

Benthic macroinvertebrate associations on a carbonate-clastic ramp in segments of the Early Jurassic back-arc basin of northern Chile (26-29° S)

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ABSTRACT

The distribution of facies and benthic fauna in segments of the marine Early Jurassic Andean Basin of northern Chile has been reconstructed based on sedimentological, taphonomic, and paleoecological evidence. In the areas studied, that is between Salar de Pedernales (26°S) and El Tránsito (29°S), the depositional system is interpreted as a homoclinal ramp, on which four environmental subdivisions can be distinguished: shallow siliciclastic ramp, mixed siliciclastic-carbonate ramp, middle carbonate ramp, and deep carbonate ramp. In an offshore direction, they reflect a general decrease in terrigenous sediment input, energy level, grain-size, and oxygen supply, and a relative increase in carbonate production. More than 200 bulk collections of benthic macroinvertebrates, dominated by bivalves and brachiopods, were grouped into 27 associations (1-27) and 3 assemblages (E,F,G) by means of a Q-mode cluster-analysis. Most associations are restricted to a single environmental subdivision and therefore proved to be useful indicators of general environmental conditions and bathymetry. This is also true for guild-assemblages. Higher numbers of dominant guilds and a relatively broad guild-spectrum within highly-diverse associations are found in the more onshore settings. Due to a stable and consolidated substrate, on the middle carbonate ramp only pedunculate brachiopods and epifaunal bivalves could gain high abundances in associations of moderate diversity. An even higher dominance of only a few guilds is found on the oxygen-controlled deep ramp. Typical representatives of low-diversity associations were deposit-feeding nuculid bivalves in the upper dysaerobic biofacies zone and small, flat-valved pectinacean bivalves in the lower dysaerobic zone.

Key words: Jurassic, Macrobenthos, Association, Paleoecology, Guild, Oxygen, Facies, Northern Chile.

RESUMEN

Asociaciones de macroinvertebrados bentónicos en una rampa carbonatada-clástica en segmentos de la cuenca de trasarco jurásica inferior, norte de Chile (26-29°S). Sobre la base de evidencias sedimentológicas, tafonómicas y paleoecológicas se reconstruye la distribución de las facies y la fauna bentónica en segmentos del Jurásico Inferior marino de la cuenca andina del norte de Chile. En las áreas estudiadas, entre Salar de Pedernales (26°S) y El Tránsito (29°S), el sistema de deposición se interpreta como una rampa homoclinal en la cual se distinguen cuatro subdivisiones ambientales: rampa somera siliciclástica, rampa mixta siliciclástica-carbonatada, rampa media carbonatada y rampa profunda carbonatada. En dirección costa afuera, se manifiesta un decrecimiento general en el aporte de sedimentos terrígenos, del nivel energético, del tamaño de grano, del suministro de oxígeno, y un incremento relativo de la producción de carbonato. Más de 200 muestras, estadísticamente representativas de macroinvertebrados

bentónicas, dominadas por bivalvos y braquiópodos, han sido agrupadas en 27 asociaciones (1-27) y 3 ensamblajes (E,F,G) por medio del 'Q-mode cluster-analysis'. La mayoría de las asociaciones están restringidas a una subdivisión ambiental única y, por lo tanto, demuestran ser indicadores útiles de las condiciones ambientales generales y de la batimetría. Esto también resulta servídido para las asociaciones de gremios. En las asociaciones de mayor diversificación, correspondientes a las regiones marinas más marginales, se encuentra un mayor número de gremios dominantes y un espectro de gremios relativamente amplio. En la rampa media carbonatada, debido a la presencia de un substrato estable y consolidado, sólo son abundantes braquiópodos pedunculados y bivalvos epifaunales, en asociaciones de diversidad moderada. Un predominio aún mayor de sólo unos pocos gremios se encuentra en la rampa profunda, controlada por el tenor de oxígeno. Representantes típicos de las asociaciones de baja diversidad son los nucúlidos depositivos de la zona disaeróbica superior y pequeños pectínidos, de valvas aplanadas, en la zona disaeróbica inferior.

Palabras claves: Jurásico, Macrobentos, Asociaciones, Paleoecología, Gremios, Oxígeno, Facies, Norte de Chile.

INTRODUCTION

The marine Early Jurassic sequence of the Andean back-arc basin of Chile and Argentina is well known for its rich and diverse benthic fauna. Bivalves form the numerically most important group and have been repeatedly illustrated in the literature. In particular, major parts of the class have been revised recently by Damborenea (1987a; 1987b). Brachiopods, the second conspicuous benthic group, and corals have been recently documented monographically by

Manceñido (1981, 1991) and Prinz (1991), respectively.

In contrast to taxonomic analyses, paleo-synecological work on the Jurassic macrobenthos of South America is rare. Damborenea *et al.* (1975) studied the biofacies of the Argentine Liassic. They already used cluster-analysis and a 'biotype' approach on the basis of presence and absence of genera. Detailed information on distribution patterns of benthic

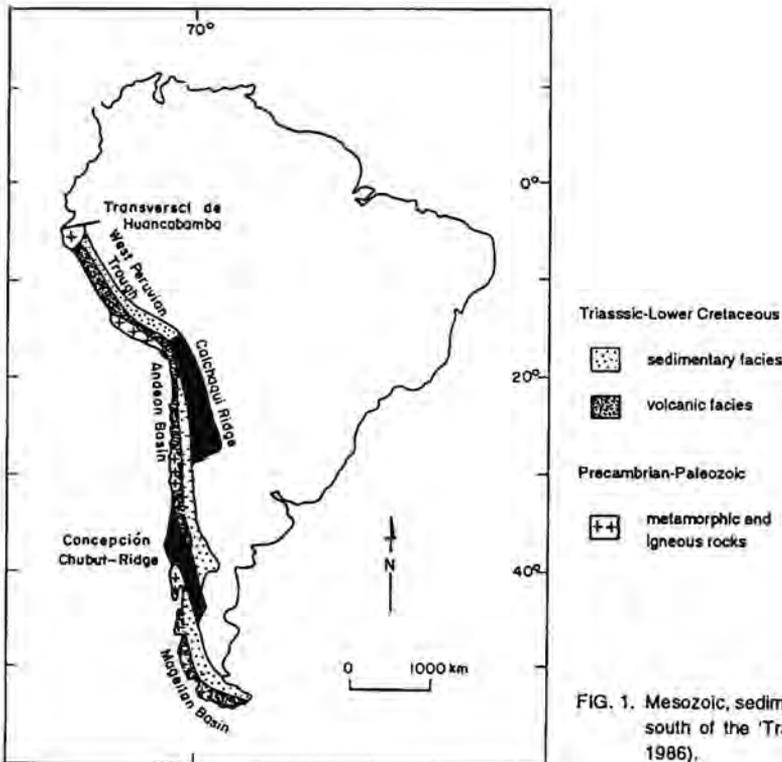


FIG. 1. Mesozoic, sedimentary basins of the Cordillera de los Andes south of the 'Transversal de Huancabamba' (after Dalziel, 1986).

associations from the Liassic of northern Chile is known by the work of Aberhan (1992). Otherwise, no paleoecological studies have been carried out.

The purpose of this paper is to summarize the information given by Aberhan (1992) with special emphasis on the spatial and temporal distribution of benthic macroinvertebrates within the Andean Basin

and on the environmental interpretation of the recognized benthic associations. The results may serve as a useful basis for the analysis of benthic distribution patterns through space and time in the Andean Basin and hopefully allow comparison with other Mesozoic back-arc basins in the future.

GEOLOGICAL SETTING

The Mesozoic paleogeography of the Andes (Fig. 1) consisted of several elongated, north-south trending basins which were bordered by Paleozoic basement ridges (e.g. Riccardi, 1983; Dalziel, 1986; Riccardi *et al.*, 1993). The north Chilean-Argentine back-arc basin, the so-called Andean Basin, was bordered by a large continental block in the east. To the west full water exchange with the Paleo-Pacific was restricted by an active volcanic arc (e.g. Hervé *et al.*, 1987; Riccardi *et al.* 1993). However, narrow connections to the open ocean obviously existed during most of the Jurassic (von Hillebrandt *et al.*, 1986; Quinzio, 1987; Gröschke *et al.*, 1989). More detailed

paleogeographic maps for various time slices have been provided by Riccardi (1983) and more recently by Riccardi *et al.* (1993).

The Upper Triassic to middle Cretaceous evolution of the Mesozoic marginal sea of Argentina and Chile can be subdivided into several transgressive-regressive cycles of different orders (e.g. Riccardi, 1983; Riccardi *et al.*, 1993). In the studied area between 26° and 29°S the sea transgressed in an eastern direction from the Sinemurian to the Toarcian. The subsequent regression started during the late Toarcian and continued until late Bajocian times (von Hillebrandt, 1971; 1973; Riccardi *et al.*, 1993).

STUDY AREAS AND MAIN SECTIONS

Sedimentologic and ecological data have been obtained by a bed by bed analysis of six sections through characteristic Liassic deposits of northern Chile (Fig. 2). The three main sections under study, comprising between 220 and 280 m of upper Sinemurian to Toarcian sediments, are schematically illustrated in figure 3. Section 2 from the Lower Quebrada E Asiento, forming part of the Montandón Formation (Harrington, 1961), has been described previously by von Hillebrandt and Schmidt-Effing (1981) and Pérez (1982) who also clarified the stratigraphy. In addition, Pérez (1982) provided a detailed description of litho- and biofacies and interpreted the depositional environments. According to Pérez (1982), the inferred bathymetry of the Liassic environments ranged from a few meters at the lowermost upper Pliensbachian to more than 100 m

near the Pliensbachian/Toarcian boundary. Note, that about 80 m above the base a gently dipping thrust fault causes the repetition of about 35 m of upper Pliensbachian sediments. Section 5 and section 6 from Quebrada Pinte, located about 5 km apart from each other, have been described and illustrated by von Hillebrandt (1973). They can be easily correlated using both litho- and biostratigraphic criteria.

The remaining sections 1, 3, and 4 are not reproduced here, since they either cover relatively short stratigraphical ranges (sections 3, 4) or are only represented by single bulk samples of particularly fossiliferous horizons (section 1). The interested reader is referred to Aberhan (1992, p. 9, Fig. 4, and Appendix 1).

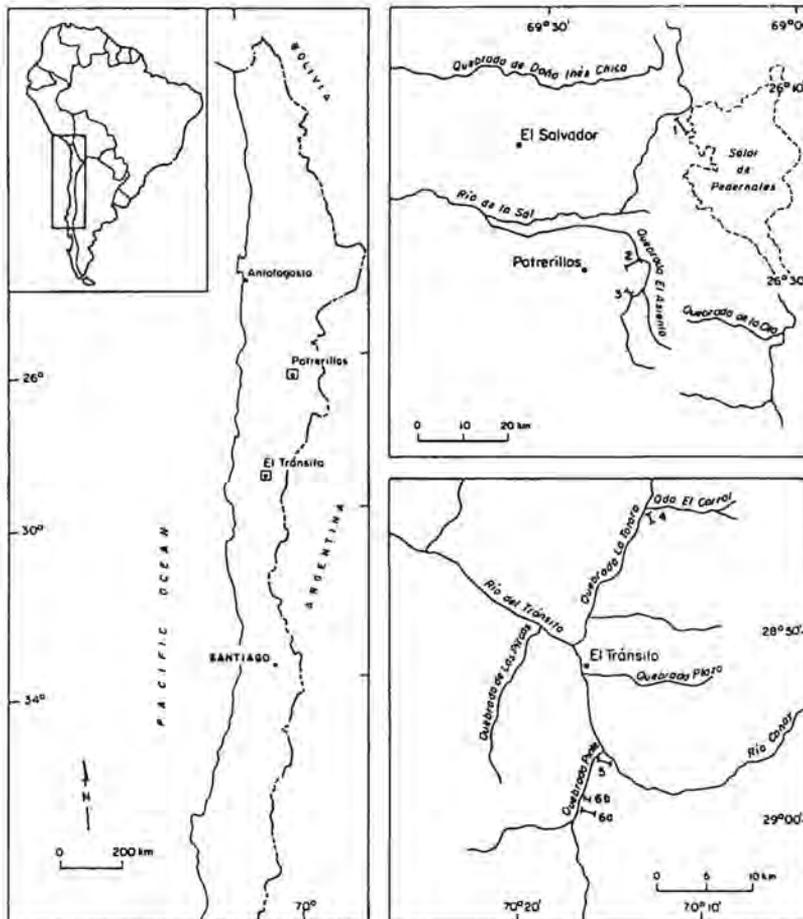


FIG. 2. Location of working areas and studied sections (1-6).

SEDIMENTARY FACIES AND DEPOSITIONAL ENVIRONMENTS

In the studied sections of the Early Jurassic of northern Chile, twelve facies types have been recognized which range from pure siliciclastics through mixed carbonate/siliciclastics to pure carbonates. The facies types are summarized in table 1 and their stratigraphic distribution can be drawn from figure 3. They have been interpreted in terms of physical processes and can be assigned to distinct depositional environments. Below, a brief overview of the main facies and an interpretation of the spatial arrangement of their corresponding environments is presented.

The dominating facies types, that is, types A-G of table 1, are characterized by uniform, relatively thick sedimentary packets with gradual transitions between various facies. They are interpreted to represent different environments on a more or less gradually sloping sea floor, exhibiting a continuous increase in

water depth with progressive distance from the shore. Four facies zones can be distinguished:

- a- an onshore facies belt, including facies A-C, was characterized by a high input of siliciclastic material which prevailed over the rate of carbonate production. Unfossiliferous, large-scale cross-bedded, coarse-grained sandstones reflect a high energy level and episodically high sedimentation rates in an environment above fair-weather wave-base. With increasing distance from the shore, grain size decreased, thus giving rise to fine-grained sandstones and siltstones bearing a rich benthic fauna. They can be attributed to environments of intermediate water energy and sedimentation rates;
- b- a second facies belt, which is situated more offshore than a-, comprises the spectrum of micritic

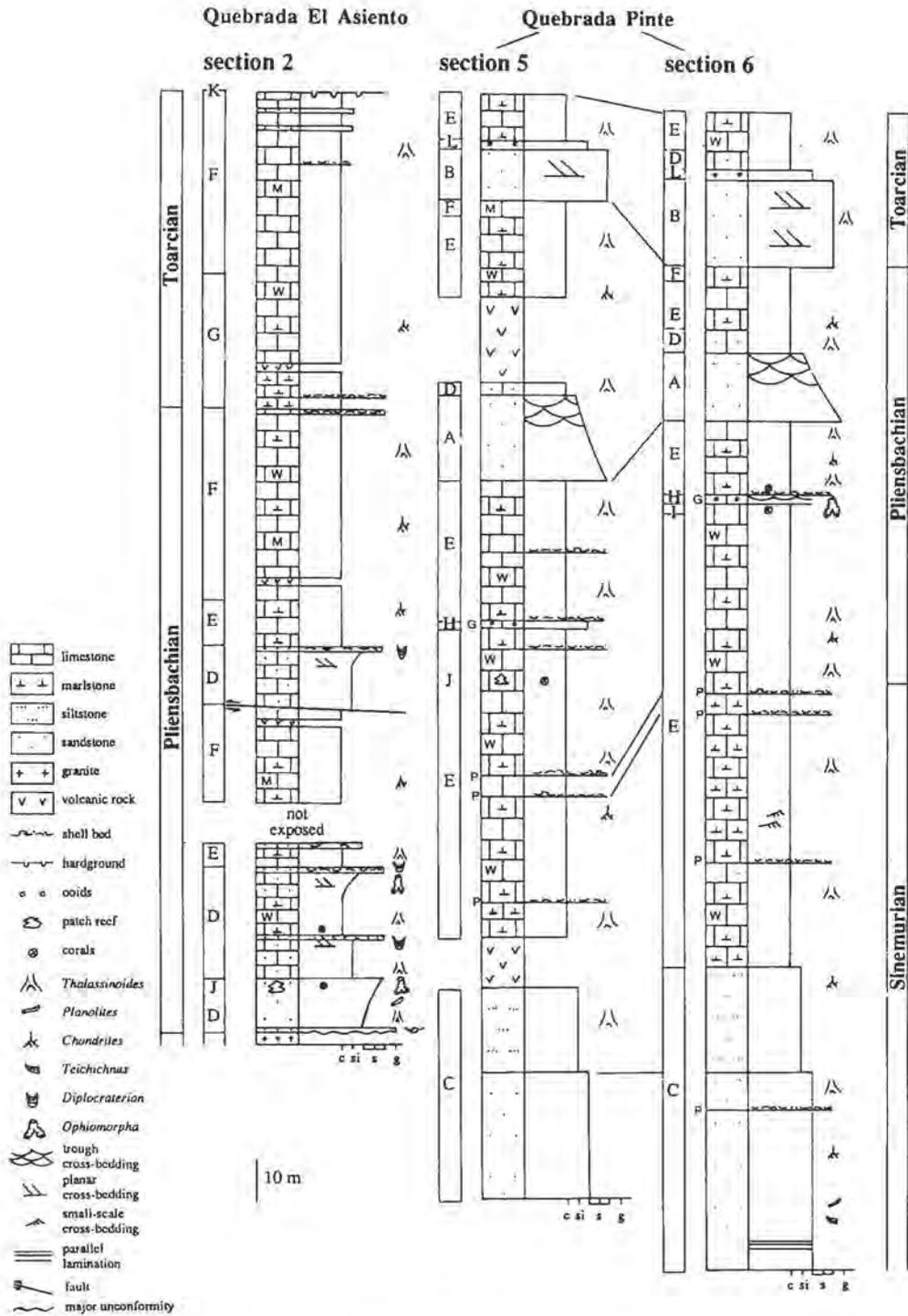


FIG. 3. Main studied sections through the Liassic of Quebrada El Asiento (section 2) and Quebrada Pinté (sections 5, 6). A to L denote facies types as defined in table 1. Grain size: c = clay; si = silt; s = sand; g = gravel. Carbonate lithology: M = mudstone; W = wackestone; P = packstone; G = grainstone.

TABLE 1. MAIN FEATURES OF THE 12 FACIES TYPES RECOGNIZED IN THE EARLY JURASSIC OF NORTHERN CHILE AND INTERPRETATION OF CORRESPONDING DEPOSITIONAL ENVIRONMENTS.

Facies types	Composition	Physical sedimentary structures	Bioturbation	Trace fossils	Body fossils	Sedimentation rate	Energy level	Interpretation of depositional environment
A - unfossiliferous, moderately sorted, coarse-grained sandstones to fine conglomerates; cobbles common, up to 8 cm in length	quartz; rarely feldspar and bioclasts; matrix: silty micrite to sparite	erosive base; trough cross-bedding	absent		very rare marine bivalves	high	high	marginal marine (an delta); strong influence of currents/waves
B - unfossiliferous, well-sorted, medium-grained sandstones	quartz; matrix: sparite	erosive base; planar cross-bedding	occur	<i>Thalassinoides</i>	absent	high	high	migrating shallow subtidal sand bar, strong influence of currents/waves
C - well-sorted, fine-grained sandstones to siltstones	quartz and bioclasts; matrix: silty marl to micrite	parallel lamination	abundant	<i>Thalassinoides</i> <i>Planolites</i> <i>Chondrites</i> <i>Teichichnus</i>	bivalves gastropods plant debris	intermediate	intermediate	shallow siliciclastic ramp; below wave base, influence of currents
D - micritic sandstones to sandy wackestones	quartz and bioclasts; rarely feldspar, mica, granitic rock fragments; matrix: micrite	generally rare; erosive base, trough and planar cross-bedding	common	<i>Ophiomorpha</i> <i>Planolites</i> <i>Thalassinoides</i> <i>Diplocraterion</i>	bivalves brachiopods gastropods corals	intermediate	intermediate	mixed siliciclastic-carbonate ramp; intermittent influence of currents
E - wacke- to packstones	bioclasts, peloids; rarely quartz		abundant	<i>Thalassinoides</i> <i>Chondrites</i>	brachiopods bivalves crinoids	intermediate to low	intermediate to low	middle carbonate ramp; winnowing common
F - brownish mud- to wackestones	rarely bioclasts, quartz, and feldspar		rare	<i>Planolites</i> <i>Chondrites</i> <i>Thalassinoides</i>	ammonoids nuculid bivalves	low	low	deep offshore carbonate ramp
G - bituminous mud- to wackestones; intercalation of winnowed lags	rarely bioclasts, quartz, and feldspar		absent		ammonoids <i>Posidonotis</i>	low	low	deepest part of ramp; oxygen-controlled benthic fauna
H - well-sorted grainstones	peloids, aggregate grains, bioclasts	trough cross-bedding	occur	<i>Thalassinoides</i> <i>Ophiomorpha</i>	brachiopods bivalves crinoids	high	high	turbulent environment on a shallow carbonate ramp, most likely shoals far from any clastic influence
I - coral-stromatoporoid biostrome	matrix: micrite		rare	<i>Thalassinoides</i> bivalve borings in organisms	corals stromatoporoids bivalves brachiopods	low	low	low energy environment on a shallow carbonate ramp, far from clastic influence
J - moderately diverse patch-reefs				bivalve borings in organisms	corals stromatoporoids bivalves brachiopods	low to intermediate	intermediate	shallow nearshore ramp
K - hardgrounds	ferruginous crusts		common	<i>Thalassinoides</i> bivalve borings in substrate	encrusting oysters and serpulids <i>Lithophaga</i>	extremely low; omission	low to intermediate	deep offshore ramp
L - Fe-oolites	Fe-oolites, bioclasts quartz; matrix: micrite		common		bivalves ammonoids	low	low	mixed siliciclastic-carbonate ramp

sandstones to sandy or silty wackestones. These mixed siliciclastic-carbonate deposits are summarized in facies type D. They reflect roughly corresponding rates of terrigenous sediment accumulation and autochthonous carbonate production. In this respect they act as a link between the siliciclastic-dominated facies zone a- and the carbonate-dominated facies zone c-. Sedimentation rate and energy level are interpreted to have been intermediate;

- c- a third facies belt is defined by the widely spread facies type E and replaced zone b- in a still farther offshore direction. It is characterized by a reduced input of terrigenous material and a high rate of carbonate production. Whilst coarse-grained material was deposited in onshore settings, a considerable amount of clay- and silt-sized particles was bypassed to environments still farther offshore towards the basin centers. Consequently, the dominant lithofacies are wacke- and packstones which are rich in bioclasts. They are interpreted to have been deposited at times of intermediate to low, but rather continuous sedimentation rates, under the influence of weak currents;
- d- an offshore facies belt, formed by facies types F and G, occupied a position still further offshore than zone c-, in the deepest parts of the basin. Low rates of sedimentation of fine-grained terrigenous clastics and autochthonous lime mud under low energy conditions led to the sedimentation of monotonous series of mud- to wackestones and silty marls. In part, bituminous sediments point towards a restricted water circulation and oxygen-deficient conditions on the sea floor.

The relative spatial position of the less common facies types H-L can be drawn from table 1 and figure 3. Most commonly, they represent spatially and temporally limited environments which were associated with one of the above mentioned main

facies types.

The organization of facies belts more or less parallel to the coastline and continuously grading into each other suggests depositional environments which spatially were passing into each and which temporally were replacing each other. Accordingly, the depositional system has been interpreted as a ramp rather than a rimmed shelf or an isolated platform. Ramps are gently sloping platforms on which shallow, high-energy facies onshore pass downslope into deeper-water, low-energy facies offshore (Ahr, 1973). Accordingly, facies belts a- to d- from above can be assigned to a shallow siliciclastic ramp, a mixed siliciclastic-carbonate ramp, a middle carbonate ramp, and a deep carbonate ramp, respectively.

It has been distinguished between homoclinal ramps and distally steepened ramps (Read, 1982; 1985). Homoclinal ramps generally lack significant sediment gravity flow deposits as well as slumping structures in the deep-water facies. Due to the apparent absence of a slope break and associated mass flow deposits, the Early Jurassic ramp of northern Chile is interpreted as a homoclinal ramp.

Due to the lack of protecting reef belts and barrier systems, facies organization and stratification types on ramps are usually highly influenced by storm activity (e.g. Aigner, 1985; Wright, 1986; Lee and Kim, 1992; Holland, 1993). However, typical features of a storm-dominated sedimentation, such as sandstone-mudstone couplets, sharp bases of beds, graded bedding, hummocky cross-bedding, and shell beds with a high percentage of articulated shells, were of subordinate importance in the studied sections. The obvious scarcity of hurricanes and winter storms can be explained by the paleogeographic position of the Andean Basin on the eastern margin of an ancient ocean behind a volcanic arc (see paleogeographic maps of Barron *et al.*, 1981; Smith *et al.*, 1982; Ziegler *et al.*, 1982; Scotese, 1991).

BENTHIC ASSOCIATIONS

Using relative abundances of individual taxa, 202 bulk collections of benthic macroinvertebrates from Early Jurassic sections of northern Chile, comprising more than 40,000 specimens, have been grouped

into 27 associations by means of a Q-mode cluster-analysis (Aberhan, 1992). Bulk samples have been taken from single layers of uniform lithology. Obviously transported, mixed, or diagenetically biased samples

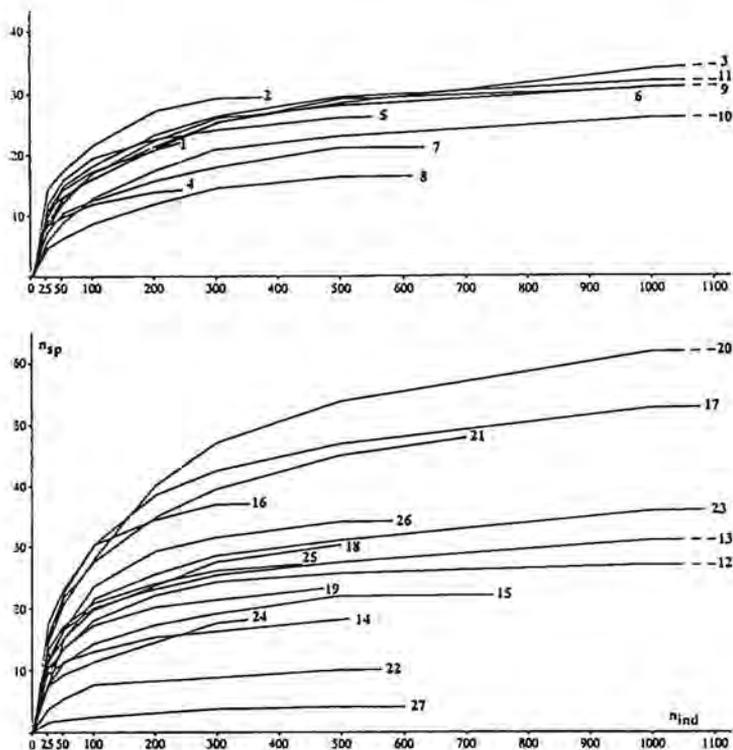


FIG. 4. Rarefaction curves of associations n_{sp} = numberspecies; n_{ind} = number of individuals. For key see Appendix 1.

were excluded from the analysis. Therefore, the associations as well as three assemblages, which are statistically less significant, are regarded to represent the autochthonous to parautochthonous relics of ancient communities.

As a rule, associations of the geological past suffered loss of soft-bodied elements. Consequently, taxonomic and trophic composition as well as diversity values are more or less biased if compared to former living communities. Furthermore, fossil associations represent time-averaged community relics of non-contemporaneous ancient communities (Walker and Bambach, 1971; Fürsich and Aberhan, 1990). As such they cannot record short-term fluctuations but rather reflect the general environmental conditions which persisted over longer time periods.

Despite these restrictions, community paleoecology has proved in numerous case studies, to be a sensitive tool in reconstructing Phanerozoic marine paleoenvironments, if used in combination with sedimentological and taphonomic data (e.g. Ziegler *et al.*, 1958; Rhoads *et al.*, 1972; Scott, 1974; 1990; Duff, 1975; Fürsich, 1977; 1981; 1984a; 1984b; Fürsich and Werner, 1986; Hurst and Watkins, 1981; Oschmann, 1988; Wignall, 1990a; Aberhan and

Fürsich, 1991). On the whole, information loss appears to be predictable within certain limits and the bias is likely to be constant within distinctive time-environmental units.

In order to avoid the repetition of long descriptions here, only the trophic nucleus of each association and assemblage (that is, the numerically most important elements that make up 80% of an association) is listed in appendix 1 (the identification of rhynchonellid brachiopods has been carried out according to the preliminary results of a Ph.D. thesis (V. Lüdemann; Berlin University) and an unpublished manuscript on Liassic rhynchonellids from Calama, North Chile (X. Shi; China University of Geosciences, Beijing). The publication of new species from the Liassic of Argentina, based on detailed morphometric analysis and thin sections, makes a revision of the Chilean material necessary. Judging from the figured specimens in Manceñido (1991) some species which prevail in assemblage zones from Argentina also dominate in associations from northern Chile of the same age. In order to avoid the use of *nomina nuda*, an open nomenclature has therefore been adopted for some rhynchonellids in this study).

Also included in appendix 1 is information on the

1, 2, and 6 (Fig. 5; Appendix 1). In order to convey an impression of the benthic colonization of the Sinemurian sea floor, the reconstruction of the *Parallelodon hirsonensis* association is given as an example in figure 6. The dominant faunal elements of the shallow siliciclastic ramp are the semi-infaunal filter-feeding bivalves *Gervillella araucana*, *Parallelodon hirsonensis*, and *Bakevellia waltoni*, the pedunculate, suspension-feeding brachiopod *Lobothyris* cf. *ovatissima*, and the shallow infaunal, filter-feeding bivalves *Protocardia* sp. A and *Anisocardia* sp. A. Consequently, the dominating guilds are semi-infaunal, shallow infaunal and pedunculate suspension-feeders. A less common guild is represented by epifaunal, presumably herbivorous gastropods, which are essentially restricted to this environment (Fig. 13).

In the various associations one-fourth to one-fifth of the bivalves is preserved with both valves. The degree of abrasion and breakage is generally low. Encrustation of shells by serpulids occurs very rarely and no traces of bioerosion have been found on shells. Most forms with aragonitic shell mineralogy are preserved as steinkerns.

Interpretation

The good preservation of the fauna and the presence of articulated bivalves indicate that lateral transport was insignificant in the formation of these associations. The preservation of aragonitic forms as steinkerns shows that a taphonomic bias of the fauna through selective solution of aragonitic shells can be ruled out. Therefore, the associations are regarded as the parautochthonous relics of the preservable part of former communities.

Lithofacies and taphonomic data point to an intermediate energy level and the influence of moderately strong currents. According to the high percentage of suspension-feeders water energy must have been sufficient enough to keep nutrients in suspension. The relatively common herbivorous gastropods let presume, that the sea bottom was colonized by benthic algae, thus indicating an environment well within the photic zone. The high percentages of epifaunal and semi-infaunal forms suggest a fairly stable substrate. At the same time substrate consistency must have been soft enough to allow the colonization by a burrowing infauna. A

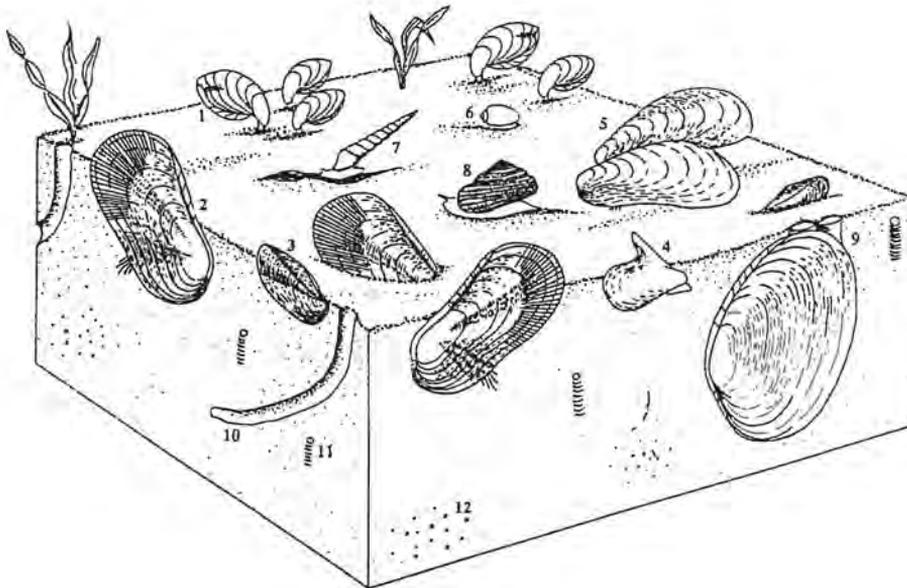


FIG. 6. Biotope reconstruction of the *Parallelodon hirsonensis* association. Illustrated are those species which form the trophic nucleus. 1- *Terebratula* cf. *ovatissima*; 2- *Parallelodon hirsonensis*; 3- *Gervillella araucana*; 4- *Bakevellia waltoni*; 5- *Modiolus giganteus*; 6- *Striactaeonina transatlantica*; 7- high-spired gastropod; 8- *Lithotrochus? andinus*; 9- *Cardinia andium*; 10- *Planolites* sp.; 11- *Teichichnus* sp.; 12- *Chondrites* sp.; benthic algae hypothetical.

relatively stable low-stress environment is also corroborated by the intermediate to high diversity values (Fig. 4; Appendix 1). The nearly complete absence of encrusters and borers points out, that shells did not remain exposed on the sea bottom for a long time and that the rate of sedimentation, therefore, was rather continuous. However, to enable the settlement of fixo-sessile brachiopods, sedimentation rates cannot have been particularly high.

In summary, the associations characterize a relatively onshore depositional environment on a shallow siliciclastic ramp below fair-weather wave base with intermediate rates of sedimentation.

MIXED SILICICLASTIC-CARBONATE RAMP BIOFACIES

Description

Common associations of the mixed siliciclastic-

carbonate ramp are association 4 in the upper Sinemurian, associations 16, 17, 20 and 21 in the upper Pliensbachian, and associations 23, 24, 25, and 26 as well as assemblage F in Toarcian strata (Fig. 5; Appendix 1). The upper Pliensbachian *Weyla alata*/*Entolium corneolum* association, which is reconstructed in figure 7, is regarded as a characteristic representative. As is typical for most associations of this environment, it exhibits a comparatively broad spectrum of life habits, a high diversity (Fig. 4; Appendix 1), and its constituent samples possess a high faunal density. The dominant organisms of the mixed siliciclastic-carbonate ramp are bivalves, which are represented by different guilds and morphotypes. In particular, these are the deep infaunal suspension-feeders *Pholadomya hemi-cardia*, *Pholadomya fidicula*, *Pleuromya uniformis*, *Pachymya rotundocaudata*, and *Gresslya peregrina*, the shallow infaunal suspension-feeder *Protocardia striatula*, the free-lying epifaunal suspension-feeders

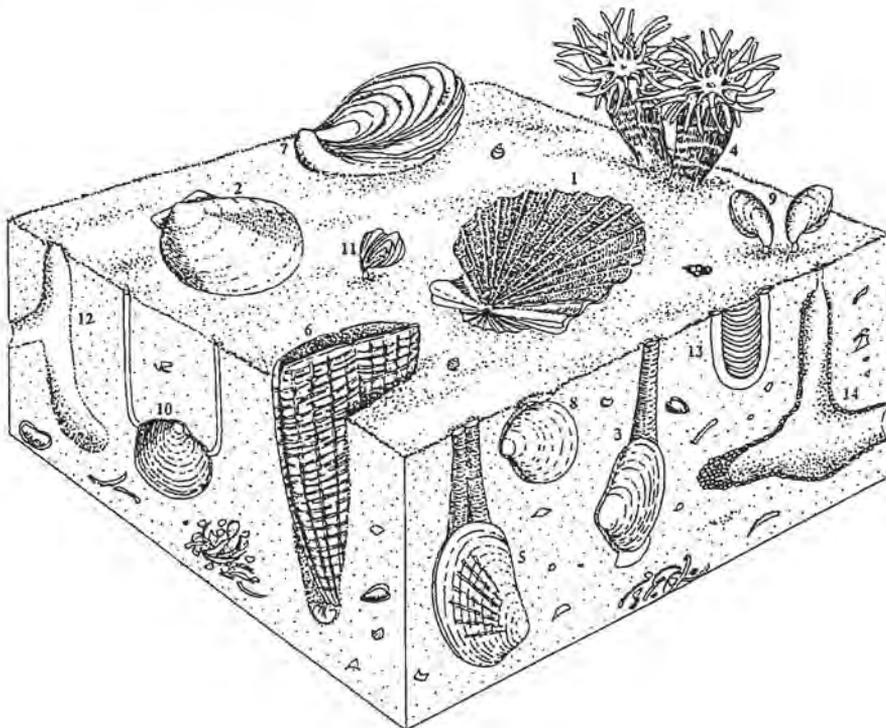


FIG. 7. Biotope reconstruction of the *Weyla alata*/*Entolium corneolum* association. Illustrated are the species from the trophic nucleus 1- *Weyla alata*; 2- *Entolium corneolum*; 3- *Pleuromya uniformis*; 4- *Montlivallia* sp.; 5- *Pholadomya corrugata*; 6- *Pinna* cf. *radiata*; 7- *Gryphaea* cf. *darwinii*; 8- Articiidae gen. et sp. nov.; 9- 'Terebratula' sp. A; 10- *Mesomiltha bellona*; 11- *Quadratrhyynchia* sp. B; 12- *Thalassinoides* sp.; 13- *Diplocraterion* sp.; 14- *Ophiomorpha* sp.

Entolium corneolum, *Weyla alata*, and *Gryphaea darwini*, the cemented epifaunal suspension-feeder *Actinostreon solitarium*, and finally the lucinids *Mesomiltha bellona* and *Mesomiltha? huayquimilli* (see also figure 13). The latter two are classified as infaunal surface deposit- and/or suspension-feeders via mucus tubes (for a discussion of feeding strategies in Lucinacea see e.g. Liljedahl, 1991).

As a rule, more than half and up to 85% of the bivalves are preserved with both valves. Many of them, especially deep infaunal forms, occur in life position. The level of abrasion and breakage of shells is very low. Encrusting serpulids, small oysters, and bryozoans as well as boring bivalves and algae occur occasionally, but in general the degree of bioerosion and encrustation of shells is low. The aragonitic fauna is represented as steinkerns and in some samples also carries original shell material.

Interpretation

As for the fauna of the shallow siliciclastic ramp, the taphonomic data show that we clearly deal with the time-averaged *in situ* remnants of former communities whose soft body fauna has been removed. The good preservation quality of fossils and the dominance of filter-feeders indicate an intermediate energy level. The well-balanced percentage of faunal elements living upon and within the sediment is suggestive of a substrate, which was sufficiently stable for a sessile epifauna and on the other hand soft enough to enable a rich endobenthic life. High faunal densities, high species richness and evenness, and an equitable distribution of guilds within the various associations, indicate a stable and predictable environment which, for the most part, was free of physical stress. Most niches were occupied and a clear structure according to the partitioning of spatial resources has been developed. Such biologically-controlled environments, which are close to their carrying capacity are typically dominated by K-strategists. K-strategists are characterized by a relatively long life span, a relatively low reproduction rate and a high level of specialization (MacArthur and Wilson, 1967). In this case, for example, *Weyla alata* seems to have followed up this strategy.

MIDDLE CARBONATE RAMP BIOFACIES

Description

Benthic associations of the middle carbonate ramp are the Sinemurian associations 3, 5, 7, 8, and 9, the lower Pliensbachian associations 10, 11, 12, 13, 14, and 15, and the upper Pliensbachian association 18 and assemblage E (Fig. 5; Appendix 1). They are dominated by epifaunal suspension-feeders, in particular pedunculate brachiopods (*Lobothyris* cf. *ovalissima*, *Lobothyris subpunctata*, *Quadratirhynchia crassimedia*, *Quadratirhynchia* sp. A, *Gibbirhynchia curviceps*, *Spiriferina chilensis*), free-lying bivalves (*Weyla alata*, *Weyla titan*, *Entolium corneolum*), and crinoids ('*Pentacrinites*' sp.) (Fig. 13). More rarely, the cemented oyster *Exogyra* sp. A occurs; representatives of the infauna are very rare. On the other hand, the degree of bioturbation is fairly high. Trace fossils, however, basically *Thalassinoides*, exhibit a very low diversity. Some of the dominant species of the middle carbonate ramp are illustrated in figure 8, the reconstruction of the *Spiriferina chilensis* association. Standing also for other associations of the middle carbonate ramp, it reflects the conspicuous lack of infauna apart from trace fossils, a high faunal density of epifauna, and a relatively low diversity, if compared to associations from the mixed siliciclastic-carbonate ramp (see also figure 4; Appendix 1).

Almost all brachiopods are articulated and often occur as small clusters on bedding surfaces. Bivalves are commonly found single-valved, more rarely bivalved and in life position. The degree of breakage is moderate to low. In some samples the percentage of shell-encrusting serpulids, oysters, and bryozoans as well as the number of bivalve and brachiopod borings, as indicated by *Gastrochaenolites* and *Podichnus* reach intermediate levels. Shells are preferentially oriented in a concave-up position within the sediment. Calcitic brachiopod and bivalve shells are preserved. In contrast, aragonitic forms are rare and, primarily they exist as steinkerns only. In some cases aragonitic gastropods and the solitary coral *Montlivaltia* are preserved with recrystallized shell material.

Interpretation

The largely component-supported sediment fabric and high concentrations of skeletal elements are interpreted to have been caused by winnowing of fine-grained sediment by moderate currents. However, general good preservation and the occurrence of brachiopods in small clusters, which are likely to reflect the original colonization pattern on the ancient sea floor, indicate that destruction of shells by currents and extensive lateral transport have not taken place. This is further corroborated by the size frequency distribution of brachiopods in

various samples (e.g. Fig. 9), which reflects a rather low degree of sorting and by the predominantly concave-up orientation of shells within the sediment.

Low sedimentation rates can be inferred from the predominance of epifauna, an intense bioturbation, and occasionally higher levels of encrustation. Consequently, the high faunal densities are interpreted as autochthonous to parautochthonous accumulations of hard parts due to a combination of low rates of sedimentation, high rates of bioproduction, and winnowing of fine-grained material.

These factors obviously resulted in a stable and consolidated, bioclast-rich substrate upon which

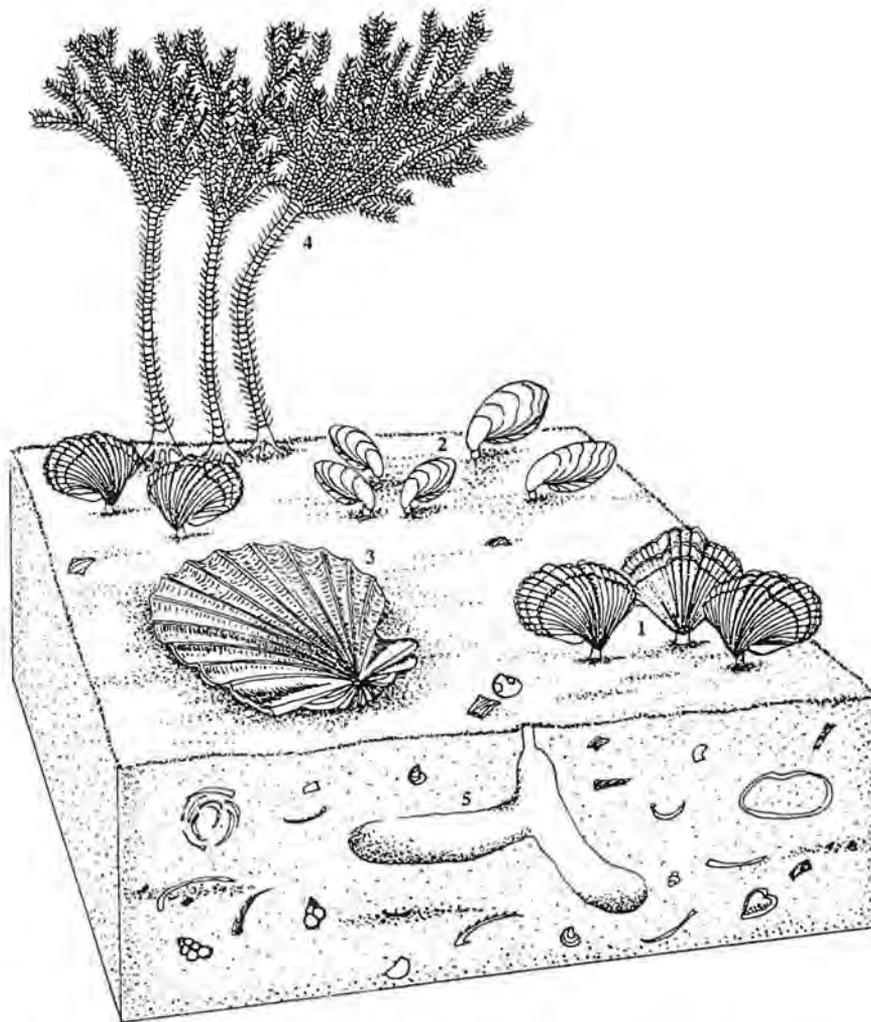
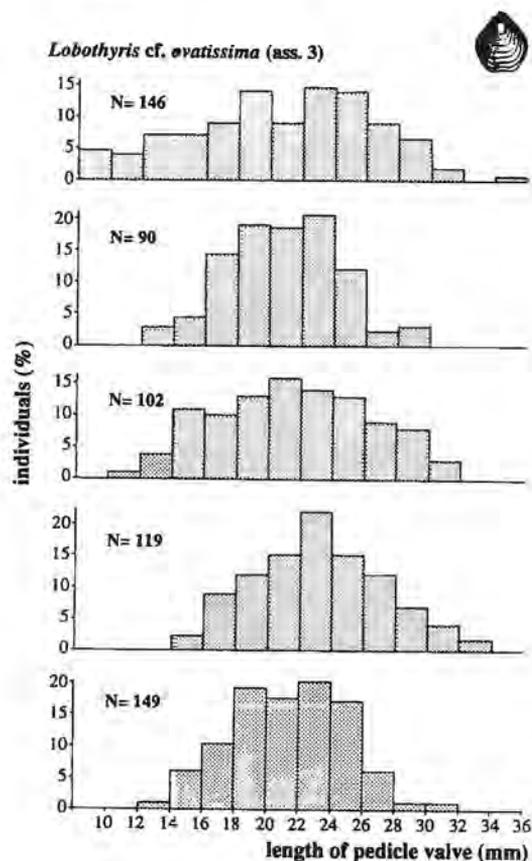


FIG. 8. Biotope reconstruction of the *Spiriferina chilensis* association with species from the trophic nucleus 1- *Spiriferina chilensis*; 2- *Lobothyris cf. ovatissima*; 3- *Weyla alata*; 4- '*Pentacrinites*' sp.; 5- *Thalassinoides* sp.; 6- shell pod.

extensive brachiopod- and epifaunal bivalve-associations were able to thrive, covering large parts of the ancient sea floor. At least some of the brachiopods were growing upon each other as indicated by abundant traces of *Podichnus* on the shells of *Lobothyris subpunctata*.

As aragonitic shells of the infauna occur only sporadically in various samples, some preservational bias, that is most of the aragonitic shells dissolved during diagenesis, cannot be ruled out. However, since aragonitic gastropods and scleractinian corals are sometimes preserved with recrystallized shells, the absence of the burrowing forms appears to reflect an original feature of these communities. As indicated by an abundant, but poorly-diverse ichnofauna, some specialized organisms - most likely crustaceans - must have been able to penetrate the substrate while it apparently was unsuitable for burrowing bivalves.

FIG. 9. Size frequency distribution of *Lobothyris cf. ovatissima* in five samples of the *Lobothyris cf. ovatissima* association. N: number of studied individuals.



DEEP CARBONATE RAMP BIOFACIES

Description

The associations represented on the deep carbonate ramp are associations 19 and 22 from the upper Pliensbachian and association 27 as well as assemblage G from the Toarcian (Fig. 5; Appendix 1). As the four associations differ markedly from each other, they are described and discussed separately.

The *Nuculana ovum* association (22) is characterized by the high dominance of a mobile, shallow infaunal, deposit-feeding nuculid bivalve, *Nuculana ovum*, which occurs in moderately bioturbated dark-coloured mud- to wackestones. The diversity of the association and the number of guilds are very low (Fig. 4; Appendix 1). Deep infaunal forms are completely lacking. Nearly half of the bivalves are articulated without evidences of encrustation or bioerosion; aragonitic fauna is preserved with shell.

The *Gryphaea sp. A* association (19) is dominated by the small, free-lying oyster *Gryphaea sp. A* (Appendix 1). Further common elements are brachiopods. Epifaunal diversity is intermediate (Fig. 4), infauna occurs only sporadically. Nearly all organisms are epifaunal filter-feeders. A relatively low percentage of bivalves has been found articulated. The degree of breakage is low; signs of encrustation and bioerosion are absent. Aragonitic fauna is preserved as steinkerns. The association occurs in moderately bioturbated wackestones.

The *Posidonotis cancellata* association (27) has an extremely low diversity (Fig. 4; Appendix 1) and is essentially formed by a single species, the epibyssate and/or free-lying, filter-feeding bivalve *Posidonotis cancellata*. It occurs in non-bioturbated, fine-bedded, black mud- and wackestones. The individuals are mainly single-valved and often concentrated as shell pavements. They are mainly preserved as internal and external molds.

The *Propeamussium pumilum* assemblage (G) is characterized by a moderately diverse epifauna, dominated by the free-lying, suspension-feeding pectinaceans *Entolium corneolum* and *Propeamussium pumilum*. On the other hand, infaunal life has been restricted to a single bivalve, the lucinid *Mesolinga sp.*, which might have lived in symbiosis with sulfide-oxidizing bacteria. Apart from a relatively low degree of articulation in bivalves, the preservation of fossils is fair. The faunal samples are from brownish

mud- to wackestones which are bioturbated by *Chondrites*. They alternate with black marls which are devoid of fossils.

Interpretation

Taphonomic data, monotonous lithofacies, and faunal composition point to a quiet offshore environment distinctly below wave-base for the four associations. They are all interpreted to have been structured by more or less lowered levels of free oxygen, as shall be demonstrated below.

The *Nuculana ovum* association is the only association where infaunal deposit-feeders, in this case nuculid bivalves, are significant. According to the facies in which they occur in the Chilean Liassic, nuculids preferred a fine-grained substrate rich in organic matter, indicative of low energy conditions. This bivalve group is known as a dominant component of oxygen-controlled environments from the Paleozoic to the Recent (e.g. Bader, 1954; Kammer *et al.*, 1986; Wignall, 1990b). In particular, in an analysis of the Lower Jurassic of England, *Nuculana ovum* has been only found in high abundance in an environment where oxygen-deficiency was evident (Morris, 1979). Low diversity, the environmental tolerances of the dominant species, and the structure of the association which completely lacks deep infaunal guilds indicate a lowered oxygen-supply of the benthic fauna. Accordingly, the O_2/H_2S interface has been reconstructed at a position a few centimeters below the surface of the substrate (Fig. 10). Below the O_2/H_2S interface, the presence of toxic H_2S prevented settlement of any infauna. Above the interface the O_2 -level increased giving rise to an impoverished fauna consisting basically of nuculids.

The low percentage of epifauna, however, is not interpreted as a consequence of low-oxygen conditions at the seafloor. Rather, biogenic reworking of the muddy substrate by nuculids most likely resulted in a water-rich, thixotropic sediment surface. This excluded most filter-feeding as well as epifaunal sessile organisms, a case of faunal interaction which is known from the Recent as trophic group amensalism (e.g. Rhoads and Young, 1970; Bloom *et al.*, 1972; Aller and Dudge, 1974).

Propeamussium pumilum, being characteristic of the assemblage of the same name, has been interpreted as a benthic opportunistic bivalve which preferred low-energy conditions and was able to tolerate lowered oxygen conditions (Johnson, 1984). Low oxygen supply is further indicated by the very low

infaunal diversity, which is essentially restricted to the lucinid *Mesolinga*. Recent representatives of this bivalve family are known to live in symbiosis with chemo-autotrophic bacteria. These oxidize H_2S to sulphate or thiosulphate and thus protect their hosts against poisonous effects (e.g. Felbeck *et al.*, 1983; Reid and Brand, 1986; Vetter *et al.*, 1991). In order to simultaneously meet the metabolism of bivalves and bacteria, chemosymbiosis requires long-term stable conditions with a balanced juxtaposition of both O_2 and H_2S (Felbeck *et al.*, 1983; Oschmann, 1993). These demands are realized close to the O_2/H_2S interface. In addition, the frequently occurring trace fossil *Chondrites* is regarded as an indicator of lowered O_2 -conditions (Bromley and Ekdale, 1984; Seilacher, 1990).

In summary, composition and structure of the benthic fauna suggest an oxygen-controlled environment with a position of the O_2/H_2S interface fairly close to the surface of the substrate (Fig. 10). Recent propeamussiids are most commonly found on the continental slope and in the deep sea and are rare in environments shallower than 60 m (Waller, 1972). This may also serve as an upper bathymetric value for the former habitat of the *Propeamussium pumilum* assemblage.

In the *Gryphaea* sp. A association diversity and dominant elements of the epifauna are - apart from *Propeamussium* - essentially the same as for the *Propeamussium pumilum* assemblage. This points to similar living conditions for the inhabitants of the surface of the substrate in both associations. The nearly complete lack of infauna indicates high stress conditions within the sediment, which are interpreted to have been caused by a shortage of free oxygen and raised concentrations of toxic H_2S . Accordingly, the O_2/H_2S interface has been placed close to the surface of the substrate in a similar position to that of the *Propeamussium pumilum* assemblage (Fig. 10).

In the *Posidonotis cancellata* association, the extreme dominance of *Posidonotis cancellata* which occurs in high numbers points to an opportunistic life strategy of that species (see also Hallam, 1977). Opportunists are characterized by rapid growth rates and high fertility rates (Levinton, 1970). This enables them to occupy free niches or habitats with high densities within a short period of time. Possibly, *Posidonotis cancellata* also lived in symbiosis with chemo-autotrophic bacteria, a mode of feeding that has been considered for the morphologically and ecologically related *Bositra* from the Posidonien-schiefer of south-west Germany (Savrda and Bottjer,

1987; Seilacher, 1990). Here, extremely low diversities, the dominance of an opportunistic species, and the absence of a shelly infauna and trace fossils are indicators of anoxic conditions within the substrate and of poor O_2 -concentrations on the surface of the

substrate. Even on the sea floor oxygen-supply never has been sufficient to give rise to a more diverse epibenthic life. For these reasons, the O_2/H_2S interface has been reconstructed in a position at, to immediately above, the sediment/water interface (Fig. 10).

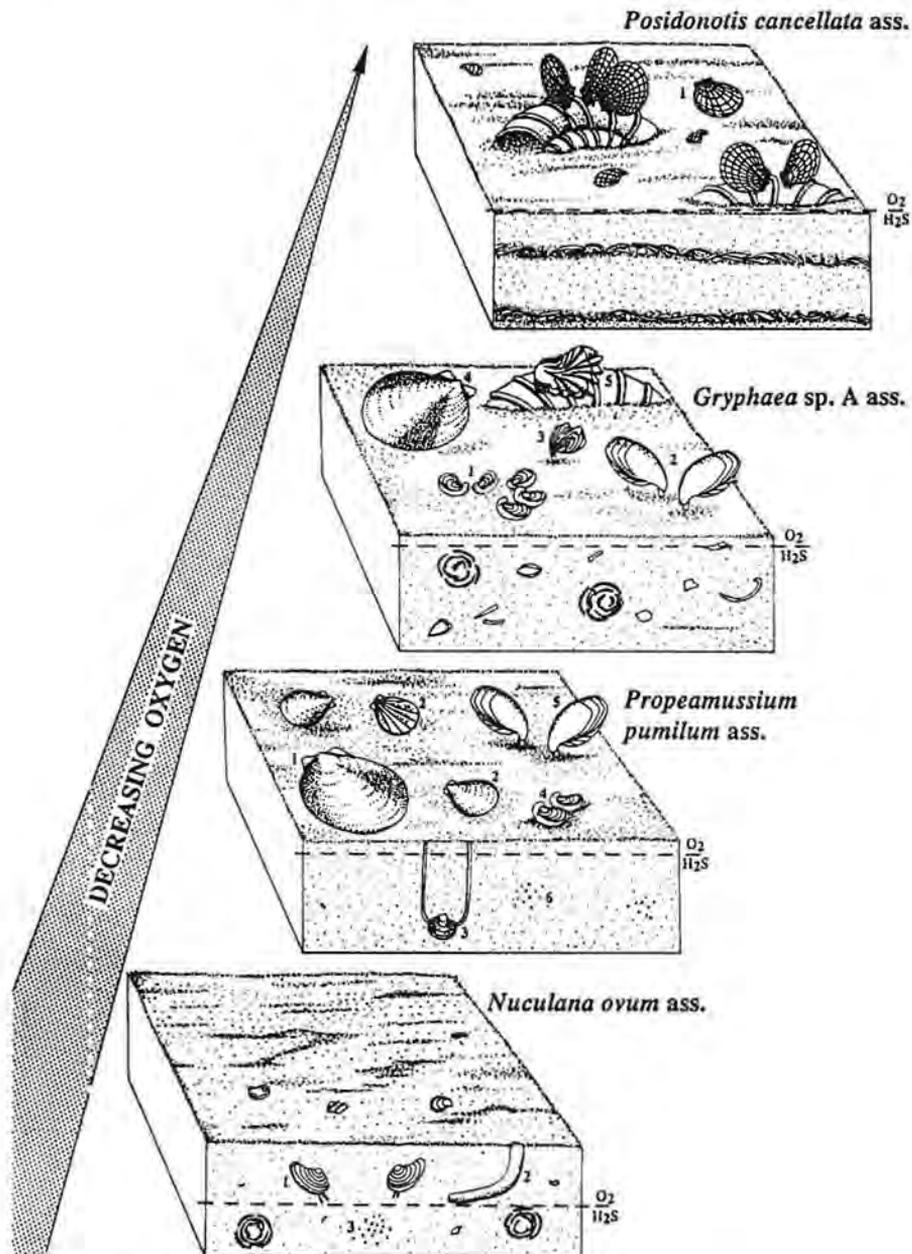


FIG. 10. Reconstruction of oxygen-controlled associations and arrangement along an oxygen gradient. *Nuculana ovum* ass.: 1: *Nuculana ovum*; 2: *Planolites* sp.; 3: *Chondrites* sp.; 4: shell pod; *Propeamussium pumilum* ass.: 1: *Entolium corneolum*; 2: *Propeamussium pumilum*; 3: *Mesolinga* sp.; 4: *Gryphaea* sp. A; 5: *Lobothyris* cf. *subpunctata*; 6: *Chondrites* sp.; *Gryphaea* sp. A ass.: 1: *Gryphaea* sp. A; 2: *Lobothyris subpunctata*; 3: *Rudirhynchia* aff. *rudis*; 4: *Entolium corneolum*; 5: *Actinostreon solitarium*; 6: shell pod; *Posidonotis cancellata* ass.: 1: *Posidonotis cancellata*. Note the position of the O_2/H_2S interface.

OXYGEN GRADIENTS ON A DEEP CARBONATE RAMP

As it has become clear from the foregoing interpretation the fauna of the deep carbonate ramp was controlled by a restricted water circulation which resulted in a reduced supply of oxygen of the benthic fauna. According to their taxonomic composition and ecological structure the associations can be arranged along an oxygen gradient (Fig. 10). This is expressed by a successively higher position of the O_2/H_2S interface within the sediment. The interface ranges from a few centimeters below the surface of the substrate to a position where it coincides with the surface of the substrate or even lies slightly above it.

Traditionally, oxygen-controlled environments have been subdivided into three biofacies zones, mainly depending on water depth (Rhoads and Morse, 1971; Byers, 1977): **a-** The aerobic biofacies (>1 ml/l O_2) is characterized by a diverse shelly and soft-bodied benthic fauna and bioturbation; **b-** the dysaerobic biofacies ($0.1-1$ ml/l O_2) consists of a small, low diversity fauna dominated by infauna with little or no elements with hard parts and moderate bioturbation, and **c-** the anaerobic biofacies (<0.1 ml/l O_2) lacks a macrobenthic fauna and bioturbation and the corresponding environment typically exhibits laminated sediments.

Further studies revealed a gradational transition between the aerobic and dysaerobic biofacies. Several authors described dysaerobic, low-diversity associations which were composed of shelly organisms of different taxonomic composition in the various case studies (e.g. Savrda *et al.*, 1984; Thompson *et al.*, 1985; Kammer *et al.*, 1986). Consequently, the definition of the dysaerobic biofacies has been extended.

A further subdivision, the exaerobic biofacies, has been added by Savrda and Bottjer (1987; 1991). It is characterized by the unusual occurrence of shelly epibenthic bivalves in laminated, organic-rich sediments. The bivalves are interpreted to have lived in symbiosis with sulphur-oxidizing bacteria at the anaerobic-cyaerobic transition. Here, the exaerobic biofacies is treated as a special development of the dysoxic environment, being characterized by the occurrence of sulphide-oxidizing bacterial mats.

This classical oxygen zonation has been elaborated on the continental slope and basin environments, which are characterized by long-term stable conditions. In contrast, many modern and

ancient shelf and epeiric basin anoxia are more dynamic. Accordingly, a modified oxygen zonation concept has been defined for these environments (see Tyson and Pearson, 1991). In particular, Oschmann (1990; 1991a; b) proposed a poikiloaerobic environment to accommodate environments with seasonally fluctuating oxygen conditions. It is characterized by micro-laminated sediments, the dominance of opportunistic species which are able to extend their planktonic larval stages (in particular shallow infaunal, filter-feeding bivalves), and a stochastically-controlled faunal non-equilibrium.

Faunal composition and dynamics of oxygen-controlled environments from the Chilean Liassic can neither be interpreted with the classical oxygen zonation concept of the dysaerobic biofacies nor with the poikiloaerobic model. While in both models endobenthic fauna dominates, in the Chilean Liassic epibenthic bivalves prevail. (Note, that the low percentage of epifauna in the *Nuculana ovum* association does not directly result from a low oxygen supply, but presumably was caused by trophic group amensalism).

The absence of micro-laminated sediments and the long-term stability in faunal composition indicate oxygen-deficient conditions which - in contrast to the poikiloaerobic environment - existed over longer periods. For example, in the uppermost Pliensbachian to lowermost Toarcian beds of Quebrada El Asiento, the *Posidonotis cancellata* association is the only benthic fauna that occurs for some tens of meters of sediment. These are interpreted to correspond to a period of several hundred thousand years. The lack of short-term fluctuations in oxygen supply may be explained by the paleogeographic position of the Andean Basin (see above): water exchange with the open ocean most likely was restricted and short-term events such as storms were rare.

Due to their temporal stability, the Chilean associations are assigned to the modified version of the dysaerobic biofacies and further demonstrate the variability in faunal composition of this environment. Based on the faunal distribution in the studied sections, a faunal zonation along an oxygen gradient can be reconstructed (Fig. 11). It may serve as an example of faunal distribution in oxygen-controlled ramp environments which are characterized by a long-term relative environmental stability. Four biofacies

zones can be distinguished, with emphasis on an upper and a lower dysaerobic biofacies (Fig. 11).

a- the aerobic zone is characterized by a highly diverse fauna which is dominated by K-strategists. It is composed of variable percentages of infaunal and epifaunal filter-feeders and exhibits high faunal densities. Important environmental factors which influenced composition and structure of associations are rate of sedimentation, rate of biogenic reworking, substrate consistency and stability, and energy level;

b- an upper dysaerobic zone is formed by low-diversity benthic associations which are dominated by nuculids. As deposit-feeders they are regarded as K-strategists (see Levinton, 1972). Deep infaunal forms are absent which is also true for the following two zones. Faunal densities are considerably tuned down in comparison with the aerobic zone.

Nuculid bivalves formed an integral part of oxygen-controlled communities since the Late Paleozoic and can be traced as a dominant component of this environment until mid Jurassic times. This evolutionary conservative bivalve group (Levinton, 1974) was obviously able to thrive successfully in

longer-term stable environments with the position of the O_2/H_2S interface only a few centimeters below the surface of the substrate;

c- the lower dysaerobic zone harbours low-diversity benthic associations, which almost exclusively consist of epifaunal filter-feeders. The fauna becomes increasingly dominated by r-strategists, which belong to the group of small, flat-valved pectinaceans. Also organisms which incorporate chemo-autotrophic bacteria as symbionts gain in importance.

Besides the *Posidonotis cancellata* association from the Liassic of Chile, similarly structured associations are known from Europe which occur in sediments of the same age. These are Kauffman's '*Posidonia*' paleocommunity from the Posidonienschiefer (Kauffman, 1981), an analogous benthic fauna from the lower Opalinuston (Aalenian) of Switzerland (Etter, 1990), and the fauna of the bituminous shale facies of northern England (Morris, 1979; 1980);

d- an anaerobic zone is characterized by the complete absence of benthic organisms and a rich ammonite fauna.

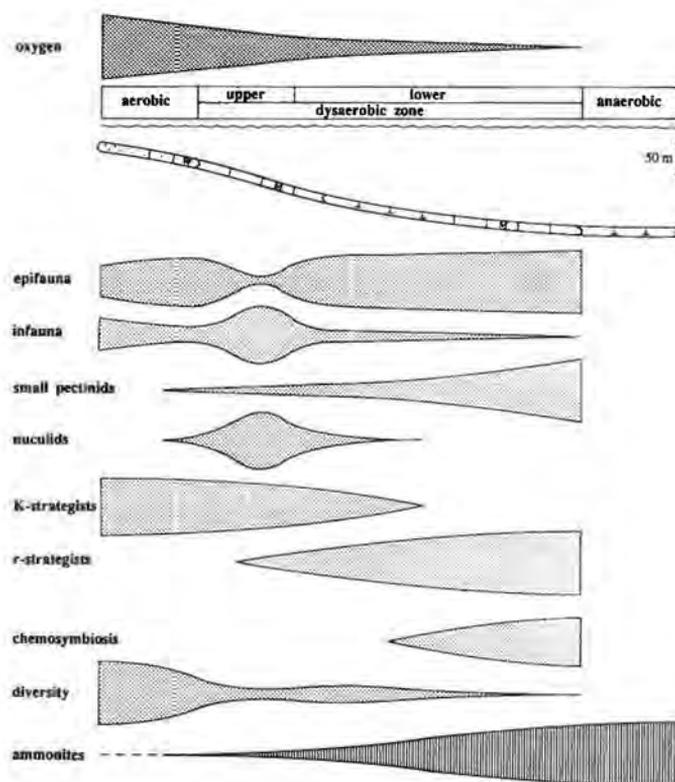


FIG. 11. Faunal distribution along an oxygen gradient. For explanations see text.

ENVIRONMENTAL SIGNIFICANCE OF GUILD-ASSEMBLAGES

From the spatial distribution of associations (Fig. 5) it becomes evident that, as a rule, associations and assemblages can be clearly assigned to one out of four environmental subdivisions of the ramp. In other words, benthic associations are fairly useful indicators of bathymetry. This appears to be in contrast to other studies (e.g. Fürsich, 1976), which showed that different associations were occupying similar environments and similar associations lived in different environments. Accordingly, the macroinvertebrate fauna by its own is not regarded as a useful tool interpreting bathymetry (Fürsich, 1976).

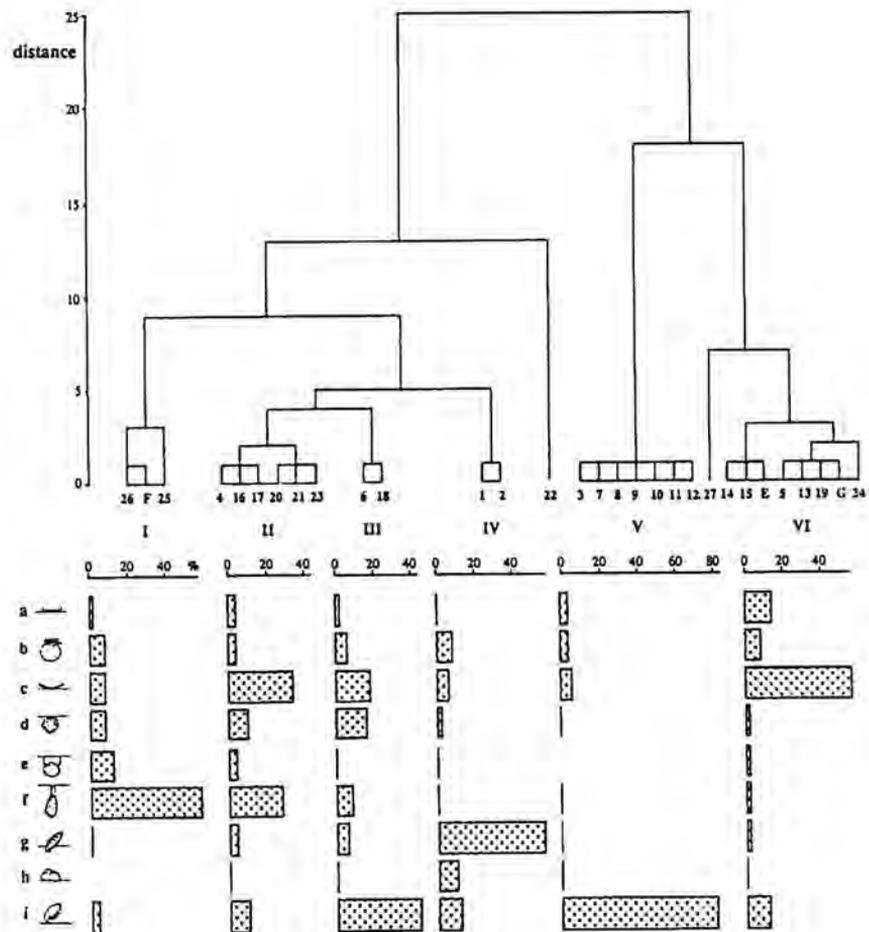
The relatively low bathymetric significance of associations e.g. from the Corallian of England and Normandy (Fürsich, 1976) is interpreted to be due to a morphologically more differentiated sea floor,

exhibiting subtidal and near-intertidal sand bars, shoals, shallow lagoons and an offshore shelf environment. In addition, variations in depth of these shallow water habitats have been on y moderate. In contrast, the ramp model proposed here for the Early Jurassic of northern Chile is characterized by a morphologically rather uniform, gently dipping sea floor and by a water depth ranging from a few meters to at least several tens of meters. Consequently, these differences in the suitability of associations for bathymetric interpretations can be explained by two differing models of platform topography. On a ramp, environmental factors are distributed more linear than on a morphologically strongly subdivided shelf and correspondingly this is reflected in the faunal distribution.

FIG. 12.

Dendrogram of a Q-mode cluster-analysis (hierarchical agglomerative method after Ward, program SPSS/PC+) and guild-composition of resulting guild-assemblages (I-VI). Associations (1-27) and assemblages (E-G) are cases; guilds are variables:

- a = cemented epifaunal suspension-feeder
- b = epibyssate suspension-feeder
- c = free-lying epifaunal suspension-feeder
- d = shallow infaunal suspension-feeder
- e = infaunal surface deposit and/or suspension-feeder
- f = deep infaunal suspension-feeder
- g = semi-infaunal suspension-feeder
- h = epifaunal herbivore and/or detritus-feeder
- i = pedunculate suspension-feeder.



GUILD-ASSEMBLAGES IN THE EARLY JURASSIC OF CHILE

To explore the relationship between benthic fauna and environments still further, it will be examined whether the associations of a particular subenvironment can be characterized by a specific guild-structure and whether the complexity of adaptive strategies varies between the four subenvironments. For this purpose, the relative percentage of guilds has been calculated for each association and assemblage. Subsequently, the associations have been grouped into guild-assemblages by means of a Q-mode cluster-analysis with the relative abundances of guilds serving as variables (Fig. 12). Each of the resulting six guild-assemblages groups together related associations with a very similar percentage of the various guilds. In contrast to associations which are defined on the basis of relative abundances of taxa only, this classification adds a further dimension to environmental interpretation since guild-assem-

blages stress the ecological structure of the benthic fauna.

The dendrogram of figure 12 reveals, that only two associations, the *Nuculana ovum* association and the *Posidonotis cancellata* association, cannot be assigned to any of the identified guild-assemblages. All other associations exhibit a high degree of similarity to, at least, one other association. This becomes most evident in guild-assemblage V, in which seven associations - all of them strongly dominated by pedunculate, suspension-feeding brachiopods - are grouped together. The relative abundance of guilds in other guild-assemblages can be depicted from figure 12.

Next, the spatial distribution of associations from a single guild-assemblage shall be examined. In the majority of cases the associations forming a guild-assemblage can be assigned to the same environmental subdivision (Fig. 5). However, all environments harboured faunas from more than a single guild-assemblage. The shallow siliciclastic ramp carried

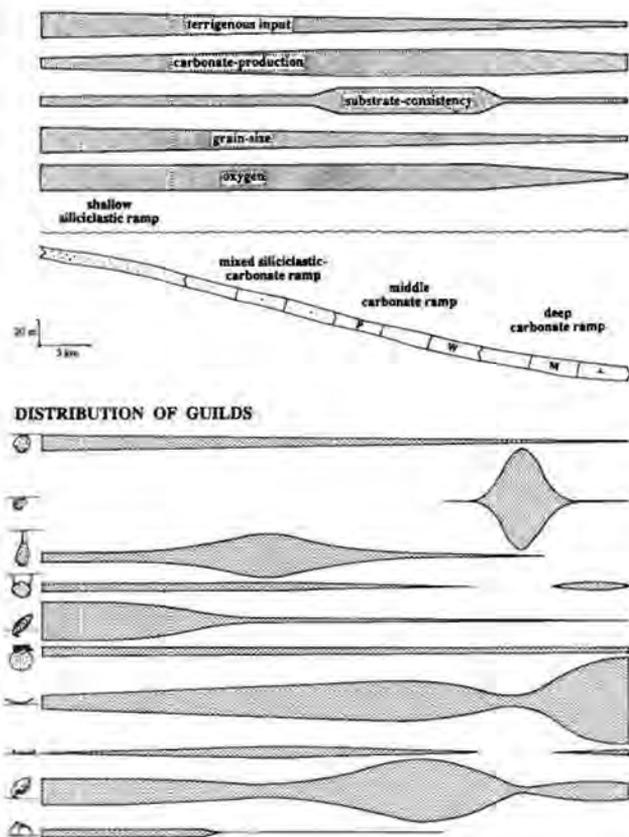


FIG. 13. Onshore-offshore changes of environmental factors and semi-quantitative distribution of guilds on an Early Jurassic ramp of northern Chile. For key of guilds see figure 12. Second guild from above; shallow infaunal deposit-feeder.

representatives of guild-assemblage III and IV, which are characterized by the dominance of pedunculate filter-feeders and semi-infaunal filter-feeders respectively. The mixed siliciclastic-carbonate ramp was the preferred habitat of guild-assemblages I and II, which exhibit high abundances of deep infaunal filter-feeders and epifaunal free-lying filter-feeders. The middle carbonate ramp harboured guild-assemblages V and the majority of associations of VI, which are dominated by pedunculate and epifaunal, free-lying suspension-feeders respectively. Finally, the deep carbonate ramp was inhabited by a minor part of guild-assemblage VI and the associations 22 and 27, which could not be assigned to any of the established guild-assemblages and are characterized by the extreme dominance of a single guild. The distribution of guilds along an onshore-offshore gradient and their relative importance are illustrated in figure 13.

DISCUSSION

The good correlation of guild-assemblages and facies zones proves, that they can be used as environmental indicators. This is particularly true of depositional settings with a fairly linear distribution of environmental factors. This is the case on platforms with a ramp topography, as discussed in this study. It also might be expected on the continental slope or in deep sea basins, if rather linear environmental

gradients exist, *e.g.* with regard to bathymetry and distance from a sediment source.

In general, the number of dominant guilds is higher and the guild-spectrum within associations is broader in the more onshore habitats of the shallow siliciclastic and mixed ramp as compared to the offshore settings of the middle and deep carbonate ramp (Fig. 13). This can be explained by a relatively high degree of environmental heterogeneity in more onshore settings. There, important environmental factors such as rate of sedimentation, consistency and stability of the substrate, water energy, salinity, temperature, and supply with nutrients are subject to stronger temporal and spatial fluctuations than in more offshore habitats. Accordingly, the specific composition of a given association is thought to reflect a distinct combination of environmental conditions within a multi-dimensional continuum of environmental factors.

In contrast, the low variability in guild-composition on the middle ramp corresponds to a spatially and temporally more homogeneous environment. Due to a consolidated substrate, only the niches on top of the substrate could be occupied in high densities. Finally, in the deep ramp, the high dominance of a single guild within associations indicates a high-stress environment. Under these rigorous conditions ecospace has been utilized considerably less intensely than in the more hospitable environments further onshore.

SPATIAL DISTRIBUTION OF BIVALVES VERSUS BRACHIOPODS

Faunal samples from the Early Jurassic of northern Chile most commonly are either dominated by bivalves or by articulate brachiopods. However, while bivalve-dominated associations occurred in all four environmental subdivisions of the ramp, brachiopod-dominated associations are restricted to the middle carbonate ramp (Fig. 13). In order to achieve a more thorough understanding of this distribution pattern, the biological adaptations and requirements of both groups shall be briefly discussed below.

In most quantitative paleoecological studies of Jurassic benthic macroinvertebrates, brachiopod-dominated associations are rare or absent (*e.g.* Duff, 1975; Fürsich, 1977; 1984b; Fürsich and Werner, 1986; Oschmann, 1988; Wignall, 1990a; Heinze,

1991). On the other hand, brachiopods occur in high abundances in eastern Europe (*e.g.* Tchoumatchenco, 1972; Dzik, 1979; Heliasz and Racki, 1980), in the submediterranean province (Fürsich and Sykes, 1977), and in some other parts of Europe (see Ager, 1965). In contrast to the more eurytopic bivalves (*e.g.* Rudwick, 1970; Steele-Petrovic, 1979) the occurrence of brachiopods in high abundances appears to be bound to a specific combination of environmental parameters.

Above all, a stable and firm substrate is regarded as an important prerequisite for a successful survival of brachiopods (see also Aberhan, 1992, p. 71). Articulate brachiopods further require a relatively stable environment. They are largely excluded from

environments with fluctuating or extreme conditions concerning oxygen supply or salinity. Due to their fixo-sessile life habitat they are restricted to environments with low to moderate rates of sedimentation. In particular, they avoid habitats in which mud and silt are actively deposited (Rudwick, 1970). Jurassic articulate brachiopods presumably had a non planktotrophic larval development (Valentine and Jablonski, 1983) and therefore a lower dispersal potential than planktotrophic bivalves. In contrast to bivalves, brachiopods failed to develop mechanisms to cope with advanced predators such as thick shells, spines, and swimming ability. In summary, the adaptable superiority of eurytopic bivalves over more stenotopic brachiopods appears to provide a plausible explanation for the observed distribution pattern of both groups (see also Stanley, 1974; Gould and Calloway, 1980; Thayer, 1985; Rhoads and Thayer, 1991).

Having these factors in mind, the striking abundance of brachiopods on the Early Jurassic middle carbonate ramp of northern Chile becomes more plausible. This fully marine environment was

characterized by a reduced input of terrigenous material and the accumulation of skeletal hardparts caused by a high rate of carbonate production, moderate winnowing of fine-grained sediment and low rates of sedimentation. This resulted in a stable and consolidated substrate. Relative distance from the shore, bathymetric position, and a fairly constant, moderate to low energy level guaranteed a relatively high stability and predictability of living conditions.

Competition with epifaunal bivalves for space may well have occurred and possibly is reflected in the fluctuating dominance pattern of both groups. However, also other biological factors such as the activities of predators or stochastic influences in the recruitment of larvae may have played an important role. Furthermore, variations in relative abundance of taxa can also be due to slight fluctuations of physical environmental parameters such as temperature, light, water energy, or primary production (e.g. Rees *et al.*, 1977; Buchanan *et al.*, 1978; Gray, 1977; 1984), which normally remain undetected in the fossil record.

CONCLUSIONS

- The Early Jurassic of northern Chile is represented by shallow to deep subtidal marine environments. The depositional system has been reconstructed as a homoclinal ramp. Reflecting the distribution of environmental factors (water energy, input of terrigenous material, carbonate production, oxygen supply, and others), four depositional facies have been recognized: shallow siliciclastic ramp, mixed siliciclastic-carbonate ramp, middle carbonate ramp, and deep carbonate ramp.
- Benthic associations can clearly be assigned to distinct subenvironments on a ramp. Furthermore, guild-assemblages proved to be of high environmental significance in environments with a relatively linear distribution of environmental factors, as is the case on a ramp.
- In the Early Jurassic of Chile the more onshore shallow siliciclastic and mixed siliciclastic-carbonate ramp harboured highly-diverse associations which indicate hospitable, low-stress conditions. They were dominated by K-strategists which belong to semi-infaunal, deep infaunal, and epifaunal, free-lying filter-feeders.
- Further offshore, reduced input of terrigenous material and low rates of sedimentation characterized the middle carbonate ramp. It was colonized by associations dominated by epifaunal free-lying bivalves or articulate brachiopods. As a stenotopic group which depended on a relatively firm and stable substrate, stable and normal marine oxygen and salinity conditions, and low to moderate sedimentation rates, articulate brachiopods were able to thrive on the consolidated substrates of this subenvironment.
- In the offshore habitats of the deep carbonate ramp, a low-diversity benthic fauna has been controlled by low oxygen concentrations. Three associations and one assemblage can be assigned to a long-term stable dysoxic environment. According to the position of the O_2/H_2S interface, they can be arranged qualitatively along an oxygen gradient. An upper dysaerobic biofacies zone has been recognized, which is dominated by deposit-feeding nuculid bivalves. In the lower dysaerobic zone thin-shelled, flat-valved filter-feeding pectinacean bivalves prevailed exhibiting an opportunistic larval strategy.

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APPENDIX 1

TROPHIC NUCLEI OF THE BENTHIC ASSOCIATIONS AND ASSEMBLAGES OCCURRING IN THE EARLY JURASSIC OF NORTHERN CHILE. Life habit: E = epifaunal; ls = shallow infaunal; ld = deep infaunal; SI = semi-infaunal; b = byssate; bo = boring; c = cemented; f = free-lying; m = mobile; p = pedunculate. Trophic group: D = deposit-feeder; H = grazing herbivore or detritus-feeding; MC = microcarnivore; S = suspension-feeder; SDS = surface deposit- and/or suspension-feeder. Diversity values: N = range of species richness, mean values in brackets; D = evenness.

Species	rel. abundance %	presence %	life habit	trophic group
1 <i>Gervillella araucana</i> association				
(2 samples; 239 individuals; N = 14-19 (16.5); D = 3.9; facies C)				
<i>Gervillella araucana</i> Damborenea, 1987b	46.0	100.0	SI	S
<i>Parallelodon hirsonensis</i> (d'Archiac, 1843)	18.8	100.0	SI	S
<i>Bakevellia (Bakevellia) waltoni</i> (Lycett, 1863)	6.7	100.0	SI	S
<i>Modiolus (Modiolus) giganteus</i> Quenstedt, 1857	6.2	100.0	Eb	S
<i>Lithotrochus ? andinus</i> (Möricke, 1894)	4.2	100.0	Em	H
2 <i>Parallelodon hirsonensis</i> association (see figure 6)				
(3 samples; 371 individuals; N = 13-21 (16.6); D = 10.6; facies C)				
<i>Lobothyris</i> cf. <i>ovatissima</i> Quenstedt, 1858	22.1	100.0	Ep	S
<i>Parallelodon hirsonensis</i> (d'Archiac, 1843)	17.8	100.0	SI	S
<i>Gervillella araucana</i> Damborenea, 1987b	12.1	100.0	SI	S
<i>Bakevellia (Bakevellia) waltoni</i> (Lycett, 1863)	10.8	100.0	SI	S
<i>Modiolus (Modiolus) giganteus</i> Quenstedt, 1857	4.3	100.0	Eb	S
<i>Striactaeonina transatlantica</i> (Behrendsen, 1891)	4.3	66.7	Em	H
high-spired gastropod	3.5	33.3	?Em	?H
<i>Lithotrochus? andinus</i> (Möricke, 1894)	3.5	100.0	Em	H
<i>Cardinia andium</i> (Giebel, 1861)	3.2	33.3	ls	S
3 <i>Lobothyris</i> cf. <i>ovatissima</i> association				
(35 samples; 4553 individuals; N = 5-15 (9.1); D = 1.6; facies D, E)				
<i>Lobothyris</i> cf. <i>ovatissima</i> Quenstedt, 1858	78.9	100.0	Ep	S
<i>Quadratihynchia crassimedia</i> Buckman, 1918	3.4	57.1	Ep	S
4 <i>Pholadomya hemicardia</i> association				
(2 samples; 236 individuals; N = 11-12 (11.5); D = 3.4; facies D)				
<i>Pholadomya (Pholadomya) hemicardia</i> Roemer, 1836	35.6	100.0	ld	S
<i>Entolium (Entolium) comeolum</i> (Young and Bird, 1828)	19.9	100.0	Ef	S
<i>Lobothyris</i> cf. <i>ovatissima</i> Quenstedt, 1858	14.4	100.0	Ep	S
<i>Weyla (Weyla) alata</i> (von Buch, 1838)	14.0	100.0	Ef	S
<i>Pachymya (Arcomya) sp. A</i>	5.9	100.0	ld	S
5 <i>Weyla alata/Lobothyris</i> cf. <i>ovatissima</i> association				
(6 samples; 544 individuals; N = 8-17 (11.8); D = 5; facies E)				
<i>Weyla (Weyla) alata</i> (von Buch, 1838)	38.1	100.0	Ef	S
<i>Lobothyris</i> cf. <i>ovatissima</i> Quenstedt, 1858	17.3	100.0	Ep	S
<i>Plagiostoma laeviusculum</i> J. Sowerby, 1822	11.0	83.3	Eb	S
<i>Pholadomya (Pholadomya) hemicardia</i> Roemer, 1836	6.1	66.7	ld	S
<i>Chlamys (Chlamys) textoria</i> (Schlotheim, 1820)	5.3	66.7	Eb	S
<i>Entolium (Entolium) comeolum</i> (Young and Bird, 1828)	3.3	100.0	Ef	S

Species	rel. abundance %	presence %	life habit	trophic group
6 <i>Protocardia</i> sp. A association				
(8 samples; 975 individuals; N = 12-16 (13.0); D = 5.1; facies C)				
<i>Lobothyris</i> cf. <i>ovatissima</i> Quenstedt, 1858	39.3	100.0	Ep	S
<i>Protocardia</i> (<i>Protocardia</i>) sp. A	13.3	75.0	Is	S
<i>Anisocardia</i> sp. A	10.5	75.0	Is	S
<i>Modiolus</i> (<i>Modiolus</i>) <i>giganteus</i> Quenstedt, 1857	8.6	100.0	Eb	S
<i>Entolium</i> (<i>Entolium</i>) <i>comeolum</i> (Young and Bird, 1828)	8.5	62.5	Ef	S
<i>Pleuromya</i> <i>uniformis</i> (J. Sowerby, 1813)	2.6	50.0	Id	S
7 <i>Quadratirhynchia crassimedia</i> association				
(5 samples; 633 individuals; N = 7-13 (10.2); D = 3.1; facies E)				
<i>Quadratirhynchia crassimedia</i> Buckman, 1918	46.0	100.0	Ep	S
<i>Lobothyris</i> cf. <i>ovatissima</i> Quenstedt, 1858	31.9	100.0	Ep	S
<i>Gibbirhynchia curviceps</i> (Quenstedt, 1858)	9.0	80.0	Ep	S
8 <i>Gibbirhynchia curviceps</i> association				
(3 samples; 607 individuals; N = 8-12 (9.7); D = 1.7; facies E)				
<i>Gibbirhynchia curviceps</i> (Quenstedt, 1858)	74.3	100.0	Ep	S
<i>Quadratirhynchia crassimedia</i> Buckman, 1918	13.8	100.0	Ep	S
9 <i>Spiriferina chilensis</i> association (see figure 8)				
(15 samples; 1884 individuals; N = 7-14 (10.0); D = 2.4; facies E)				
<i>Spiriferina chilensis</i> (Forbes, 1846)	63.2	100.0	Ep	S
<i>Lobothyris</i> cf. <i>ovatissima</i> Quenstedt, 1858	14.1	80.0	Ep	S
<i>Weyla</i> (<i>Weyla</i>) <i>elata</i> (von Buch, 1838)	3.6	93.3	Ef	S
10 <i>Lobothyris subpunctata</i> association				
(16 samples; 2102 individuals; N = 5-13 (7.5); D = 1.7; facies E)				
<i>Lobothyris subpunctata</i> (Davidson, 1851)	76.6	100.0	Ep	S
<i>Weyla</i> (<i>Weyla</i>) <i>elata</i> (von Buch, 1838)	8.0	93.6	Ef	S
11 <i>Quadratirhynchia</i> sp. A association				
(16 samples; 1844 individuals; N = 5-17 (11.3); D = 3.4; facies E)				
<i>Quadratirhynchia</i> sp. A	51.8	100.0	Ep	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	12.6	93.8	Ep	S
<i>Weyla</i> (<i>Weyla</i>) <i>elata</i> (von Buch, 1838)	6.9	100.0	Ef	S
<i>Weyla</i> (<i>Weyla</i>) <i>litan</i> (Möncke, 1894)	4.0	68.8	Ef	S
<i>Exogyra</i> sp. A	3.6	43.8	Ec	S
<i>Plagiostoma laeviusculum</i> J. Sowerby, 1822	3.3	93.8	Eb	S
12 <i>Lobothyris subpunctata/Quadratirhynchia</i> sp. A association				
(10 samples; 1329 individuals; N = 7-14 (10.1); D = 3.5; facies E)				
<i>Lobothyris subpunctata</i> (Davidson, 1851)	47.9	100.0	Ep	S
<i>Quadratirhynchia</i> sp. A	22.9	100.0	Ep	S
<i>Montlivaltia</i> sp.	4.5	70.0	Ec	MG
<i>Weyla</i> (<i>Weyla</i>) <i>elata</i> (von Buch, 1838)	3.8	80.0	Ef	S
<i>Spiriferina chilensis</i> (Forbes, 1846)	2.9	20.0	Ep	S

Species	rel. abundance %	presence %	life habit	trophic group
13 <i>Exogyra</i> sp. A association (10 samples; 1246 individuals; N=12-19 (14.6); D=8.1; facies E)				
<i>Exogyra</i> sp. A	23.5	100.0	Ec	S
<i>Weyla</i> (<i>Weyla</i>) <i>alata</i> (von Buch, 1838)	16.1	100.0	Ef	S
<i>Weyla</i> (<i>Weyla</i>) <i>titan</i> (Mörnicke, 1894)	15.9	90.0	Ef	S
<i>Plagiostoma laeviusculum</i> J. Sowerby, 1822	7.0	100.0	Eb	S
<i>Chlamys</i> (<i>Chlamys</i>) <i>textoria</i> (Schlotheim, 1820)	6.3	90.0	Eb	S
<i>Ctenostreon wrighti</i> Bayle, 1878	5.4	90.0	Ef	S
<i>Quadratirhynchia</i> sp. A	4.4	60.0	Ep	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	3.1	60.0	Ep	S
14 <i>Weyla</i> association (4 samples; 5-2 individuals; N=4-13 (9.0); D=2.7; facies E)				
<i>Weyla</i> (<i>Weyla</i>) <i>alata</i> (von Buch, 1838)	54.3	100.0	Ef	S
<i>Weyla</i> (<i>Weyla</i>) <i>titan</i> (Mörnicke, 1894)	12.5	75.0	Ef	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	8.4	75.0	Ep	S
<i>Quadratirhynchia</i> sp. A	4.7	50.0	Ep	S
<i>Exogyra</i> sp. A	4.3	75.0	Ec	S
15 <i>Entolium comeolum</i> association (3 samples; 740 individuals; N = 7-16 (10.9); D = 3.2; facies E)				
<i>Entolium</i> (<i>Entolium</i>) <i>comeolum</i> (Young and Bird, 1828)	40.8	100.0	Ef	S
<i>Weyla</i> (<i>Weyla</i>) <i>alata</i> (von Buch, 1838)	38.1	100.0	Ef	S
<i>Montivaltia</i> sp.	2.8	51.7	Ec	MC
16 <i>Pachymya rotundocaudata</i> association (3 samples; 349 individuals; N = 21-29 (25.7); D = 14.4; facies D)				
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	15.5	100.0	ld	S
<i>Pachymya</i> (<i>Pachymya</i> ?) <i>rotundocaudata</i> (A. Leanza, 1942)	13.8	100.0	ld	S
<i>Cardinia andium</i> (Giebel, 1861)	8.3	100.0	ls	S
<i>Weyla</i> (<i>Weyla</i>) <i>alata</i> (von Buch, 1838)	7.4	100.0	Ef	S
<i>Rudirhynchia</i> aff. <i>rudis</i> Buckman, 1918	5.2	100.0	Ep	S
<i>Gryphaea</i> (<i>Gryphaea</i>) <i>darwini</i> (Forbes, 1846)	4.9	100.0	Ef	S
<i>Tetrahynchia tetrahedra</i> (J. Sowerby, 1812)	4.9	66.7	Ep	S
<i>Pseudotraperzium ancaturzi</i> (A. Leanza, 1942)	4.0	100.0	ls	S
<i>Pinna</i> (<i>Pinna</i>) cf. <i>radiata</i> Münster, 1837	3.7	100.0	Sl	S
<i>Pholadomya</i> (<i>Pholadomya</i>) <i>fidicula</i> (J. Sowerby, 1821)	3.4	66.7	ld	S
<i>Protocardia</i> (<i>Protocardia</i>) <i>striatula</i> (J. de C. Sowerby)	3.2	66.7	ls	S
<i>Chlamys</i> (<i>Chlamys</i>) <i>textoria</i> (Schlotheim, 1820)	2.9	66.7	Eb	S
<i>Pholadomya</i> (<i>Pholadomya</i>) <i>corrugata</i> Koch and Dunker, 1877	2.6	66.7	ld	S
<i>Plagiostoma laeviusculum</i> J. Sowerby, 1822	2.0	100.0	Eb	S
17 <i>Pleuromya uniformis</i> association (8 samples; 1068 individuals; N = 9-34 (23.0); D = 7.9; facies D)				
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	28.3	100.0	ld	S
<i>Weyla</i> (<i>Weyla</i>) <i>alata</i> (von Buch, 1838)	18.3	100.0	Ef	S
<i>Protocardia</i> (<i>Protocardia</i>) <i>striatula</i> (J. de C. Sowerby)	6.5	87.5	ls	S

Species	rel. abundance %	presence %	life habit	trophic group
<i>Pholadomya (Pholadomya) corrugata</i> Koch and Dunker, 1877	4.3	62.5	ld	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	3.9	87.5	Ep	S
<i>Cardinia andium</i> (Giebel, 1861)	3.5	62.5	ls	S
<i>Plagiostoma laeviusculum</i> J. Sowerby, 1822	2.8	87.5	Eb	S
<i>Tetrahyntia tetrahedra</i> (J. Sowerby, 1812)	2.4	62.5	Ep	S
<i>Montlivaltia</i> sp.	2.3	62.5	Ec	MC
<i>Mesomiltha bellona</i> (d'Orbigny, 1850)	2.3	62.5	ld	SDS
<i>Ctenostreon wrighti</i> Bayle, 1878	2.2	100.0	Ef	S
<i>Pinna (Pinna) cf. radiata</i> Münster, 1837	2.2	100.0	Sl	S
<i>Rudirhynchia aff. rudis</i> Buckman, 1918	2.2	50.0	Ep	S
18 <i>Lobothyris subpunctata/Rudirhynchia aff. rudis</i> association (4 samples; 489 individuals; N = 14-18 (15.5); D = 5.0; facies E)				
<i>Lobothyris subpunctata</i> (Davidson, 1851)	39.5	100.0	Ep	S
<i>Weyla (Weyla) alata</i> (von Buch, 1838)	15.7	100.0	Ef	S
<i>Rudirhynchia aff. rudis</i> Buckman, 1918	8.8	100.0	Ep	S
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	8.6	100.0	ld	S
<i>Gervillaria pallas</i> (A. Lanza, 1942)	4.7	50.0	Sl	S
<i>Gryphaea (Gryphaea) darwini</i> (Forbes, 1846)	3.1	75.0	Ef	S
19 <i>Gryphaea</i> sp. A association (see figure 10) (4 samples; 414 individuals; N = 5-15 (9.5); D = 4.0; facies F)				
<i>Gryphaea</i> sp. A	45.7	100.0	Ef	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	15.5	75.0	Ep	S
<i>Rudirhynchia aff. rudis</i> Buckman, 1918	10.9	75.0	Ep	S
<i>Entolium (Entolium) corneolum</i> (Young and Bird, 1828)	6.0	50.0	Ef	S
<i>Actinostreon soliarium</i> (J. de C. Sowerby, 1824)	5.1	75.0	Ec	S
20 <i>Weyla alata/Entolium corneolum</i> association (see figure 7) (11 samples; 1254 individuals; N = 14-29 (19.0); D = 7.4; facies D)				
<i>Weyla (Weyla) alata</i> (von Buch, 1838)	32.2	100.0	Ef	S
<i>Entolium (Entolium) corneolum</i> (Young and Bird, 1828)	12.2	100.0	Ef	S
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	6.1	90.9	ld	S
<i>Montlivaltia</i> sp.	5.8	81.8	Ec	MC
<i>Pholadomya (Pholadomya) corrugata</i> Koch and Dunker, 1877	5.4	72.7	ld	S
<i>Pinna (Pinna) cf. radiata</i> Münster, 1837	4.5	100.0	Sl	S
<i>Gryphaea (Gryphaea) cf. darwini</i> (Forbes, 1846)	3.8	72.7	Ef	S
Arcticidae gen. et sp. nov.	3.4	81.8	ls	S
' <i>Terebratula</i> ' sp. A	3.2	36.4	Ep	S
<i>Mesomiltha bellona</i> (d'Orbigny, 1850)	2.5	63.6	ld	SDS
<i>Quadrirhynchia</i> sp. B	2.5	45.5	Ep	S
21 <i>Mesomiltha bellona</i> association (3 samples; 697 individuals; N = 9-40 (26.8); D = 12.9; facies D)				
<i>Mesomiltha bellona</i> (d'Orbigny, 1850)	16.2	100.0	ld	SDS
<i>Weyla (Weyla) alata</i> (von Buch, 1838)	13.1	100.0	Ef	S
<i>Entolium (Entolium) corneolum</i> (Young and Bird, 1828)	11.5	100.0	Ef	S
<i>Gryphaea (Gryphaea) cf. darwini</i> (Forbes, 1846)	9.2	66.7	Ef	S

Species	rel. abundance %	presence %	life habit	trophic group
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	5.5	100.0	ld	S
<i>Myophorella</i> (<i>Myophorella</i>) <i>araucana</i> (A. Leanza, 1942)	5.0	66.7	ls	S
<i>Pholadomya</i> (<i>Pholadomya</i>) <i>corrugata</i> Koch and Dunker, 1877	4.7	66.7	ld	S
' <i>Terebratula</i> ' sp. A	4.2	66.7	Ep	S
<i>Montivaltia</i> sp.	3.6	66.7	Ec	MC
' <i>Terebratula</i> ' sp. B	3.0	66.7	Ep	S
<i>Pholadomya</i> (<i>Pholadomya</i>) <i>fidicula</i> (J. Sowerby, 1821)	2.3	100.0	ld	S
<i>Quadratirhynchia</i> sp. B	2.0	66.7	Ep	S
22 <i>Nuculana ovum</i> association (see figure 10)				
(4 samples; 563 individuals; N = 3-7 (4.8); D = 1.4; facies F)				
<i>Nuculana</i> (<i>Nuculana</i>) <i>ovum</i>	85.3	100.0	Im	D
23 <i>Gryphaea darwini</i> association				
(6 samples; 1079 individuals; N = 9-19 (15.3); D = 5.5; facies D, L)				
<i>Gryphaea</i> (<i>Gryphaea</i>) <i>darwini</i> (Forbes, 1846)	37.3	100.0	Ef	S
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	15.6	100.0	ld	S
<i>Rhynchonelloidea</i> sp. A	9.4	100.0	Ep	S
<i>Actinostreon solitarium</i> (J. de C. Sowerby, 1824)	7.0	100.0	Ec	S
<i>Lithophaga</i> sp.	3.9	16.7	lbo	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	3.9	83.3	Ep	S
<i>Vaugonia</i> (<i>Vaugonia</i>) <i>exotica</i> (Mörnicke, 1894)	3.4	66.7	ls	S
24 <i>Actinostreon solitarium</i> association				
(3 samples; 545 individuals; N = 7-13 (9.7); D = 3.0; facies D)				
<i>Actinostreon solitarium</i> (J. de C. Sowerby, 1824)	54.2	100.0	Ec	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	11.0	33.3	Ep	S
<i>Gryphaea</i> (<i>Gryphaea</i>) <i>darwini</i> (Forbes, 1846)	10.4	100.0	Ef	S
<i>Entolium</i> (<i>Entolium</i>) <i>comeolum</i> (Young and Bird, 1828)	9.3	100.0	Ef	S
25 <i>Mesomiltha ? huayquimili</i> association				
(3 samples; 435 individuals; N = 12-17 (15.0); D = 6.9; facies D)				
<i>Mesomiltha ? huayquimili</i> (A. Leanza, 1942)	29.0	100.0	ld	SDS
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	20.9	100.0	ld	S
<i>Modiolus</i> (<i>Modiolus</i>) <i>imbricatus</i> J. Sowerby, 1818	6.0	100.0	Eb	S
<i>Vaugonia</i> (<i>Vaugonia</i>) <i>exotica</i> (Mörnicke, 1894)	5.7	66.7	ls	S
<i>Gresslya peregrina</i> (Phillips, 1829)	5.5	100.0	ld	S
<i>Chlamys</i> (<i>Chlamys</i>) <i>textoria</i> (Schlotheim, 1820)	3.9	66.7	Eb	S
<i>Gryphaea</i> (<i>Gryphaea</i>) <i>darwini</i> (Forbes, 1846)	3.9	100.0	Ef	S
<i>Lobothyris subpunctata</i> (Davidson, 1851)	3.9	66.7	Ep	S
<i>Mesomiltha bellona</i> (d'Orbigny, 1850)	3.4	33.3	ld	SDS
26 <i>Gresslya peregrina</i> association				
(3 samples; 579 individuals; N = 15-26 (19); D = 5.9; facies D)				
<i>Gresslya peregrina</i> (Phillips, 1829)	28.2	100.0	ld	S
<i>Pleuromya uniformis</i> (J. Sowerby, 1813)	21.2	100.0	ld	S
<i>Pholadomya</i> (<i>Pholadomya</i>) <i>fidicula</i> (J. Sowerby, 1821)	20.0	100.0	ls	S

Species	rel. abundance %	presence %	life habit	trophic group
<i>Cercomya (Cercomya) undulata</i> (J. de C. Sowerby, 1827)	3.6	100.0	Id	S
<i>Mesomiltha bellona</i> (d'Orbigny, 1850)	3.5	100.0	Id	SDS
<i>Modiolus (Modiolus) imbricatus</i> J. Sowerby, 1818	3.5	100.0	Eb	S
27 <i>Posidonotis cancellata</i> association (see figure 10)				
(4 samples; 599 individuals; N = 1-3 (2.0); D = 1.0; facies G)				
<i>Posidonotis cancellata</i> (A. Leanza, 1943)	98.2	100.0	Eb/f	S

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