine influence in the system.

Discussion

The faunistic character of the counted samples from Santa Rosa de Pichana is very similar to that of the faunistic character of 285 samples from Pebas Formation exposures in northeast Peru and southeast Colombia (Wesselingh *et al.*, 2002). The stable isotope ratios measured in the Santa Rosa de Pichana shells also are representative for the Pebas Formation (Vanhof *et al.*, 1998, 2003). The sequences in Santa Rosa are well developed (thick), but otherwise comply with the dominant type of sedimentary sequence found in the Pebas Formation (Räsänen *et al.*, 1998; Gingras *et al.*, 2002; Vanhof *et al.*, 2003). The studied sequences contain three intervals, a transgressive, maximum flooding and regressive/prograding interval.

Transgressive interval – The base of the transgressive interval is formed by organic-rich clays or (partially) reworked peat commonly containing molluscs that may be

concentrated in lenses, as well as sandstone intervals. In one case a channel is developed in the basal transgressive interval. The base of the transgressions are usually characterised by burrowed firmgrounds. The *Thalassoides* type of burrowing suggests substantial elevation of salinity (up to mesohaline; Gingras *et al.*, 2002). Upwards, the sediments grade into blue-grey massive or bioturbated fossiliferous mudstones or silty, fine-grained sandstones. The presence of *Asterosoma* burrows just below level F532 again suggests elevated salinities for this interval. Terrestrial snails occur in the basal lignites. In the overlying/intervening sandy interval, low diversity faunas occur that are attributed to the Tall-*Dyris* and *Tryonia* assemblages, with indications of considerable reworking. Indications for (episodically) low pH values, also indicating freshwaters, exist in the form of common dissolution marks and softening of shell carbonate. Stable oxygen and carbon isotope ratios show large variations, but ratios are in general less negative than those of the late transgressive and highstand faunas. Strontium isotope ratios of two specimens from level F538#1 (*Dyris lintea* and *Pachydon tenuis*; Vonhof *et al.*, 2003) show typical values of Andean freshwater sources and exclude any substantial mixing with seawater for that interval. This implies that relatively high carbon and oxygen isotope ratios can only be explained by plant growth and/or evaporation in combination with outgassing of CO₂, similar as seen in *Anodontites* living in present-day Amazonian floodplain lakes (Kaandorp *et al.*, 2003). The presence of juvenile specimens of *Corbula cotuhensis* in samples 98RK65 and 98RK66 indicates that the species, which is representative of marginal marine settings (Wesselingh, 2006a), managed to become settled, but apparently did not survive to adulthood. The rare occurrence of such one-year old marginal marine species elsewhere in the Pebas Formation shows that the system was open to marine settings during the early phase of transgression.

The upper part of the transgressive interval is usually a mollusc-rich siltstone layer that yields faunas attributed to the Small-*Dyris* assemblage *sensu* Wesselingh *et al.* (2002). Faunas are diverse and well preserved. The faunas lived in little agitated bottoms, between the fair-weather and storm wave base or below the latter. Judging from the common occurrence of charophytic oogenia, these waters must have been clear. The shelly mud intervals can also directly overlay the basal lignite/peat, in which case considerable quantities of shells can be mixed in from the Tall-*Dyris* and *Tryonia* assemblages (level 98RK65).

Interval of maximum flooding – These intervals are dominated by dark grey mudstones with dispersed organic matter and *in situ* mollusc faunas (dominated by *Pachydon obliquus*). The Small-*Dyris* assemblages of the late transgressive intervals grade into the *Pachydon obliquus* assemblage of the maximum flooding intervals. Diversity drops as the faunas become dominated by *P. obliquus*. Preservation of the molluscs is good, apart for variation in the shell integrity. The *Pachydon obliquus* assemblage is thought to represent dysoxic lake bottom communities (Wesselingh *et al.*, 2002) below storm wave base. Low stable isotope values exclude the possibility of substantial marine influence during deposition of this interval.

Regressive/prograding interval – The dark grey mudstones of the highstand interval grade into a succession of dark grey and blue mudstones, and laminated, fine-grained sandstone lenses and laminae, with rare burrows (*Gyrolithes*, *Arenicolites*, *Planolites*).

Sandstone intercalations increase upward, and (sometimes massive) sandstone layers dominate the upper part of the regressive/prograding interval, reflecting the shallowing of the shoreface. The shore eventually became emerged, allowing the development of a soil in the upper part of sequence III. The regressive/prograding interval of sequence III is unusually thick for the Pebas Formation. Shells are almost entirely absent in regressive/prograding intervals. In the studied section a few fossil molluscs were observed only in sequence III, but could not be sampled. In other sections, the regressive/prograding interval is usually devoid of molluscs and, judging from the excellent preservation of fine-scale sedimentary structures, burrowing faunas (including corbulid bivalves) must have been extremely rare or absent. In one section (Santa Teresa I, Loreto, Peru: locality data in Wesselingh *et al.*, 2002), we observed thin strings or pavements consisting of juvenile *Pachydon* specimens preserved in butterfly position (valves lying in plane attached through ligament). These juveniles apparently represent single settlement events followed by mass mortality in the same year. The presence of *Gyrolithes* in the lower shoreface of sequence IV might indicate strong salinity fluctuations.

A number of indications exist that oxygen levels in waters in the Pebas system played a crucial role in the determination of faunal distributions. Low oxygen levels are indicated by common preservation of organic matter, possible presence of chemosymbiosis in Pachydontinae (Wesselingh, 2006b), absence of oxyphyllic taxa such as *Corbicula* spp., low carbon isotope ratios, and uncommon elevated barium and iron concentrations in shell carbonate (Kaandorp *et al.*, 2006). Oxygen levels seem to have been high in the transgressive phase, but dropped during highstand intervals. With decreasing depositional depths upwards in the sequences, oxygenation also should have increased.

Little agreement exists over the predominant salinity regimes in the Pebas system. Based on ichnofossil assemblages and the presence of tidal sedimentary structures, Gingras *et al.* (2002) argued for predominantly oligohaline-mesohaline salinities during deposition of the Pebas Formation. Based on molluscs, strontium and stable isotopes, Wesselingh *et al.* (2002) and Vonhof *et al.* (2003) argued for almost exclusively freshwater settings in the Pebas Formation with only very few oligohaline incursion levels. We have investigated possible salinity variations on a range of scales in Santa Rosa de Pichana.

Oligohaline-polyhaline conditions throughout are excluded in intervals bearing molluscs, based on strontium isotope ratios, low oxygen and carbon isotope ratios, and the presence of strict freshwater taxa in low numbers in half of the samples. Oxygen and carbon isotope ratios are particularly low in faunas from the late transgressive and maximum flooding intervals. The relatively high, but nevertheless negative, oxygen isotope ratios found in mollusc assemblages in the basal part of the transgressive horizons might indicate some marine influence. However, strontium isotope measurements, low carbon isotope ratios and the presence of strict freshwater species at the same levels rule elevated salinities out. The clearest indications for possible elevated salinities are from *Thalassinoides*-demarcated *Glossifungites* surfaces in firmgrounds at the base of sequences and from *Asterosoma* burrows in sandstones in the basal transgressive interval. Molluscs are absent in the latter sandstones, but mollusc faunas from strata directly overlying the *Asterosoma*-bearing sandstones show an admixture of shells representa-

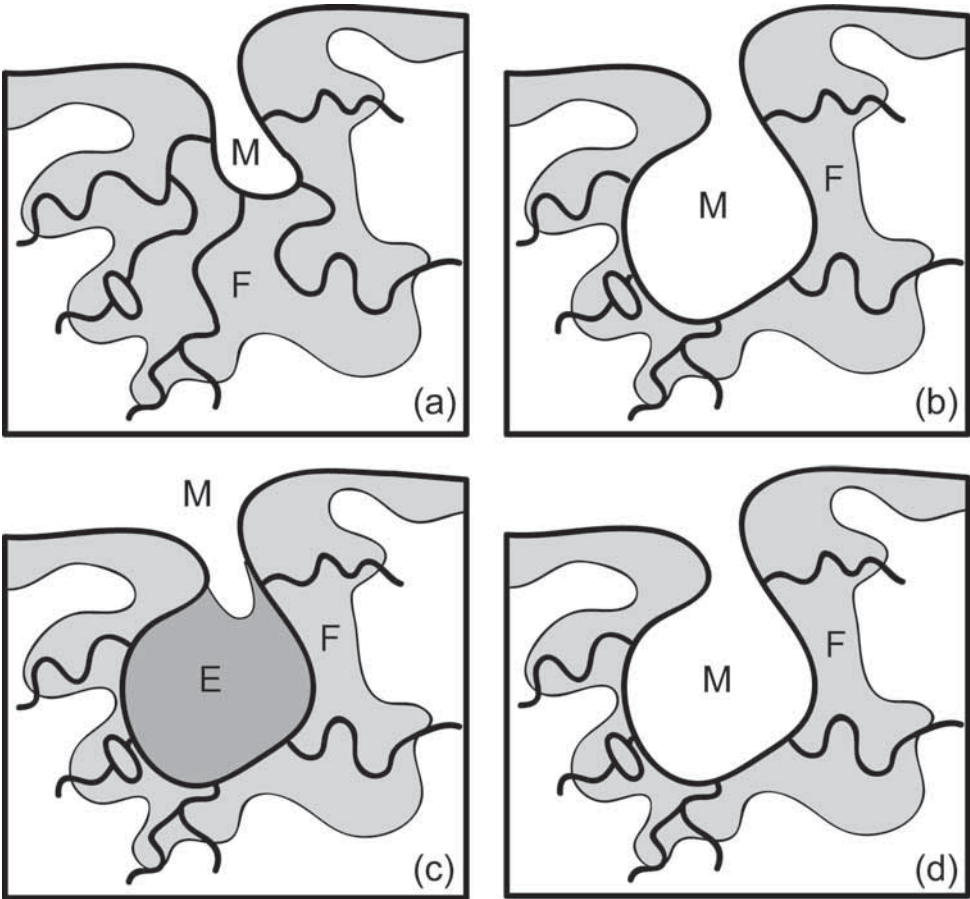


Fig. 8. (a) In a low-gradient coastal plain, fluvial faunas can become restricted towards the basin margins during maximum marine transgressions (b). In the case of the Pebas system, a highly diverse endemic freshwater fauna existed between the marine and fluvial freshwater settings (c). Such endemic faunas are not adapted for living in fluvial environments. If substantial marine transgressions occur, the endemic faunas would be expected to become squashed between marine and fluvial regimes (d). Key: M = marine faunas; E = endemic (freshwater) faunas; F = fluvial and fluviolacustrine faunas.

tive of fluvial, marginal lacustrine and lacustrine settings, while lacking marine species, with a single exception. In the base of sequence II some juvenile specimens of *Corbula cotuhensis* were found, indicating the ability of settlement of marginal marine species there. The presence of juveniles only indicates that the species were able to settle, but died before reaching adulthood. This is a clear sign that the Pebas system was open to marginal marine settings during at least the initial phase of transgression. Fully-grown marginal marine species do occur in the Pebas Formation in younger stratigraphic intervals (Vermeij & Wesselingh, 2000; Wesselingh *et al.*, 2002; Wesselingh, 2006a). The apparent incompatible salinity indications can be explained in two ways. The first possibility is that *Thalassinoides* were emplaced at elevated salinities under depositional

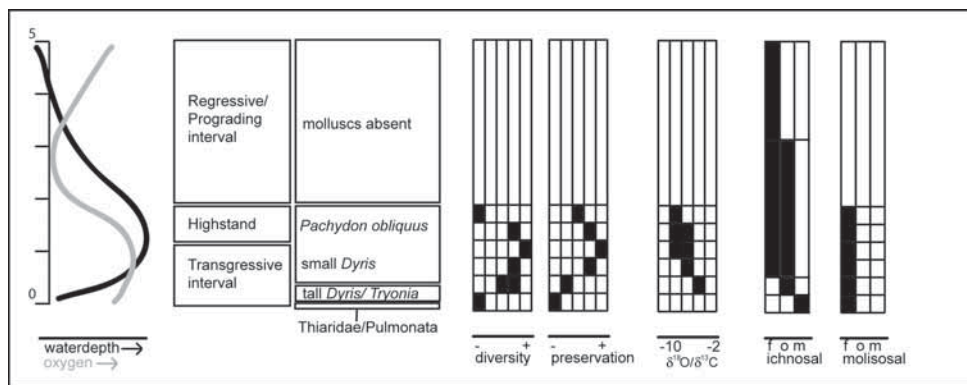


Fig. 9. Schematic representation of depositional and faunistic characteristics in sequences from Santa Rosa de Pichana. Salinity indications from combined molluscan/isotope data and from ichnofossil occurrences are also outlined. The height of a sequence (in this case 5.0 m) ranges between 4 and 6.5 m in Santa Rosa. In other Pebas outcrops such sequences are often only 2.5–4.0 m thick. Key: f = freshwater; o = oligohaline; m = mesohaline; ichnosal = salinity estimates based on ichnofossil data; molisosal = salinity estimates based on mollusc and isotope data. Other abbreviations explained under Figure 2.

conditions where carbonate faunas did not live or were not fossilized. In that case, marine incursions might be preserved only in association with the flooding surfaces, after which the embayed water rapidly freshened due to poor circulation and accumulation of river waters. The second possibility is that the animals responsible for these burrows (burrowing shrimps) adapted to freshwater settings, in a manner similar to the corbulid pachydontine bivalves (Wesselingh, 2006b).

A very similar situation comprising marine ichnofossils in deposits with freshwater molluscs and ostracods has been described lately from the Paleocene Fort Union Formation of the United States (Belt *et al.*, 2005). Here, three freshwater ostracod and two freshwater bivalve species, one of which is a *Pachydon*, occur in deposits that also yield a diverse array of marine ichnogenera. Belt *et al.* (2005) showed that, in the Fort Union Formation, the different assemblages were deposited in separate time intervals, and concluded that a very low gradient coastal lowland, susceptible to sea level variations, explains the occurrence of both freshwater and marine indicators in successive layers, like the first scenario outlined above for the Pebas Formation. A difference with the Pebas system is the high diversity, and especially endemism and stratigraphic continuity, of the mollusc and ostracod faunas in the latter system. To date no indications have been found that these faunas could cope with elevated salinities and it is unlikely that they could have taken shelter in 'normal' (fluvial) freshwater environments during marine incursions (Fig. 8). The evolutionary continuity of the endemic Pebasian faunas (especially from c. 17 to c. 9 Ma: Wesselingh & Salo, 2006; Wesselingh *et al.*, 2006a) in western Amazonia argues against repeated basin-wide establishment of mesohaline or normal marine settings.

On the other hand, the sporadic occurrence of (typically) brackish-water trace fossils is an argument indicating that the fauna did not evolve into stable infaunal, freshwater niches in Miocene Amazonia; that is, if depositional conditions were consistently fresh

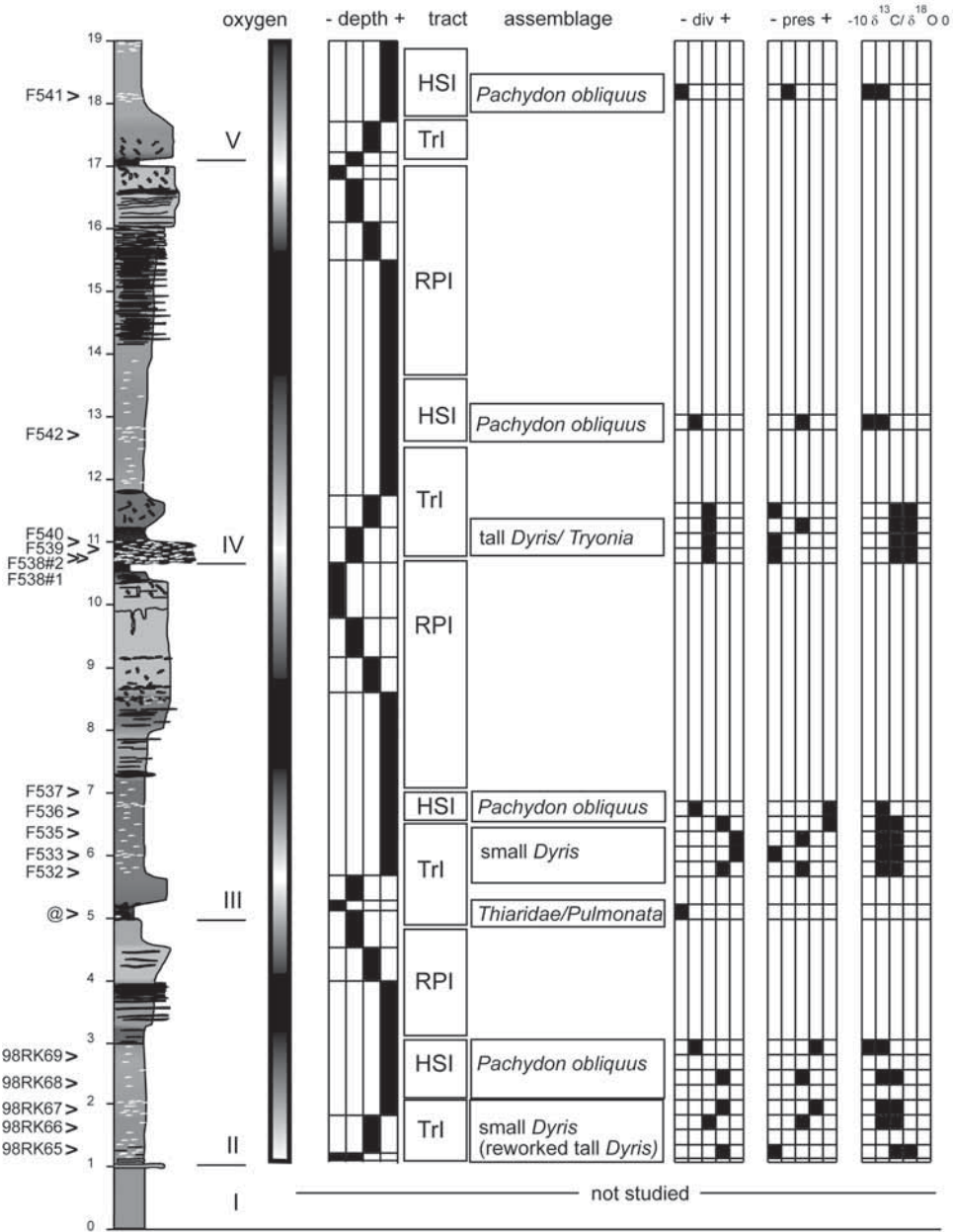


Fig. 10. Interpretation of the Santa Rosa de Pichana section. Key: HSI = highstand interval; TrI = transgressive interval; RPI = regressive/prograding interval; div = diversity; pres = preservation; $\delta^{13}\text{C} / \delta^{18}\text{O}$ = average values for samples. Depth ranges from left to right: below storm wave base, between fair weather and storm wave base, above fair-weather wave base, terrestrial; grain-size in lithological column as in Figure 2.

and burrowing animals evolved into increasingly freshwater environments, then their success should be recorded in the sedimentary record as pervasive and dominant fabrics. Likewise, the relatively rare occurrence of highly burrowed deposits suggests the depositional system was not consistently brackish. This leaves us with the possibility that the brackish-water character of the depositional system has been previously overstated (Gingras *et al.*, 2002), but that regular brackish-water incursions did occur. This possibility would imply that fossil shells represent only 'snapshots' of the entire depositional (including geochemical) system. Possible salinity variations on a seasonal scale in shell-bearing intervals have been excluded by isotope work in successive growth bands of bivalves including the specimens from Santa Rosa de Pichana (Kaandorp *et al.*, 2006).

In general, waters of the Pebas system must have been non-acidic, given the common and very delicate preservation of carbonate fossils. Kaandorp *et al.* (2006) attributed the very large $\delta^{13}\text{C}$ variation observed in some *Pachydon* specimens (Fig. 7) to pH values of the water at around pH 6.4. Episodic lowering of pH may have occurred in environments during the early stages of the transgressive phases, as indicated by the presence of dissolution holes on shells. In shallow waters with abundant plant production, the degradation of organic matter may produce interstitial lowering of pH, dissolving carbonate shells (Aller, 1982). Dissolution may also result from bacterial degradation, but this type of dissolution often provides a corroded surface, not large dissolution holes that characterise some of the samples from Santa Rosa de Pichana. Also, local drainage of black water creeks or rivers from swampy backlands may have caused lowering of pH values in the water, as may have substantial rainwater input in shallow (isolated) marshes and ponds. Furthermore, pH values may have been depressed in the vicinity of cratonic rivers, but no indication was found in the Santa Rosa section for these. A model for the depositional sequences and faunal development of the Santa Rosa de Pichana sequences is illustrated in Figure 9 and a full interpretation of the section is given in Figure 10.

Conclusions

A common type of succession of transgressive, highstand and regressive/prograding intervals is found in depositional sequences of the non-marine Miocene Pebas Formation of western Amazonia. Mollusc faunas are almost entirely limited to the transgressive and highstand intervals. In the transgressive to highstand intervals a succession of assemblages is found, from the Thiaridae/Pulmonata assemblage, through the *Tryonia* and Tall-*Dyris* assemblages in the early transgressive intervals and Small-*Dyris* assemblage in the late transgressive intervals, to the *Pachydon obliquus* assemblage in the highstand interval. Reworking during the early transgressive phase was common. With increasing water depth, the preservation of the molluscs improved. Diversity increased to its zenith in the Small-*Dyris* assemblage and then decreased towards the *Pachydon obliquus* assemblage.

Dissolved oxygen levels in the water probably played a major role in the determination of fauna successions, with dysoxia becoming important during highstand intervals and dominant in the early regressive/prograding intervals. Molluscs and stable isotope profiles show no indications of elevated salinities, not even on seasonal time scales.

Thalassinoid ichnofossils of the *Glossifungites* ichnofacies at the base of sequences may represent up to lower mesohaline salinities, but also may reflect evolution of lowered salinity tolerances for the constructors (crustaceans and possibly polychaetes).

The Santa Rosa de Pichana section appears representative for large parts of the Pebas Formation. Based on molluscan and stable isotope evidence we think that the system consisted of predominantly freshwater swamp to lacustrine conditions in a long-lived lake/wetland system at sea level and open to marginal marine settings. However, discrepancies with ichnofossil data from the same stratigraphic intervals, which consistently indicate elevated salinities, are in need of further study.

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Appendix 1

Species composition of the Santa Rosa de Pichana samples

Sample	98RK65	98RK66	98RK67	98RK68	98RK69	F532	F533	F535	F536	F537	F539	F538#1	F538#2	F540	F542	F541
<i>Anodontites capax</i>	10												8			
<i>Anodontites batesi</i>						1										
<i>Diplodon longulus</i>								3								
Hyriidae sp. indet.												1				
Unionoidea sp. indet.											3		4			
<i>Mytilopsis scripta</i>	8	17	7			19	50	5	16					11	3	
<i>Mytilopsis sallei</i>	80	13	6	3	2	50	43	120	180	13	20	110	42	12	23	
<i>Corbula cotuhensis</i>	1	9														
<i>Pachydon obliquus</i>	1300	1200	48	85	73	700	500	800	1500	170	1500		270	240	1200	300
<i>Pachydon carinatus</i>	3	7	3		2		5	9	5	1						
<i>Pachydon tenuis</i>	4	3	3	3	6	3	6	7	11		12	120	60	11	7	
<i>Pachydon ellipticus</i>	2						3	16	8	3						
<i>Pachydon amazonensis</i>	20	49	9	7	1	50	37	180	15		22	35	14	31	6	1
<i>Pachydon cuneatus</i>		4		1	1	3	6	7	9			1			4	
<i>Pachydon erectus</i>	2	12	2	1		11	5	7	1	2			1	1	1	
<i>Pachydon ledaeformis</i>	105	13				14	11	28	16		5	13	18	3		
<i>Pachydon iquitensis</i>	3	2				6	12	65	16				1	5		
<i>Pachydon telliniformis</i>	45	10	3	1	1						7	2	1			
<i>Pachydon</i> sp. indet.												1				
<i>Exallocorbula dispar</i>	10	19		3		4	8	32	24		1			12	2	
<i>Ostomya papyria</i>		8	1			31	22	35	110	1						
<i>Ostomya myiformis</i>		2						2								
<i>Ostomya carinata</i>			2			4	21	23	18	1						
<i>Pachyrotunda rotundata</i>									4						1	
<i>Concentricavalva concentrica</i>						2	7	41	13	1						
<i>Neritina ortonii</i>	15	3	3	1			1	3	1						2	
<i>Neritina etheridgei</i>		1				3	1			1						
<i>Tryonia minuscula</i>	170	16		1		1	4	110	260	31	540	450	225	650	33	
<i>Tryonia scalarioides</i>																
<i>tuberculata</i>	103	20														
<i>Tryonia acicularis</i>		3		1		3	3	6	12	1					2	
<i>Dyris ortonii</i>	2	10		1		3	1	1	6							
<i>Dyris tricarinata</i>	155	215	5	22	2	70	60	400	60		310			53	4	1
<i>Dyris lintea</i>	260	1									3	240	21	1		
<i>Dyris hershleri</i>											70	1500	850	3		
<i>Dyris pebasensis</i>	1															
<i>Dyris gracilis</i>	2	3		1	1	7	8	6	1						3	
<i>Dyris hauxwelli</i>	125	58		3	1	25	30	75	4						97	
<i>Dyris lanceolatus</i>															1	
<i>Dyris acicularis</i>								2								
<i>Dyris regularis</i>						6		10	1							
<i>Dyris microbispiralis</i>	2	2				21	29	16	4						17	
<i>Dyris</i> sp. indet.				1			3	3						2	1	1
<i>Onobops communis</i>	26	65		3	2	39	62	70	35						28	2
<i>Onobops bispiralis</i>	2	1					1	3							2	

Cont.	98RK65	98RK66	98RK67	98RK68	98RK69	F532	F533	F535	F536	F537	F539	F538#1	F538#2	F540	F542	F541
<i>Onobops microconvexus</i>	1	2						1		1						
<i>Onobops minissimus</i>															1	
<i>Pyrgophorus</i> sp.			1				2									
<i>Toxosoma eboreum</i>	6	45	3	2	1	65	58	65	60		1				27	1
<i>Longosoma curtum</i>								1							2	
<i>Littoridina pebasana</i>		1				2		2								1
<i>Littoridina</i> sp. indet.								1								
<i>Sioliella bella</i>								1								
<i>Sioliella crassilabra</i>			1			1		10	3				1			
<i>Sioliella woodwardi</i>		1				7	4					1				
<i>Sioliella</i> sp. indet.												3			1	
<i>Tropidobora tertiana</i>		2	1			2		6	1							
<i>Cochliopina?</i> <i>bourguyi</i>		2				2	2	2								
<i>Cochliopina?</i> <i>hauxwelli</i>	4					5	6	3	8						2	
<i>Cochliopidae</i> sp. indet.							1			1					1	
<i>Sheppardiconcha</i>																
<i>tuberculifera</i>	150	4		1												
<i>Orthalicus</i> sp.								1								
<i>Pebasiconcha immanis</i>												3				
	2617	1823	98	141	93	1159	1013	2175	2405	227	2491	2482	1513	1039	1469	307

Appendix 2
Isotope composition of the Santa Rosa de Pichana mollusc shells. Standard deviation of replicate analyses <0.05.

Level	Species	δ ¹³ C	δ ¹⁸ O	Level	Species	δ ¹³ C	δ ¹⁸ O
F541	<i>Pachydon obliquus</i>	-7.72	-6.84	F539	<i>Pachydon tenuis</i>	-5.54	-4.25
F541	<i>Pachydon obliquus</i>	-7.86	-6.77	F539	<i>Pachydon obliquus</i>	-7.06	-4.75
F541	<i>Pachydon obliquus</i>	-6.02	-6.47	F539	<i>Pachydon obliquus</i>	-7.10	-5.27
F541	<i>Pachydon obliquus</i>	-7.68	-6.93	F539	<i>Pachydon tenuis</i>	-7.38	-4.33
F541	<i>Pachydon obliquus</i>	-7.28	-6.63	F539	<i>Dyris tricarinatus</i>	-7.82	-4.84
F541	<i>Pachydon obliquus</i>	-7.51	-7.45	F539	<i>Dyris tricarinatus</i>	-5.72	-6.31
F541	<i>Pachydon obliquus</i>	-7.76	-7.07	F539	<i>Dyris tricarinatus</i>	-8.90	-6.82
F541	<i>Pachydon obliquus</i>	-7.49	-8.15	F539	<i>Tryonia minuscula</i>	-8.40	-6.75
F541	<i>Pachydon obliquus</i>	-5.64	-6.39	F539	<i>Tryonia minuscula</i>	-5.78	-3.06
F541	<i>Pachydon obliquus</i>	-7.46	-7.73	F539	<i>Tryonia minuscula</i>	-5.23	-2.74
F541	<i>Pachydon obliquus</i>	-8.87	-7.23	F538	<i>Pachydon tenuis</i>	-4.97	-4.86
F541	<i>Pachydon obliquus</i>	-8.26	-7.15	F538	<i>Pachydon tenuis</i>	-6.62	-4.83
F541	<i>Pachydon obliquus</i>	-6.44	-6.77	F538	<i>Pachydon tenuis</i>	-4.81	-5.00
F541	<i>Pachydon obliquus</i>	-7.02	-6.98	F538	<i>Pachydon tenuis</i>	-8.98	-4.79
F542	<i>Pachydon obliquus</i>	-7.90	-7.98	F538	<i>Pachydon tenuis</i>	-4.57	-4.61
F542	<i>Pachydon obliquus</i>	-7.88	-7.90	F538	<i>Mytilopsis cf. sallei</i>	-4.93	-6.07
F542	<i>Pachydon obliquus</i>	-9.54	-9.12	F538	<i>Pachydon tenuis</i>	-1.61	-4.11
F542	<i>Pachydon obliquus</i>	-7.46	-8.05	F538	<i>Pulmonata sp. indet.</i>	-4.83	-4.65
F542	<i>Pachydon obliquus</i>	-8.09	-9.01	F538	<i>Mytilopsis cf. sallei</i>	-5.79	-2.84
F542	<i>Toxosoma eboreum</i>	-6.86	-7.56	F538	<i>Pachydon obliquus</i>	-3.99	-4.04
F542	<i>Toxosoma eboreum</i>	-6.78	-7.86	F538	<i>Dyris lintea</i>	-5.20	-1.79
F542	<i>Pachydon erectus</i>	-7.90	-8.84	F538	<i>Dyris lintea</i>	-3.55	-3.17
F542	<i>Tryonia minuscula</i>	-7.48	-8.03	F538	<i>Dyris lintea</i>	-3.24	-3.05
F542	<i>Dyris lauxwelli</i>	-6.83	-8.72	F538	<i>Dyris lintea</i>	-4.84	-4.04
F542	<i>Soliella sp. indet.</i>	-7.74	-7.20	F538	<i>Dyris lintea</i>	-4.96	-5.25
F539	<i>Pachydon obliquus</i>	-8.14	-6.54	F538	<i>Dyris lintea</i>	-2.20	-3.26
F539	<i>Pachydon obliquus</i>	-5.39	-4.96	F538	<i>Dyris lintea</i>	-3.05	-2.82
F539	<i>Pachydon obliquus</i>	-5.95	-5.01	F538	<i>Tryonia minuscula</i>	-3.41	-4.16
F539	<i>Pachydon obliquus</i>	-5.75	-3.48	F538	<i>Tryonia minuscula</i>	-4.69	-4.89

Level	Species	δ ¹³ C	δ ¹⁸ O
F536	<i>Pachydon obliquus</i>	-7.34	-6.47
F536	<i>Pachydon obliquus</i>	-6.78	-7.21
F536	<i>Pachydon obliquus</i>	-8.61	-7.91
F536	<i>Pachydon obliquus</i>	-6.04	-7.11
F536	<i>Pachydon obliquus</i>	-9.87	-10.06
F536	<i>Pachydon obliquus</i>	-8.43	-8.49
F536	<i>Pachydon tenuis</i>	-7.98	-6.70
F536	<i>Pachydon tenuis</i>	-7.96	-6.35
F536	<i>Toxosoma eboreum</i>	-6.23	-6.25
F536	<i>Toxosoma eboreum</i>	-6.65	-7.16
F536	<i>Tryonia minuscula</i>	-7.17	-8.77
F536	<i>Tryonia minuscula</i>	-6.29	-6.75
F536	<i>Dyris ortonii</i>	-7.13	-7.15
F536	<i>Dyris hauxwelli</i>	-7.22	-6.99
F533	<i>Pachydon obliquus</i>	-8.29	-6.78
F533	<i>Pachydon obliquus</i>	-7.48	-7.99
F533	<i>Pachydon obliquus</i>	-8.92	-6.10
F533	<i>Pachydon obliquus</i>	-7.67	-5.73
F533	<i>Pachydon obliquus</i>	-8.01	-6.25
F533	<i>Pachydon obliquus</i>	-6.76	-5.50
F533	<i>Pachydon obliquus</i>	-9.52	-8.11
F533	<i>Mytilopsis scripta</i>	-10.33	-7.15
F533	<i>Pachydon carinatus</i>	-8.53	-5.68
F533	<i>Dyris tricarinatus</i>	-10.18	-6.98
F533	<i>Toxosoma eboreum</i>	-9.34	-7.36
F533	<i>Dyris hauxwelli</i>	-9.69	-6.49
F533	<i>Dyris tricarinatus</i>	-8.47	-6.51
F533	<i>Onobops communis</i>	-8.59	-6.93
F533	<i>Mytilopsis scripta</i>	-10.52	-7.28
98RK69	<i>Pachydon obliquus</i>	-9.30	-8.02
98RK69	<i>Pachydon obliquus</i>	-7.33	-7.52
98RK69	<i>Pachydon obliquus</i>	-10.06	-8.46
98RK69	<i>Pachydon tenuis</i>	-9.15	-7.94
Level	Species	δ ¹³ C	δ ¹⁸ O
98RK69	<i>Pachydon tenuis</i>	-9.29	-7.77
98RK69	<i>Pachydon obliquus</i>	-9.52	-8.56
98RK69	<i>Pachydon obliquus</i>	-9.01	-8.55
98RK69	<i>Pachydon obliquus</i>	-9.77	-7.60
98RK69	<i>Pachydon obliquus</i>	-10.76	-8.83
98RK69	<i>Pachydon obliquus</i>	-11.48	-9.22
98RK69	<i>Toxosoma eboreum</i>	-8.75	-7.46
98RK69	<i>Toxosoma eboreum</i>	-7.93	-7.38
98RK69	<i>Dyris tricarinata</i>	-10.03	-8.35
98RK66	<i>Pachydon obliquus</i>	-4.67	-2.62
98RK66	<i>Pachydon obliquus</i>	-5.56	-3.19
98RK66	<i>Pachydon obliquus</i>	-1.90	-2.10
98RK66	<i>Pachydon obliquus</i>	-4.55	-2.29
98RK66	<i>Pachydon obliquus</i>	-6.87	-4.46
98RK66	<i>Pachydon obliquus</i>	-6.96	-4.27
98RK66	<i>Pachydon obliquus</i>	-5.06	-2.80
98RK66	<i>Toxosoma eboreum</i>	-5.88	-3.02
98RK66	<i>Dyris tricarinata</i>	-8.55	-3.96
98RK66	<i>Dyris tricarinata</i>	-6.98	-2.67
98RK66	<i>Dyris hauxwelli</i>	-6.46	-4.19
98RK66	<i>Dyris hauxwelli</i>	-6.67	-3.34
98RK65	<i>Pachydon obliquus</i>	-7.29	-4.71
98RK65	<i>Pachydon obliquus</i>	-7.16	-4.11
98RK65	<i>Pachydon obliquus</i>	-6.14	-3.62
98RK65	<i>Pachydon obliquus</i>	-6.90	-4.41
98RK65	<i>Pachydon obliquus</i>	-6.45	-3.73
98RK65	<i>Pachydon obliquus</i>	-6.31	-5.21
98RK65	<i>Pachydon obliquus</i>	-6.90	-4.53
98RK65	<i>Pachydon obliquus</i>	-6.18	-4.16
98RK65	<i>Sheppardiconcha tuberculifera</i>	-3.07	-2.21
98RK65	<i>Sheppardiconcha tuberculifera</i>	-3.51	-0.43
98RK65	<i>Sheppardiconcha tuberculifera</i>	-5.42	-4.55
98RK65	<i>Sheppardiconcha tuberculifera</i>	-6.06	-2.79

Level	Species	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
98RK65	<i>Sheppardiconcha tuberculifera</i>	-7.25	-2.21
98RK65	<i>Sheppardiconcha tuberculifera</i>	-3.25	-1.81
98RK65	<i>Dyrus lintea</i>	-5.83	-2.35
98RK65	<i>Dyrus lintea</i>	1.88	-0.42
98RK65	<i>Dyrus lintea</i>	-4.31	-2.50

Level	Species	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
98RK65	<i>Dyrus lintea</i>	-2.60	-4.67
98RK65	<i>Dyrus lintea</i>	-2.08	-4.54
98RK65	<i>Tryonia scalarioides tuberculata</i>	-8.11	-2.81
98RK65	<i>Tryonia scalarioides tuberculata</i>	-7.27	-4.33

