

PALAEODEMECOLOGICAL ANALYSIS OF INFAUNAL BIVALVES “LEBENSSTADEN” FROM THE MULICHINCO FORMATION, LOWER CRETACEOUS, NEUQUÉN BASIN, ARGENTINA



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Abstract. The study of palaeodemecological features requires some particular taphonomic conditions. These conditions were met in the Mulichinco Formation (Valanginian), where burrowing bivalve trace fossils are widespread and often appear in cross section on bedding surfaces. Two groups of such beds were analyzed, measuring population density, spatial distribution, size distribution and horizontal orientation of the burrows. The palaeoenvironment was established by means of a detailed sedimentological analysis, and the bivalve fauna present was checked, in order to attempt identifying their potential producers. High population densities were found in the two groups, indicating favourable physical conditions and good food supply, while differences in both spatial and size distributions were noticed between them; on most surfaces there was no preferred orientation. The first group (group A) showed a uniform pattern of spatial distribution and larger traces, with a remarkable absence of small sizes. In the second group (group B), the spatial distribution pattern is indistinguishable from a random distribution (except one case in which the pattern appears to be aggregated). Group A is interpreted as a set of escape traces made by deep burrowers in response to storm deposition, while group B is considered as resting/escape traces made by shallow burrowers in tide-dominated environments. Palaeodemecological studies of this kind are potentially useful tools for sedimentary and basin analyses.

Key words. Bivalvia. Spatial distribution. Population density. Early Cretaceous. Valanginian. Argentina.

Resumen. ANALISIS PALEODEMECOLÓGICO DE SIGNOS DE ACTIVIDAD DE BIVALVOS INFAUNALES DE LA FORMACIÓN MULICHINCO, CRETÁCICO INFERIOR, CUENCA NEUQUINA, ARGENTINA. El estudio de rasgos paleodemecológicos requiere de ciertas condiciones tafonómicas particulares. En la Formación Mulichinco (Valanginiano) se cumplen dichas condiciones, siendo frecuentes los signos de actividad de bivalvos excavadores que aparecen en sección transversal sobre las superficies de estratificación. Dos grupos de tales superficies fueron analizados, midiendo densidad poblacional, disposición espacial, distribución de tamaños y orientación en planta de las excavaciones. El paleoambiente se determinó por medio de un análisis sedimentológico detallado, y se registró la fauna de bivalvos presente con la intención de identificar a los potenciales productores. Se encontraron altas densidades poblacionales para ambos grupos, lo que indica condiciones físicas favorables y buen suministro de alimento, en tanto que la disposición espacial y la distribución de tamaños difiere entre dichos grupos; no se advirtió orientación preferencial en la mayoría de las superficies. El primer grupo (grupo A) muestra un patrón uniforme de disposición espacial y trazas de mayor tamaño; llama la atención la ausencia de pequeños tamaños. En el segundo grupo (grupo B), el patrón de disposición es indistinguible de uno al azar (salvo en un caso donde parece haber un patrón agregado). Se interpreta al grupo A como un conjunto de rastros de escape realizados por excavadores profundos en respuesta a depósitos de tormenta, en tanto que el grupo B es considerado como un conjunto de rastros de reposo/escape hechos por excavadores superficiales en ambientes dominados por mareas. Estudios paleodemecológicos de este tipo representan herramientas potencialmente útiles para los análisis sedimentológicos y de cuencas.

Palabras clave. Bivalvia. Disposición espacial. Densidad poblacional. Cretácico temprano. Valanginiano. Argentina.

EXAMINATION of infaunal bivalve population size, distribution and density has offered a wealth of data for some living species, and is a key tool for proper management of culture, since many of these studies were undertaken in order to better understand the population dynamics of farmed edible species. In contrast, knowledge on *in-situ* fossil populations of marine infaunal bivalves is fragmentary and largely depends on exceptional preservation conditions. However, they may provide useful information about environmental parameters, such as depth, palaeocurrents, nutrient availabil-

ity, etc. (Liljedhal, 1991; Kitamura, 1992; Jonkers, 1999). They may also yield unique biological information, such as population density and structure. In some instances they can even reveal behavioral patterns or response to certain environmental conditions (Kranz, 1974; Mángano *et al.*, 1998).

Suitable preservation conditions are met at some levels of the Mulichinco Formation (Valanginian) which is part of the Mendoza Group. These beds bear a large variety of trace fossils which reveal different activities by the diverse producers (Rodríguez *et al.*, 2007; Pazos, 2009, 2011), and their study

suggests a reinterpretation of previous prevailing views on lithological facies. Besides their use to infer palaeoenvironments, those ichnofossils allow the analysis of some demecological features of their producers, such as their spatial distribution and density (Echevarría *et al.*, 2008).

The spatial arrangement, density, size distribution and orientation of traces found in two groups of beds from the Mulichinco Formation are analyzed in this paper. The resting/escape traces (ichnogenera *Lockeia* James/ *Scalichnus* Hanken, Bromley and Thomsen) are common in the Puerta Curaco (northern Neuquén) section of this unit (Fig. 1), and since the direction of movement of bivalves during escape is almost vertically upward (Kranz, 1974) the information provided by these associations can be considered a fair reflection of certain demecological features of their producers.

GEOLOGICAL SETTING

The Neuquén Basin developed during Mesozoic and early Cenozoic times in the southern Central Andes. It was a backarc basin which opened towards the Palaeo-Pacific and accommodated a thick marine infilling during the Jurassic and Early Cretaceous. Its epicontinental sea condition, separated from the open ocean by a magmatic arc, favoured the development of a tide-dominated platform (Legarreta and Uliana, 1991). The Mulichinco Formation (Weaver, 1931) represents a wedge-like lowstand system tract (LST) (Vergani *et*

al., 1995; Schwarz and Howell, 2005), belonging to the second of the two main sequences included in the Mendocian cycle (Mendoza Group). It developed on top of a previous ramp after a major fall in relative sea level (Gulisano *et al.*, 1984; Legarreta and Gulisano, 1989; Legarreta and Uliana, 1991; Vergani *et al.*, 1995; Schwarz *et al.*, 2006). The unit is mainly restricted to the central part of the basin, and rests on top of the Vaca Muerta-Quintuco Formations. It is in turn overlain by the widespread Agrio Formation.

The logged section (Puerta Curaco, northern Neuquén, Fig. 1) is one of the localities where the Mulichinco Formation is fully exposed (Fig. 2.1). The lowest part of the section at this locality was interpreted as deposited in a relatively deep environment (lower shoreface to shelf, Schwarz and Howell, 2005); nevertheless, recent analyses suggest a much shallower environment (Rodríguez *et al.*, 2007; Pazos, 2009). From the biostratigraphical point of view, the beds here discussed belong to the *Lissonia riveroi* Zone of Early Valanginian age.

MATERIALS AND METHODS

A detailed section of the Mulichinco Formation was logged and measured at Puerta Curaco, northern Neuquén (Fig. 3). For this purpose, lithology, geometry and sedimentary structures were carefully examined in the field, as well as the fossil and ichnofossil record. A facies analysis was performed on these data in order to establish the environment where the trace associations developed.

Study of palaeodemecological features in fossil populations such as spatial relationships, requires certain particular taphonomic conditions. Among these are the preservation of many individuals in life position (or of the fossil traces indicative of these features), an appropriate lithology, and the exposure of large bedding surfaces. These requirements are not suitable for the collection of material because of the volume of rock involved. The *in-situ* outcrops at Puerta Curaco have bivalve resting/escape traces (Figs. 4.4–6) and good cross sections, but the exposed bedding surfaces are reduced. Even though some bottom surfaces are well exposed (Fig. 2.3), their outcrop position make them awkward, if not impossible, to record. Hence, a detailed mapping was carried out on bedding surfaces exposed on some large *ex-situ* blocks which were easily referred to strata in the log of the formation; the analyzed surfaces ranged between 0.6 and 1.1 square metres. Eight top surfaces (from now on referred as sampled surfaces) of seven blocks were analyzed, two of them (referred to as 1 and 2 from now on) belong to a lower

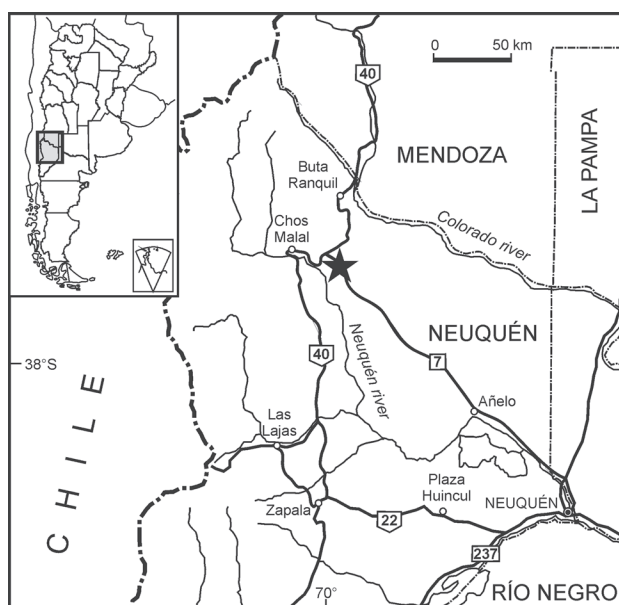


Figure 1. Location map of Puerta Curaco section in northern Neuquén/ Mapa con la localización de la sección de Puerta Curaco en el norte de Neuquén.

set of beds (group A), while sample surfaces 3 to 6 belong to a stratigraphically higher group of beds (group B). Block 7 could not be easily attributed to any of those two groups, but the demecological information recovered seems to link this block with those of group A. Only one surface was examined and measured in most samples, except in this last one. In this block, the topmost level (about 5 cm thick) was partly missing, and thus two different surfaces could be analyzed (Fig. 2.2); the data for each of them are dealt with separately as 7a and 7b. Figure 3 shows the log of the lowest part of the Mulichinco Formation with indication of the provenance of the two groups of sampled surfaces. Although some time-averaging can never be ruled out, we tried to minimize it by excluding those surfaces with features obviously related to time-averaged assemblages (such as different trace infill or cross-cutting of traces, see Mangano *et al.*, 1998: 341, fig. 9), like that illustrated on Figure 4.2; other beds show direct

evidence of at least two generations (Fig. 4.6). Nevertheless, it must be borne in mind that superposition of traces can also be produced by a single population during the same escape event.

We used sheets of tracing paper (100 x 70 cm) to record in the field the information on location and shape of trace fossils; when the size of the sampled surface required more than one sheet we established adequate overlapping margins for subsequent assembling. Each sheet was scanned by parts and then reassembled using standard drawing software, also used for digitizing the outline of the traces and the sampled surfaces, and for measuring the distances between individuals and their size. Figure 5 shows digitized surface 5 (Fig. 5.2) and its field photograph (Fig. 5.1). Use of photographs for the analysis performed was hampered by the short distance involved, a fact introducing strong deformation towards the edges. Size was estimated from the longest axis of each in-

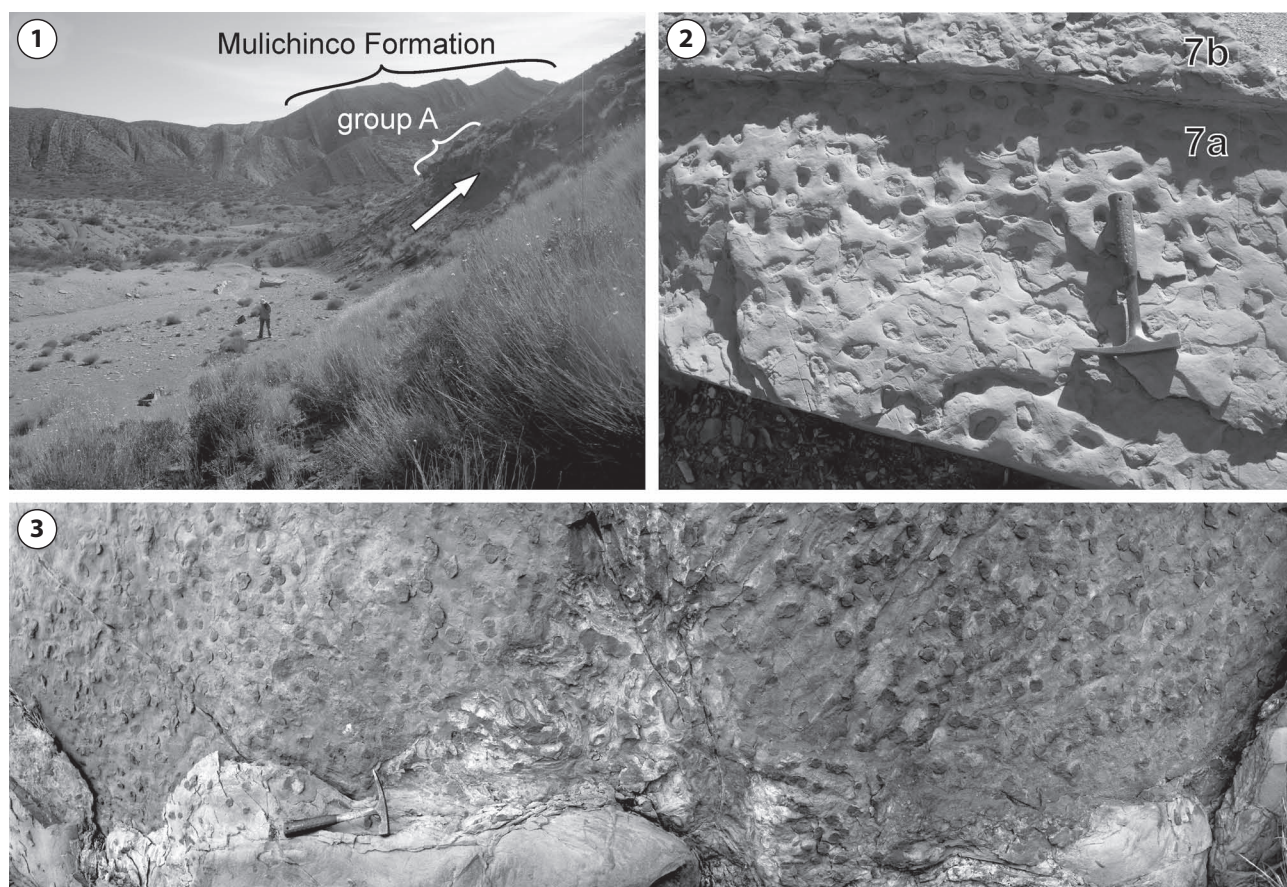


Figure 2. 1, General view of Mulichinco Formation section at Puerta Curaco in the background, with location of beds of group A in the foreground, the white arrow indicates the position of the overhanging bed sole illustrated in Figure 2.3/ Vista general de la Formación Mulichinco en Puerta Curaco de fondo, con la ubicación de los estratos del grupo A en el frente, la flecha blanca indica la posición del estrato cuya base en voladizo aparece en la Figura 2.3; 2, detail of sampled surfaces 7a and 7b with dense *Scalichnus* isp./ 2, detalle de las superficies muestreadas 7a y 7b con gran número de *Scalichnus* isp.; 3, sole of group A bedding plane, exposed as a large overhanging roof and showing a high density of infaunal bivalves escape traces/ 3, base en voladizo de una de las capas del grupo A, mostrando la alta densidad de rastros de escape de bivalvos infaunales; rock hammer length: 28 cm/ largo de la piqueta: 28 cm.

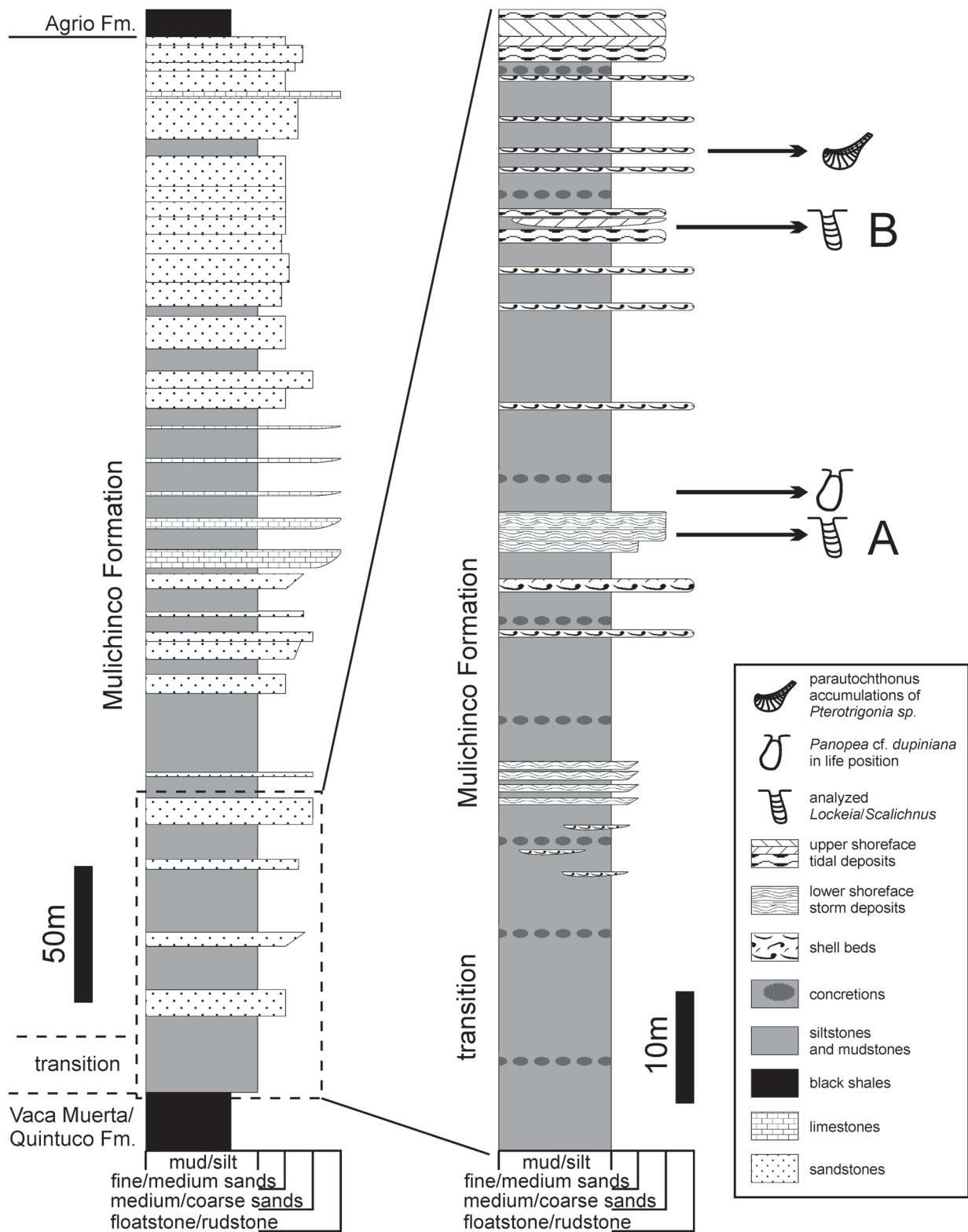


Figure 3. Stratigraphical section of the Mulichinco Formation at Puerta Curaco, Neuquén, with a detailed log of its lower-most section indicating the position of the two groups of beds with dense infaunal bivalves "Lebensspuren" studied here/ *Perfil estratigráfico de la Formación Mulichinco en Puerta Curaco, Neuquén, con un perfil de detalle de su parte inferior indicando la posición de los dos grupos de estratos con signos de actividad de bivalvos estudiados en este trabajo.*

dividual trace, a proxy to shell-height of the producer. This estimation may be somewhat biased, especially for resting traces, since the length of the cross section in the sedimentary surface may not always represent the maximum height of the organism as it depends on the position of the section along the antero-posterior axis of the shell. On the other hand, it is a much better estimator of shell height in escape traces, since any cross section must accommodate the maxi-

mum shell height all along. In order to check the accuracy of these measurements, we compared the distances obtained directly for one of the sampled surfaces with those taken on the tracing paper; a permutation test rendered no significant difference between both data sets ($p=0.89$, means of 5.4 and 5.5 cm, $N=44$). The mean difference (in absolute values) between the digital and the tracing sheets data was 1 mm. Surface areas were quantified with ImageJ 1.41o (<http://rsb>.

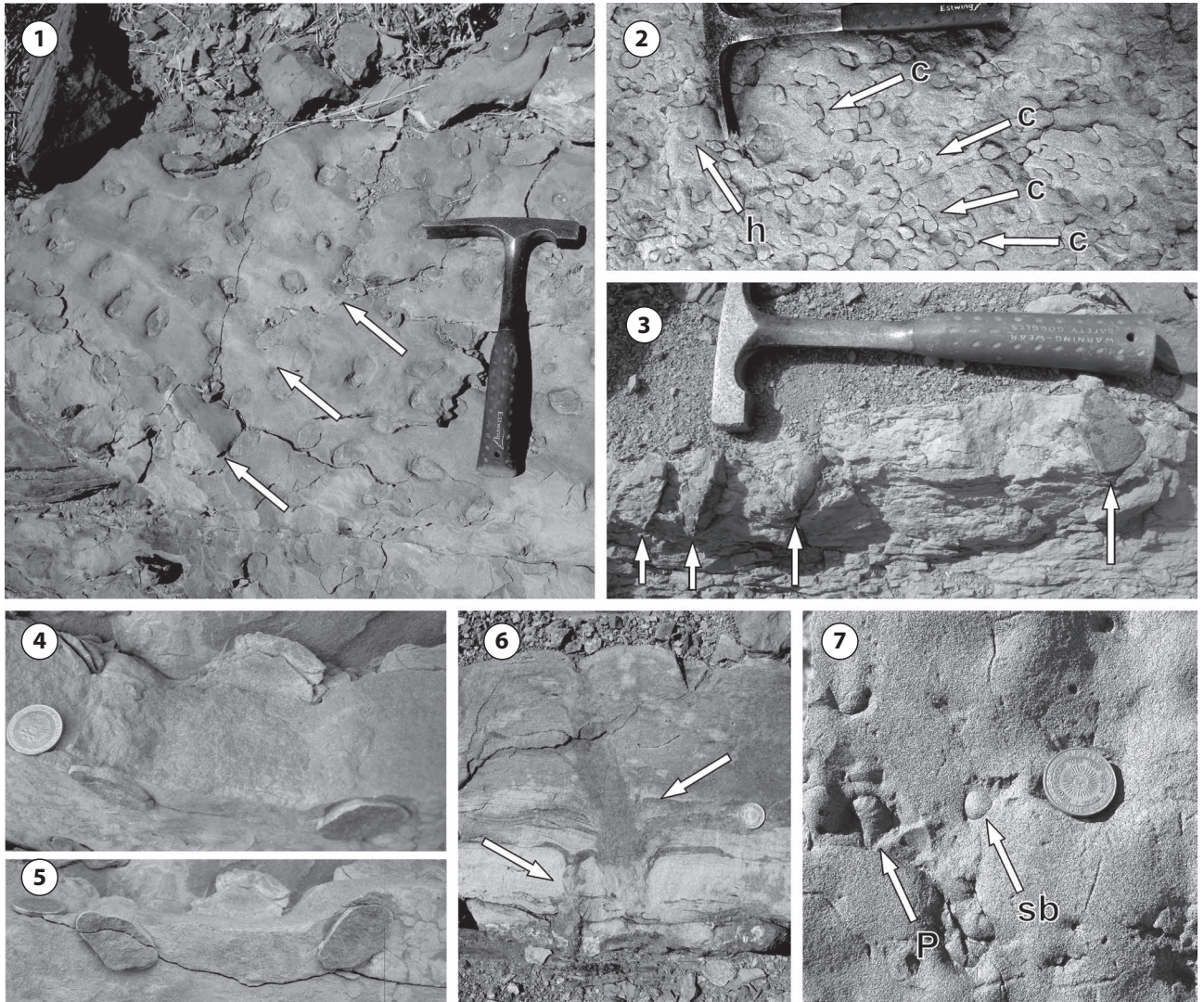


Figure 4.1. Part of sampled surface 2 showing some ripples (white arrows)/ Parte de la superficie 2 con óndulas preservadas (flechas blancas); **2**, crowded surface showing cross-cutting relationship among individual traces (c, evidence of time-averaged trace fossil association) and a heart-shaped cross section (h), ex-situ block not included in quantitative analysis/ superficie con alta densidad de icnofósiles mostrando relaciones de interferencia entre rastros individuales (c, evidencia de asociación promediada en el tiempo) y sección transversal acorazonada (h), bloque ex-situ no incluido en el análisis cuantitativo; **3**, beds 1.5 m above group A with *Panopea* cf. *dupiniana* in life position (white arrows)/ capas 1,5 m por encima del grupo A con *Panopea* cf. *dupiniana* en posición de vida (flechas blancas); **4–5**, detail of two *Scalichnus* isp. from group A/ detalle de dos ejemplares de *Scalichnus* isp. del grupo A; **4**, lateral view of the traces passing through the thickness, notice oblique view of bottom surface shown in 4.5/ vista lateral de los rastros atravesando el espesor del estrato, nótese la vista oblicua de la sección de los rastros mostrada en 4.5; **5**, cross-section of same traces as 4.4, bottom surface view/ sección transversal de los rastros de 4.4 vistos desde la base; **6**, cross-section of group B bed with resting/escape traces (white arrows)/ estrato del grupo B en sección, mostrando rastros de reposo/escape (flechas blancas); **7**, top bedding plane from group B showing *Pterotrigonia* sp. (P) and smooth-shelled bivalve (sb) remains/ superficie del techo de una capa del grupo B con restos de *Pterotrigonia* sp. (P) y bivalvos lisos (sb); rock hammer length: 28 cm; coin diameter: 2.3 cm/ largo de la piqueta: 28 cm; diámetro de la moneda: 2,3 cm.

info.nih.gov/ij) and the statistical analyses were performed using PAST 1.92 (Hammer *et al.*, 2001).

Special care was taken to interpret traces in the field and, during digitization, any dubious traces were double-checked against the photographs. Due to the scope of the study we could not afford to be too strict in the exclusion conditions, as the removal of all dubious traces would produce significant changes in the parameters to be estimated.

For spatial relationship analysis we applied the method of the nearest neighbour (Clark and Evans, 1954; Goldring, 1991). This method entails measurement of the mean distance of each individual to its nearest neighbour, and then its comparison to the expected mean distance in a population with the same density and a random distribution; this comparison was made by means of the value *R* (measured distance/expected distance). When individuals occupy a sizeable area with respect to the analyzed surface, Clark and Evans (1954) suggested that the procedure is applicable to the centres of individuals. We considered as centre of each individual the intersection between the normally disposed major and minor axis; for irregular and incomplete traces we estimated a “centroid”. Our study surfaces have limits beyond which we cannot know if there was any additional individual or not. Therefore, the traces that were nearer to the edge than to the nearest preserved neighbour might well have had a nearer unpreserved neighbour. Consequently, the distance of these individuals to their nearest preserved neighbour was not considered in the estimation of the mean distance. The significance of the departure of the distribution pattern from a random model was tested calculating the value *c* as established by Clark and Evans (1954); the absolute values

of 1.96 and 2.58 for *c* represent the 0.05 and 0.01 levels of significance respectively for a two tailed test.

In order to check for preferential orientation, we measured the direction of the major axis in each individual trace section, and grouped the values in categories of 20 degrees; we compared the results with a regular distribution using a χ^2 test. Since the sampled surfaces were not in their original position, the initial direction (the zero value) was arbitrarily chosen in each case. Only surface 2 had an independent reference structure: some preserved ripples.

RESULTS

Palaeoenvironmental setting

According to the environmental characterization, the two groups of analyzed beds were deposited in different environments. The lowest group of beds (A) is here interpreted as belonging to a lower shoreface, storm dominated environment (=facies association B, offshore-transition of Rodríguez *et al.*, 2007). It comprises siltstones interbedded with progressively thicker sandstones with hummocky cross-stratification (HCS); sandstones show erosional basal contact and may also have some ripples and cross-lamination. The presence of tetrapod scratch marks points to relatively shallow waters within this environment (see Pazos, 2009 for a discussion on environmental interpretation of such scratch marks). Regardless of the water depth, sandstones with HCS are interpreted as storm deposits, being this the main perturbation factor for benthic biota; there was also certain tidal influence as shown by ripples and cross-lamination.

Group B may represent more proximal facies, probably a subtidal upper shoreface, but still tidally influenced (=fa-

TABLE 1 - Demecological data/ Datos demecológicos

	group A		group A?		group B			
	surface 1	surface 2	surface 7a	surface 7b	surface 3	surface 4	surface 5	surface 6
<i>density (ind/m²)</i>	144.60	138.90	188.10	168.70	83.90	83.40	108.80	99.00
<i>R (obs/exp)</i>	1.21	1.15	1.32	1.38	0.97	0.86	0.93	1.00
<i>c</i>	**4.65	*2.29	**8.24	**7.22	-0.37	*-2.43	-0.69	-0.04
<i>mean distance</i>	5.05	4.90	4.83	5.29	5.32	4.70	4.46	5.01
<i>distance variance</i>	2.08	1.78	1.59	1.19	5.62	5.28	2.92	2.86
Major axis of traces								
<i>mean (cm)</i>	3.80	3.00	3.30	3.20	2.10	2.00	2.30	2.40
<i>variance</i>	0.62	0.71	0.62	0.66	0.43	0.79	0.34	0.34
<i>skewness</i>	-0.05	-0.53	-0.30	-0.18	0.23	0.97	-0.44	-0.33

R and *c* obtained as explained in Clark and Evans (1954) - **p*<0.05 ***p*<0.01

cies association C, shoreface of Rodríguez *et al.*, 2007). It is characterized by heterolithic sand-dominated sequences, with erosional basal contacts and varied trace fossils. This environment was characterized by strong tidal currents, producing asymmetrical ripples and linear marks, and also pockets with mudclasts. Decantation of fine grained sediments would have been produced during calm intervals (*i.e.* low and high tides). In this environment, tidal currents had strong influence on erosion and deposition, causing bed progradation, and being the main perturbation factor for the infaunal bivalves living there.

Density and spatial relationship

Table 1 shows the demecological data obtained for all sampled surfaces. As can be seen, both groups differ significantly in population density. Group A shows higher densities (about 140 ind/m², and even higher if we consider both surfaces 7) than group B (between 83 and 109 ind/m²). Also the spatial relationship seems to differ between groups. In group A the values of R are always significantly higher ($p < 0.05$) than those expected in a random distribution, pointing toward a uniform distribution. On the other hand, R values of group B are statistically indistinguishable from those of a random distribution, with the only exception of surface 4 which appears to present an aggregated pattern.

Size

The two groups also differ in the size range of the trace producers. Group A shows higher values (mean values between 3.0 and 3.8 cm; the mean of surfaces 7a and 7b also ranges between these two extreme values) than group B (mean values between 2.0 and 2.4 cms) (Tab. 1). Size distribution (Fig. 6) clearly shows these relationships, as well as some other important features. The scarcity of small-sized traces is noteworthy, especially in group A sampled surfaces, which seems to indicate that most individuals were of similar age. At this point, the possible bias in size estimation should be considered; such lack of small sizes is significant in group A, since it indicates that the trace cross section was approximately the maximum for all individuals. For group B interpretation may be somewhat more imprecise (see below).

Skewness is negative for all samples (*i.e.*, the smaller values are more loosely spread than the larger ones), with the exception of two from the group B (surfaces 3 and 4), which show a positive skewness (Tab. 1). This suggests the presence of “unusually large” individuals, *i.e.* an older cohort, occurring in these two populations. Mixture analysis is a statistic

method used to estimate the parameters of two or more univariate normal distributions from a pooled univariate sample (Hammer, 2009); it does not provide a test for a mixture hypothesis, but just tries to reconstruct the presumed original samples. Its application to the data from surfaces 3 and 4 results, in each case, on a large population with slightly lower mean size and negative skewness and a small population with a larger mean; this is particularly clear for surface 4. Nevertheless sample sizes are too small to arrive at any significant conclusion.

Spatial orientation

Figure 7 shows the orientation graphs for the major axis of the traces; although many of them seem to have a bimodal distribution, they were found not significantly different from a random distribution, with the only exception of surface 3 ($p = 0.0255$).

DISCUSSION

Palaeodemecology

Density. When compared to living infaunal bivalve populations, densities are high for both groups of traces. Prezant *et al.* (2008) reported densities of about one hundred individuals in a square metre for *Laternula truncata* (Lamarck) (Anomalodesmata) in Thailand mangrove flats. For *Laternu-*

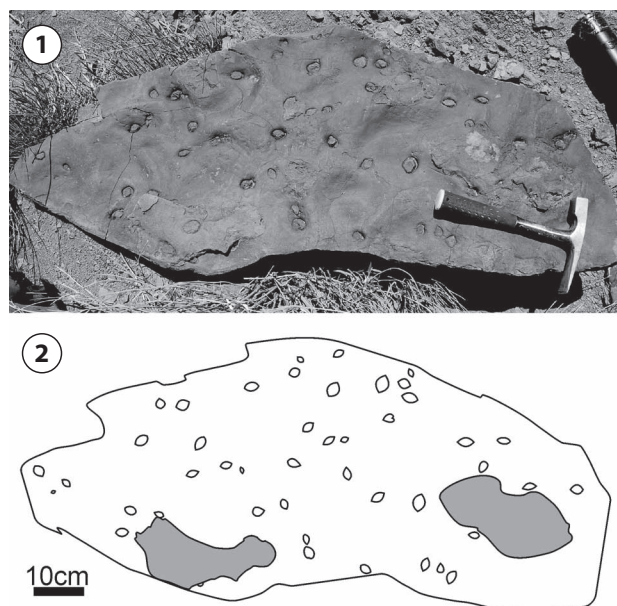


Figure 5.1. Field photograph of sampled surface 5, rock hammer length: 28 cm; **2**, the corresponding digitized drawing of traced outlines from the same surface/ **1**, Fotografía de campo de la superficie 5, largo de la piqueta: 28 cm; **2**, dibujo digitalizado de los contornos calcados de la misma superficie.

la elliptica (King and Broderip) similar values were obtained in many austral localities (Stout and Shabica, 1970; Beurois, 1989; Ahn, 1994), and an extrapolation for a Pliocene population from Antarctica resulted in similar values to those drawn from modern populations (Jonkers, 1999). Witbaard and Bergman (2003) recorded densities of up to 286 individuals per square metre for *Arctica islandica* Linné (Venerida) in the North Sea, but only for certain areas; in many localities densities were of about 23 individuals per square metre. Densities in group A are higher than those values, and although the values of group B are close to them (or even a bit lower) it must be noted that values given for extant clams are maximum. This suggests an environment with high food supply and good physical conditions for the development of these populations.

Since the optimal conditions for the settlement of a population of any species are usually a complex combination of ecological factors, we cannot advance beyond those conclusions. If we were to consider both groups of traces as produced by the very same species, we might regard group B as generated under somewhat more stressful environmental conditions. This could be due either to: a) nutrient-poorer waters; b) winnowing of juveniles by tidal currents with concomitant population density decrease (Emerson and Grant, 1991); c) higher proportion of suspended silt diminishing the food quality and thus reducing the average size of individuals (Witbaard and Bergman, 2003); or d) various combinations of the above. Nevertheless, we consider as a more plausible

explanation that each group of traces was likely produced by different bivalves (see below).

Spatial distribution. Spatial distribution differs between both groups; group A revealed a quite uniform pattern of distribution. This seems logical, as at higher densities, negative interactions should have greater influence (competition for space). Nevertheless, when establishing the method, Clark and Evans (1954) pointed out the possibility of individuals being as closely spaced as their size allows, resulting in their centres distributed non-randomly; this is not strictly the case (individuals are not in contact with each other), but the high densities could be influencing results to a certain degree. Also, as interpreted herein, the traces represent the position of the animals after escaping from an obrution event. Thus, they would not strictly reflect the behaviour of the organisms during settlement but during, or after, a rearrangement process instead.

The prevailing random pattern of distribution detected in group B suggests an absence of interactions (either negative or positive, yet in surface 4 an aggregated pattern could be present). Although the mean distances among individuals are very similar for both groups (about 5 cm), the difference in pattern between them is also evident in their variance. The variance is higher in group B (especially surfaces 3 and 4) than in group A (Tab. 1), *i.e.* the distances to the nearest neighbour are more variable in group B than in group A.

We are aware that results obtained herein are applicable only to the scale of analysis used (the surfaces of the top of blocks), since the possibility of different patterns of spatial distribution at larger scales cannot be dismissed (cf. Valentine, 1973, p. 252; Dodd and Stanton, 1981, p. 371).

Size. Average individual size is quite different between both sets, those of group A being larger; this fact, together with the inferred environmental differences, suggests that the producers of each main set of traces probably belonged to different species.

The absence of small sized individuals is noteworthy, especially in group A. Surface 2 has the highest proportion of small sizes in this set, and yet only 10 % of values are smaller than 2 cms. On the other hand, surfaces 3 and 4 show about half of the traces below that threshold value (Fig. 6). The high frequency of these small values in sampled surfaces of group B proves that their potential for preservation is rather good, suggesting at the same time a genuine lack of juveniles in the first group. In their study on the populations of *Laternula truncata*, Prezant *et al.* (2008) mentioned this same fact (they could not find individuals shorter than 1.5 cm)

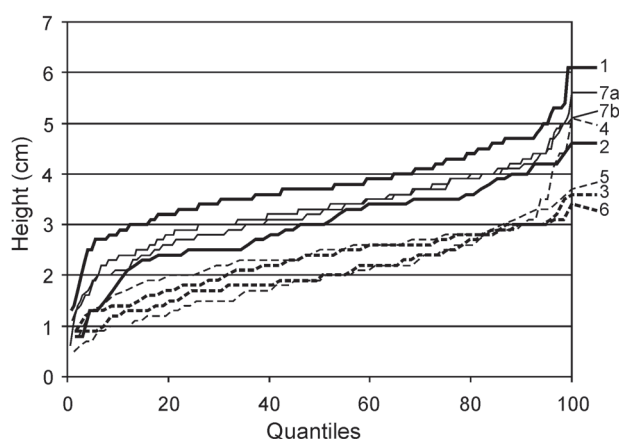


Figure 6. Size distribution by height of the traces in cross-section on the sampled surfaces; solid line: group A; dashed line: group B/ *Distribución de tamaños por altura de los rastros en sección transversal para cada superficie muestreada; líneas continuas: grupo A; líneas discontinuas: grupo B.*

and they offered as explanation a possible inhibition of larvae settlement due to fine-grained sediments. There are also references of larvae settlement inhibition by the presence of adult individuals (Lindegarth *et al.*, 2002). André and Rosenberg (1991) found that high densities of adult *Cerastoderma edule* (Linné) (Venerida) and *Mya arenaria* Linné (Myida) reduce succesful settlement of bivalve larvae, probably because they are ingested by adult suspension feeders. But not all authors agree with this last interpretation; David *et al.* (1997), analyzing a large-scale spatial distribution, considered the patchy patterns in age structure of *Spisula ovalis* Linné (Venerida) as mainly related to density-independent effects. In any case, the explanation for inhibition of settlement by mud and silt, as well as by the presence of adults are both consistent with our data. In the first case the inferred environment clearly provides a plausible scenario: storms produce the deposition of sand, which would be quickly colonized by the bivalve larvae; during fair-weather the silt and clay would deposit, and so the settlement of new larvae would be inhibited (the resultant population then representing a single cohort). The second alternative also offers a good explanation given the high densities found in the populations. A third possible explanation, taking into account the environment inferred, is that the initial erosion during a storm removed the bivalves which dwell near the surface (Kondo, 1998), including the juveniles of the population. However, if this were the case their shelly remains would be expected at the base of the sandy bodies deposited during the storm.

Group B represents a different situation; small values are well represented, with a minimum size of 0.5 cm. The absence of even smaller values in this case could be due to lower chances of preservation or the difficulty of recognizing minute traces. Winnowing of juveniles by tidal currents, although not discarded, can not be considered as a plausible explanation for the lack of small sizes in this case; if all juveniles were uprooted then the population could not be sustained through time. As pointed above, surfaces 3 and 4 may have borne more than one cohort living together. Nevertheless, the very low proportion of individuals of a presumably older cohort suggests a producer with short life cycle.

Orientation. *Lockeia* traces are sometimes found preferentially oriented (Nara, 2003; Rodríguez *et al.*, 2007), generally in response to water currents. Some of the rose diagrams of the analyzed surfaces (*e.g.* Fig. 7, surfaces 1, 2 and 7b) are reminiscent of the quadri-polar pattern recognized for Palaeozoic marine infaunal bivalves oriented under oscillating wave motion (Liljedahl, 1991, text-fig 7), in which orienta-

tion of the anterior end of each shell was recorded. Nevertheless, our data are not strictly comparable, inasmuch the traces did not provide reliable indication of anterior end. According to our results, there rather seems to be a bimodal pattern of the peaks of major-axis of the traces (Fig. 7). Only in surface 2 there is a structure indicative of current direction, namely

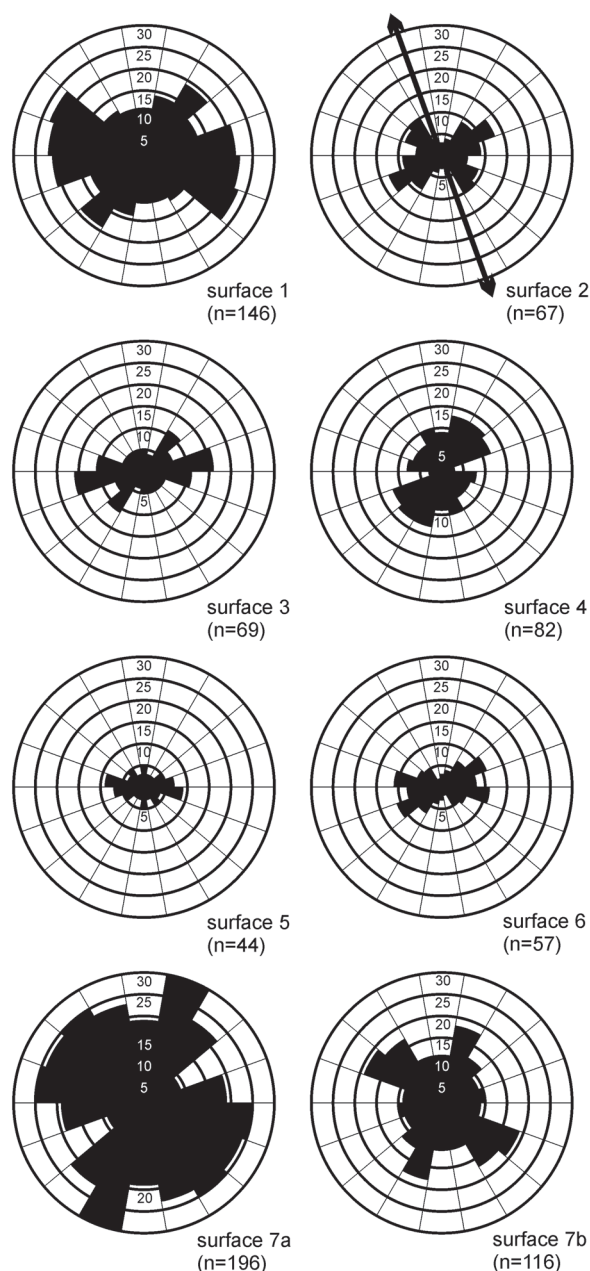


Figure 7. Orientation graphs of the traces for all sampled surfaces; double-headed arrow in surface 2 indicates the direction of ripple crests; range of category interval: 20°; a significant preferred orientation was only found for surface 3 ($p=0.0255$)./ Gráficos de orientación de los rastros para todas las superficies muestreadas; la flecha de dos puntas en la superficie 2 indica la dirección de las crestas de ondulas; rango de intervalo de las categorías: 20°; se encontró una orientación preferencial significativa únicamente para la superficie 3 ($p=0,0255$).

some asymmetrical ripples, and the trend for the major axes is almost perpendicular to their crests (Fig. 4.1, Fig. 7, surface 2), and therefore parallel to the original current. Nonetheless, only in surface 3 a pattern significantly different from a random model is recognized.

The lack of orientation is not surprising; the truncation of the topmost level in part of block 7, clearly shows that the analyzed surfaces are not necessarily the original top surfaces of the sand bodies, except when they bear other superficial sedimentary structures such as ripple marks. In any case, when the animals retreated upwards through them, they could still be covered by more sediment and thus the bivalves eventually would not respond to any current that may have affected them. Also, when bivalves escape from a burial event they usually adopt an inverted erect probing orientation (*i.e.* the reverse position they adopt when burrowing) (Schäfer, 1962: 420, 1972: 373, fig. 221 oriented as in 1962; Kranz, 1974: 257–259). As a consequence the possible preferred orientation they may have had in life position can be altered. Nevertheless, there are also references to bivalves with a large, heavy shell and a relatively small foot that do not reverse their position during their escape response to obrution (Hanken *et al.*, 2001). At another locality, but from the same unit and age as our material, Rodríguez *et al.* (2007) reported that *Lockeia* traces were located almost exclusively along ripple crests. All these data support the idea that the analyzed traces are closer to fugichnia than to cubichnia.

Ichnological evidence

Although an ichnological analysis is beyond the scope of this paper, a few notes on the evidence provided by the traces themselves are offered. The traces analyzed here can be referred to either cubichnia or fugichnia *s.l.* (*i.e.* encompassing equilibrichnia, a subtle distinction favoured by some authors, *cf.* Bromley, 1990; Buatois and Mángano, 2011), ichnogenera *Lockeia* and *Scalichnus*, both known to be produced by bivalves. *Lockeia* and unidentified escape structures had already been recognized in this formation (Rodríguez *et al.*, 2007; Pazos, 2009, 2011).

Lockeia is basically a resting trace, although intergradation with escape traces commonly occurs (Buatois and Mángano, 2011). It is almond-shaped to elliptical in cross-section, and V-shaped or rounded in vertical section (Mángano *et al.*, 1998; Radley *et al.*, 1998; Buatois *et al.*, 2002; Nara, 2003; Seilacher, 2007; Pieńkowski and Niedźwiedzki, 2009). Its populations are usually monospecific and this appears to be the case for the material studied here. Although the shape

of such traces is quite variable, this could be due to many factors, such as differences in relative position of the shell (Mángano *et al.*, 1998, fig. 11), and/or ontogenetic stages of their producers (transverse shape of bivalves can change a lot during ontogeny), and/or the physical properties of the sediment at the moment of producing the trace. Rodríguez *et al.* (2007, fig. 4.H, 4.K, 4.M) reported and figured *Lockeia* traces similar to those described here from roughly equivalent levels and facies associations of the Mulichinco Formation at Vega de Escalone, a locality about 25 km north of Puerta Curaco. It is interesting that these authors also distinguished two size-groups for the *Lockeia* traces, though their larger ones are comparable to those of group B here.

Escape traces include structures formed in response to rapid changes in sedimentation, typically event deposition (Buatois and Mángano, 2011). The fugichnia *s.l.* ichnogenus *Scalichnus*, was described by Hanken *et al.* (2001) as large, vertically oriented, subcylindrical to bottle-shaped structures, produced by the bivalve *Panopea* during retrusive and protrusive movements. It is oval in cross-section; its infilling may bear a discernable central shaft and siphonal lining, or a meniscate arrangement of laminae, or sometimes it may even be structureless (Hanken *et al.*, 2001; Pieńkowski and Niedźwiedzki, 2009).

Both kinds of traces occur in the studied log, (*cf.* Fig. 4) and commonly appear associated. The analyzed traces have the almond-shaped to oval, or even heart-shaped, cross-section that characterizes both ichnogenera (Fig. 4.1–2, 4.5). The presence of ridges or irregularities on some of them may indicate lateral movement of the organism, but this can be produced in *Lockeia* as well as in *Scalichnus*. Nara (2003) analyzed the formation mechanism of ridges and furrows in *Lockeia*, and some ichnospecies even reflect crawling activity (Mángano *et al.*, 1998; Radley *et al.*, 1998).

For group A at least the traces seem to be very long; in some of the beds it is clear that they pass through their whole thickness (Fig. 4.4–5), since they appear at the base as well as at the top. The vertical paths of the plug-shaped endichnial trails are fairly straight and simple; we did not observe any substantial spiral component related to asymmetrical extensions of the foot while crawling up (*cf.* Schäfer, 1962, 1972, fig. 222). In the traces which pass through mudstones the sandy infilling coming from upper beds can be seen; this clearly indicates an escape reaction after the deposition of the sand. The environment was prone to sudden deposition of thick layers of sediment; it is well-known that bivalves can cope with rapid burial by moving upwards to maintain their

position relative to the new substrate surface (Reineck, 1958; Schäfer, 1962, 1972; Kranz, 1974; Kondo, 1998), but they do not initiate an escape response if the sudden deposits exceed certain critical thickness (Nichols *et al.*, 1978). Therefore, in our case the traces are interpreted as true escape traces, and referred to *Scalichnus* isp. The lack of preferred orientation is congruent with this interpretation. Furthermore, considering the high densities, the lack of cross-cutting between traces and the homogeneous infilling are suggestive of the activity of a single population.

Group B is more difficult to explain; although there is evidence of lateral movement, traces tend to be more regular in cross-section, maybe pointing to greater substrate stability and/or more stationary trace makers. Long vertical traces are less common than in the previous group and, in addition, the beds themselves are thinner. Given the sustained energy of the environment, there was a continuous response of the bivalves to progradation, so probably the analyzed traces may represent transitional resting-escape traces. If this were the case, then we should bear in mind that size estimations may be biased, especially towards top surfaces in which the bedding plane may represent the actual water-sediment interface last inhabited by the organisms.

Potential producers

Studying the response of different bivalve species to anastrophic burial, Kranz (1974) established that infaunal siphonate feeders were among the most able to escape from relatively deep burials (10–50 cm of sediment), either in native or exotic sediments. Given the thickness of the obrution layers (especially in group A) that were crossed in this case and the recorded taxa for the formation (and equivalent levels), all traces studied herein were most probably made by siphonate suspension-feeding infaunal bivalves. Kondo (1998) established which adaptive strategies are more frequent in different marine environments. In a lower shoreface environment (like the one inferred for group A), he found mostly siphonate, moderately rapid, shallow burrowers and siphonate, virtually immobile deep burrowers; in the surf zone (upper shoreface, like the environment inferred for group B) only the first category was dominant. In the case under study, there are clear differences, not only in size, between the two groups of traces, which suggest that their producers were different organisms.

The shape and size of the traces in group A suggest that the most likely producers were deep burrowers. Several taxa of potential producers are recorded in equivalent levels of the Chachao Formation in southern Mendoza (Damborenea *et*

al., 1979): *Panopea dupiniana*? d'Orbigny, *Panopea gurgitis* (Brongniart), *Pholadomya* (*Pholadomya*) cf. *gigantea* (J. Sowerby), *Homomya* sp. indet. and *Plectomya* sp. indet., while in the overlying Agrio Formation *P. gurgitis* usually occurs abundantly, whereas *Pholadomya gigantea* is scarce but widely distributed (Lazo, 2007). Traditionally, adult deep burrowers were considered as sluggish forms unable to reburrow (Stanley, 1970); if this were the case, the producers could not be fully grown animals. Nevertheless, there is some evidence that they may have had certain movement capabilities (Ansell and Rhodes, 1997). Kondo (1998) found evidence of vertical migration in *Panopea* specimens from the Yabu Formation (Pleistocene of Japan) as a response to rapid burial during storm sedimentation; he even suggested that most individuals escaped successfully. Furthermore, the ichnogenus *Scalichnus* was defined for traces containing *Panopea* shells (Hanken *et al.* 2001, figs. 5–6) though much larger in size and from younger beds (Pliocene) than those studied here. No bivalve shell was found directly associated to these traces at Puerta Curaco, but beds intercalated between the two groups studied do bear *Panopea* cf. *dupiniana* d'Orbigny in life position (Fig. 4.3).

The producers of traces from group B were probably more active burrowers. They were smaller and in some beds their transverse section is somewhat variable. Occasionally, small bivalved specimens of *Pterotrignia* sp. appear at the top of some bioturbated, ripple-bearing sandy beds together with some smooth-shelled unidentified bivalves (Fig. 4.7). The local abundance of *Pterotrignia* sp. at these levels as well as in shell-beds higher up (Fig. 3), together with the evident similarity in size and shape of their shell sections with those of the observed traces, suggest that these active shallow burrowers could be regarded as potential producers. Several other shallow burrowers are reported from the Mulichinco Formation and also occur in the studied interval, such as *Aphrodina quintucoensis* Weaver and *Eriphyla argentina* Burckhardt, but these have a laterally compressed shell larger than the traces.

CONCLUSIONS

The high densities obtained in all the analyzed surfaces clearly demonstrate that physical environment was optimal for the producers of these traces, and that the food supply was plentiful. Apart from that, the rest of the data apparently reflect the influence of different environmental settings and/or producer species in each group.

Group A consist of an association of escape traces produced by populations of deep-burrowing bivalves. They rep-

resent opportunistic populations established in sandy storm-deposits, as the traces always start from the sand. Once this cohort was established, the settlement of new larvae would have been inhibited either by accumulation of fine-grained sediment during fair weather, or by the presence of already established adult individuals. High densities would have caused certain competition for space while animals were growing, resulting in a fairly uniform pattern of spatial distribution. New storm-deposits would have buried these populations, forcing the bivalves to escape and thus producing the *Scalichnus* trails.

Group B may be the resting/equilibration traces of more active bivalves in an environment with frequent progradation. Populations were more continuous through time, but with short life cycles. There is no evidence of negative interactions as revealed in the previous group, and there is even one case with a probable aggregated pattern of spatial distribution. Only one surface showed a significant non-random orientation pattern, and even this is not clearly unidirectional. This may be the result of continuous flow change in tide-dominated environments.

The study of these *in-situ* populations of infaunal bivalves provides additional valuable information to help distinguish subtle differences in environmental conditions, which in turn may become a potentially useful tool for better understanding sedimentary processes, sequence stratigraphy and detailed basin analysis. This particular case study provided information on productivity, general physical conditions and main responses by infaunal bivalves to sedimentary perturbations.

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