Palaeolatitudinal gradients along the southeastern Palaeo-Pacific margin and the distribution of Early Jurassic bivalves

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Abstract. Presence-absence bivalve species data for each Early Jurassic stage along southeastern South America between 20 and 46°S present-day latitude were processed by a set of analytical methods to analyse the palaeolatitudinal patterns of diversity and distribution. The expected decrease in species diversity towards higher latitudes is punctuated by a consistent local diversity increase between 34 and 42°, especially evident during Pliensbachian and Toarcian times, which may be due to an abrupt change in palaeogeography at that latitude, coinciding with the Curicó direct connection to the open ocean and the establishment of an increased variety of habitats within the extensive Neuquén Basin. The proportions of systematic groups show relative increases towards both higher latitudes (Crassatelloidea, Nuculanoidea, Pectinoidea, Monotoidea, Inoceramoidea) and lower latitudes (Trigonioidea, Pholadomyoidea, Limoidea, Lucinoidea). Epifaunal bivalves were dominant during the Hettangian but by Pliensbachian–Toarcian times they were less common than infaunal ones, while semi-infaunal species had low diversities during the whole Early Jurassic. This study suggests that (a) large scale geographical conditions should be taken into account for the analysis of latitudinal diversity trends among benthonic faunas; and (b) latitudinal trends of some living bivalve lineages may have a longer and more complex history than previously thought.

INTRODUCTION

One of the global-scale relationships between biogeography and ecology is the existence of latitudinal gradients in species diversity (Hillebrand, 2004; Krug *et al.*, 2009 and references therein), known both in past and living faunas. Although it is generally acknowledged that the global pattern of decreasing diversity towards higher latitudes may be obscured, disrupted or even altered locally due to several factors, a good deal of research is still needed to evaluate these.

The Jurassic Pacific southeastern palaeo-coast is a good region to study regional palaeolatitudinal faunal changes. The purposes of this paper are: to analyze diversity trends along latitude on the basis of a species distribution dataset, and to try to dissect the results both by systematic and palaeoecological groups, in an attempt to better understand the palaeolatitudinal faunal changes in the light of the regional palaeogeographical setting.

Bivalves have been fundamental in the investigation of the nature and origin of latitudinal marine diversity gradients (Crame, 1996a, 2000a, 2000b; Jablonski *et al.*, 2006; Krug *et al.*, 2008; Valentine and Jablonski, 2010, and references therein). Latitudinal diversity gradients are welldocumented for bivalves, both from the continental shelf (Jablonski *et al.*, 2000) and deep sea (Rex *et al.*, 1993, 2000) of the Northern Hemisphere. Roy *et al.* (1998) analysed various previous hypotheses to explain the origin of this major pattern, and concluded that sea surface temperature (as the result of solar energy input) is significantly correlated to the strikingly similar latitudinal gradients observed.

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The pattern of latitudinal diversity gradients shown by modern marine bivalves is not simple and it does not appear to be symmetric in both hemispheres (Rex *et al.*, 1993; Crame, 2000a, 2000b; Jablonski *et al.*, 2013). Even an inverse gradient is also regionally known for some groups (Valdovinos *et al.*, 2003; Kindlmann *et al.*, 2007; Kiel, Nielsen, 2010) along the Chilean coast. The latitudinal gradients in biodiversity are not easy to interpret because they are strongly influenced by local conditions and the history of the regions concerned (Crame, 2000b; Rivadeneira *et al.*, 2002), but it was proposed that it is maintained by high tropical origination rates (Valentine, Jablonski, 2010).

The various hypotheses proposed to explain the origin of this pattern are of a general nature and thus imply that this feature should have been present in past biotas as well. Crame (2000a, b) proved that latitudinal gradients in bivalve taxonomic diversity can be traced back to the Late Palaeozoic in both hemispheres, though the gradients were not symmetric. Furthermore, he observed that Late Palaeozoic and Late Jurassic diversity gradients were weaker than present ones (Crame, 2001, 2002), and there was a dramatic increase in these gradients during the Cenozoic.

Apart from the well-known and universally recognized diversity gradient, knowledge about other latitudinal gradients (related for instance to taxonomy, functional groups, size, speciation rates, extinction rates or intraspecific variability) is still patchy, but again living bivalves provide good arguments for their discussion (Crame, 2000a; Berke et al., 2012; Jablonski et al., 2013). Not surprisingly, many of the trends observed are not amenable to generalization since they vary between hemispheres and among coastlines, hinting at multiple and complex causes. In this context, data from the fossil record could help to test hypotheses based on living faunas. Most authors agree that patterns are more regular in the Northern Hemisphere (Rex et al., 1993; Crame, 2000a, 2000b), which is also the best known, and new data from the Southern Hemisphere in particular are needed to discuss the nature and origin of such asymmetry.

MATERIAL AND METHODS

DATASET

The distribution of bivalve species in about 200 localities from Chile and Argentina between 20 and 45°S was recorded for the four Early Jurassic stages: Hettangian, Sinemurian, Pliensbachian and Toarcian (Appendix 1¹). Though it is possible to analyse shorter time intervals for the distribution of Early Jurassic bivalves from the Neuquén Basin (Argentina), where their time ranges are determined accurately by accompanying ammonites, the same precision is not yet possible for some of the other areas. The Neuquén Basin time-ranges cannot be extrapolated to the whole area since differences may be expected due to the large geographic distances involved. Only 8 localities belong to the Coastal Cordillera of Chile; all the others are in the Andes. Presence-absence data were used throughout, since reliable quantitative records are only available for a small fraction of the occurrences. Data were compiled at the species level for this paper, since firsthand knowledge of the faunas facilitates identification and consistency. However, it should be noted that although species is the most objective of taxonomic units, in global analysis the generic or familial levels are usually preferred (Stehli et al., 1967) to avoid inconsistencies due to compilations by different authors.

The database for the analysis (Appendix 2^2) is a species list showing the distribution of 233 bivalves in thirteen areas (0–12), each with a latitudinal range of 2°, spanning a northsouth strip from 20 to 46°S present-day latitude. The dataset used is updated and thus more complete than a previous one (Damborenea, 1996), and includes information on each species taxonomic affinities as well as life habits. Though the purpose is the consideration of palaeobiogeographic issues, data were initially plotted on their present-day positions to avoid a priori bias and circular reasoning. As pointed out by Rosen (1992), present-day positions are the only universally objective reference for fossil locations available so far.

On the analysis of latitudinal gradients the main interest focuses on distribution limits, so for species that appear at two distant localities it is usual to extend their ranges along the intermediate latitudes. These extended ranges were used in some of the analysis, whilst others were based on the actual records, as explained below.

It is well known that facies control may significantly affect the distribution of some bivalves, and this should be distinguished from regional factors related to latitude. Nevertheless, the large number of records and localities taken into account (comprising a wide range of facies within each area) make this "noise" factor less of a problem.

ANALYTICAL METHODS

Cluster analysis

The first explorative technique here applied is the hierarchical cluster analysis, for which a distance or similarity measure must be chosen (Hammer, Harper, 2006). Our main

¹ See: http://www.voluminajurassica.org/.

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goal was to group together the localities according to their species content, so the Simpson's coefficient of similarity (Simpson, 1943; see also Shi, 1993) was used. This index is totally insensitive to the size of the larger sample, what makes it suitable when there are risks of incomplete sampling (Shi, 1993; Hammer, Harper, 2006), as is the case for our data-base. The localities were not equally treated in the literature, neither have the same abundance of fossils; hence they cannot be considered as equally sampled, making the Simpson's coefficient the most adequate available index of similarity to use. Cluster analysis is an ordination method, grouping elements according to their overall similarity; clusters or groups have no statistical significance associated. A support value can be obtained for the nodes by simply resampling taxa (in this case species) and building a new dendrogram; the proportion of times the node appears on the dendrograms resulting from the resampled matrices is the support value for the node. Although the general grouping and disposition of the localities are evaluated on each analysis, special value is given to groups with similarity values of 0.50 or higher (i.e. 50% of species shared or more) and to groups with support values of 0.50 or higher, as considered in other palaeobiogeographic studies (Brayard et al., 2007; Dera et al., 2011).

For this analysis the use of extended ranges may result in circular reasoning, since the latitudinal gradient would be analyzed presuming its existence; nearby localities would be similar because we assume they share species for being close to each other. To avoid this, cluster analysis was performed on the actually observed presence/absence data; this may produce some sensitivity to differences in knowledge between localities, but that is why Simpson's coefficient was used. Cluster analyses were performed on the software PAST (Hammer *et al.*, 2001).

Distribution limits of species

To check for the faunal changes along a latitudinal gradient, we analysed the distribution limits of the considered species through that gradient. Cluster analyses, although useful, are hierarchical ordination methods and hence they impose a hierarchical structure on the data, whether this exists or not. If a gradation among localities is to be expected, as happens in a latitudinal gradient, other independent approaches should be considered to check for it. A first graphic and very simple approach is to analyse the distribution limits of the considered species through that gradient. The methodology applied is similar to that used for origination/extinction analyses, counting the first and last appearance data (FAD and LAD respectively) on each stage (Hammer, Harper, 2006), although in this case the stages are substituted by the latitudinal intervals, while the FADs and LADs are replaced by the northern distribution limit data (NDL) and the southern distribution limit data (SDL). If faunal turnover presents a gradational pattern, then high values of SDL and NDL are expected in all areas. On the other hand, sudden changes in faunal distribution will be recognized as peaks on the graphic; particularly significant will be the coincidence of peaks on both curves since they will show a major faunal turnover at that latitude (i.e. there will be a lot of species that appear only to the north and a lot that appear only to the south of that point). Peaks on only one curve indicate a reduction in general diversity in one direction (either north or south) and may be informative depending on the nature of data. This reduction could be spurious if it only represents a sampling bias. Extended ranges were used for this analysis.

Generalized linear models

Another approach to check for gradational patterns is to look for changes in the proportional or count values of different species categories; data like systematic kinship (for instance, superfamilies) or ecologic groups are good raw material for this kind of analysis. Generalized linear models (GLMs) are useful for both proportion and count data (Crawley, 2007). The software R (R Development Core Team, 2008) carries out a weighted regression, using the individual sample sizes as weights and the logit (for proportion data) or log (for count data, following the Poisson distribution) link functions to ensure linearity (Crawley, 2007). As a result a linear predictor is obtained together with its significance; the significance level used here was 0.05, but significance values between 0.05 and 0.10 were considered also as potentially explanatory. Positive linear predictors will imply positive associations between variables, *i.e.* an increment in the independent value, in this case latitude, is associated to an increment in the dependent value, in this case the proportion of species or the number of species of the analysed group. Negative linear predictors will imply the opposite trend, *i.e.* an increasing proportion or number of species of the group towards lower latitudes (northwards in this context). The analyses were performed both on observed data and on extended range data. Poorly sampled localities may introduce noise instead of clearing a pattern up, therefore they were removed from the analysis. When this happened it was made clear in the discussion.

The analysis for changes in the proportion of different systematic groups was applied to the superfamilies represented on each stage. The same analysis was also applied to the ecological categories, considering the specific life habit of each taxon as well as the main relationship to the substrate (*i.e.* epifaunal, semi-infaunal and infaunal). In many cases, due to the low number of species in each group, there were no significant results, especially for the Hettangian and Sinemurian. The analyses on count data were performed only for the Pliensbachian, given the particularly good data set for that stage.

LATITUDE AND DIVERSITY

Before discussing the results in detail, it is necessary to frame the analysis in relation to some general trends through the time involved. Within the study area, there is a slight decrease in the percentage of endemic species through time from the Hettangian (67%) to the Toarcian (60%) (Damborenea *et al.*, 2012, p. 57). This decline is in agreement with similar trends observed in several areas of the Northern Hemisphere (see Hallam, 1977) for endemic bivalve genera. It is interesting to note that Hallam (1977, fig. 2) recorded an opposite trend for South America but then correctly attributed it to poorly documented data.

Overall bivalve gross diversity (species richness) through time along the whole studied area in western South America shows a sharp maximum in the Pliensbachian (Damborenea *et al.*, 2012, fig. 4.6). This fact is in agreement with plots of the number of bivalve genera worldwide along this same time interval (Hallam, 1977, fig. 1). It is interesting to note that the total number of Pliensbachian species recorded in the studied geographical range (150) is comparable to the general species richness in present-day marine bivalves occurring in continental shelf depths at similar latitudes (Stehli *et al.*, 1967; Crame, 1996a, fig. 1; Jablonski *et al.*, 2013, fig. 1).

For living bivalves, taxonomic diversity at family, genus and species levels are covariant with latitude (Stehli *et al.*, 1967; Stehli, 1968), and this can be extrapolated to fossil faunas, even during times when climatic belts were apparently ill-defined (Stehli *et al.*, 1969) as seems to have been the case during the Early Jurassic. The general decreasing diversity trend towards higher latitudes was also recorded for the main ecological types (Roy *et al.*, 2000b), as this aspect had not been explored in ancient faunas previously.

Concerning general diversity latitudinal gradients, our data do not show the expected continuous decrease in species diversity towards higher latitudes in the geographic range considered here. Instead, the general decreasing trend is punctuated by a local diversity increase between 34 and 42°, which is especially evident for Pliensbachian and Toarcian times (Fig. 1).

At the scale of our data, discontinuities are recognizable by the concurrence of latitudinal breaks of different species. In this way, the evolution of the observed patterns through the Early Jurassic (c. 25 Ma) can be described stage by stage as well.

HETTANGIAN

As a result of the Late Triassic extinction, bivalve data for the Hettangian are very few; only 29 species were recorded in the study area (Fig. 2A). This considerably limited



Fig. 1. Latitudinal diversity through time

Number of bivalve species every two degrees of latitude along the study area for each time interval, using extended ranges. Left hand map shows (diagonal hatching) the maximum extension of marine Early Jurassic deposits during the interval studied

the analysis, which was nevertheless performed with the same methods as the other time intervals for comparison. No deposits of this age bearing marine bivalves are known to the south of 36°S, and thus the analysis is constrained to the northern regions of our range. Latitudinal ranges are discontinuous as two separate depocentres are recognised, one in

northern Chile and the other in central Chile and Argentina, which share only 10 taxa (Fig. 2A).

Cluster analysis (Fig. 2B) shows certain latitudinal gradient, discriminating between northern (20–24°S) and southern (32–36°S) bivalve faunas, roughly corresponding to the two depocentres.



Fig. 2. Latitudinal diversity for Hettangian times

Left hand map shows the localities with bivalves and the inferred extension of marine deposits for the Hettangian along the study area (compiled from several sources). **A.** Latitudinal occurrences of bivalve species along the study area. **B.** Cluster analysis, hierarchical clustering of the observed presence-absence of bivalve species in 2° latitudinal bands, using Simpson's similarity coefficient and paired group algorithm. **C.** Faunal turnover analysis scale: diversity in number of species, using extended ranges. **D.** Latitudinal variation in the proportion of species, generalised linear model for Trigonioidea, see linear predictor values in Table 1. **E.** Latitudinal variation in the proportion of species groups

SINEMURIAN

Although northern and southern limits of distribution (Fig. 2C) show some turnover between 26–28°S, it must be pointed out that there are no data for the latitudes between 28–32°S, so the peak for southern limits of distribution may be overestimated.

Likewise, there are not enough data to perform generalized linear models of the distribution of most superfamilies. Nevertheless, there is a significant trend of decreasing relative diversity at higher latitudes for the superfamily Trigonioidea (Table 1) when either range extensions (Fig. 2D) or actual records are used.

Although no significant results were obtained for the proportions of the different ecological categories (Fig. 2E), it is remarkable that shallow burrowers occur mostly at low latitudes (less than 26° except for one species between 34 and 36°) while deep burrowers were only recorded at latitudes higher than 26°. There is a good data base for the Sinemurian, with 109 species distributed from 20 to 36° , with a region of low data density between 30 and 34° . During the Sinemurian (Fig. 3) there seems to have been a southwards shift of the main turnover region, as indicated by the cluster analysis (grouping the zones between 26 and 32° S on one hand, and those between 32 and 36° S on the other, Fig. 3B). This is also evident from the limits of distribution analysis (showing a clear peak of northern and southern limits between 28 and 30° S). The minor inconsistency between both types of analyses may be due to the scarcity of records along the boundary regions, being more reliable the limit suggested by the faunal turnover.

Concerning the gradational proportional distribution of superfamilies (Table 1), there is again a significant trend of

Table 1

Significant results of generalized linear model analysis performed for superfamilies. Linear predictors (lp) with significance levels (p) lower than 0.05 are shown (those between square brackets have significance levels between 0.05 and 0.10)

Superfamily	Gen	eralized linear n	nodel analysis res	sults	Relative	Comparable trends	Comparable trends
Superfamily	Hettangian	Sinemurian	Pliensbachian	Toarcian	diversity	in living faunas	in Late Jurassic faunas
Trigonioidea	lp = -1.09 p = 0.025	[lp = -0.10] [p = 0.067]	lp = -0.66 * p = 0.033	lp = -0.09 p = 0.026		no data	
Limoidea				lp = -0.09 p = 0.048	decreasing		Limidae (Crame, 2002)
Lucinoidea				lp = -0.31 p = 0.027	latitudes	lucinoids (Crame, 2000a)	lucinoids (Crame, 2002)
Pholadomyoidea			lp = -0.05 p = 0.08				Pholadomyidae (Crame, 2002)
Pectinoidea				lp = 0.07 p = 0.009		Pectinidae (Roy <i>et al.</i> , 2000a)	
Crassatelloidea		lp = 0.41 p = 0.048		lp = 0.09 p = 0.033		Astartidae (Roy <i>et al.</i> , 2000a)	
Nuculanoidea			lp = 0.10 p = 0.048		decreasing towards lower	Nuculanidae (Roy <i>et al.</i> , 2000a) protobranchs (Crame, 2000a)	protobranchs (Crame, 2002)
Monotoidea				lp = 0.15 p = 0.001	latitudes	extinct	Inoceramidae, Oxytomidae
Inoceramoidea			lp = 0.30 p = 0.042			extinct	(Crame, 1993, 2002)
Arcoidea			lp = 0.06 $p = 0.036$				

* Calculated excluding interval areas 1 and 2.



Fig. 3. Latitudinal diversity for Sinemurian times

Left hand map shows the localities with bivalves and the inferred extension of marine deposits for the Sinemurian along the study area (compiled from several sources). **A.** Latitudinal occurrences of bivalve species along the study area. **B.** Cluster analysis, hierarchical clustering of the observed presence-absence of bivalve species in 2° latitudinal bands, using Simpson's similarity coefficient and paired group algorithm. **C.** Faunal turnover analysis scale: diversity in number of species, using extended ranges. **D.** Latitudinal variation in the proportion of species, generalised linear model for Trigonioidea and Crassatelloidea, see linear predictor values in Table 1. **E.** Latitudinal variation in the proportion of species, generalised linear model for life habits groups. Other references in Figure 2

decreasing relative diversity at higher latitudes for the superfamily Trigonioidea when range extension data were used (Fig. 3D), although these results seem strongly influenced by the datum between 20 and 22°, which is a trigoniid species. On the other hand, the superfamily Crassatelloidea showed the opposite trend only when range-extension data were used, despite its low overall diversity.

During this stage there was a diversification of epifaunal life habits, which were dominated by epibyssate species during the Hettangian. Also, infaunal life habits seem to have increased their proportional diversity towards the south (linear predictor: 0.064, p = 0.094); the trend observed for deep burrowers in the previous stage was maintained during the Sinemurian, being present only at latitudes higher than 26°; on the other hand shallow burrowers occurred through the whole range. Among semi-infaunal life habits (Fig. 3E) reclining species show a trend to reduce proportional diversity towards the south (linear predictor: -0.13; p = 0.038), while endobyssate species probably increased in proportional diversity in that same direction (linear predictor: 0.28; p = 0.067).

PLIENSBACHIAN

Reliable data to the north of 26° are very scarce and have only been included for the sake of completeness. Otherwise, bivalve faunas of this age are by far the best known for the Early Jurassic of the southern Andean region (Fig. 4), with 150 species. As already said, bivalve faunas show a sharp rise in overall diversity during the Pliensbachian which may be only partially attributed to the intensity of studies. All elements of the fauna participate in this increase in species numbers.

The complete Pliensbachian database allows the most detailed analysis of the palaeobiogeography of the west margin of southern South America. Cluster analysis (Fig. 4B) discriminates northern latitudes $(22-32^{\circ}S)$ from southern ones $(32-46^{\circ})$, although the best defined biogeographic region is between 34 and 44°S (*i.e.* coinciding with the Neuquén embayment at the time). According to the limits of distribution (Fig. 4C), and in coincidence with the cluster analysis, the main biogeographic turnover seemed to have been between 3° and 36°S during this stage, showing an





Left hand map shows the localities with bivalves and the inferred extension of marine deposits for the Pliensbachian along the study area (compiled from several sources). **A.** Latitudinal occurrences of bivalve species along the study area. **B.** Cluster analysis, hierarchical clustering of the observed presenceabsence of bivalve species in 2º latitudinal bands, using Simpson's similarity coefficient and paired group algorithm. **C.** Faunal turnover analysis scale: diversity in number of species, using extended ranges. **D.** Latitudinal variation in the proportion of species, generalised linear model for Arcoidea, Nuculanoidea, Inoceramoidea, Trigonioidea and Pholadomyoidea, see linear predictor values in Table 1. **E.** Latitudinal variation in the proportion of species, generalised linear model for life habits groups. Other references in Figure 2

even greater displacement towards the south. There is a high peak on the NDL curve between 24 and 26°S, but data for the areas between 20 and 24°S are scarce, and hence many of the considered species may have had a broader range, extending northwards; similarly, the SDL peak between 40 and 42°S can be partly attributed to a rather poor knowledge of the faunas in Chubut.

The gradational distribution analysis shows that during the Pliensbachian (Fig. 4D; Table 1) the superfamilies Arcoidea, Nuculanoidea and Inoceramoidea had a southward increasing trend in proportion of species, while Pholadomyoidea and possibly Trigonioidea showed the opposite trend. These results were obtained using the extended ranges. When actual records are used the linear predictor values change but the trends are maintained and are still significant, except for Inoceramoidea and Trigonioidea. The low values in the proportion of species of the different families are remarkable for this stage, and they were not restricted only to the superfamilies mentioned.

The latitudinal variations just pointed out may be explained, at least in part, on ecological grounds. During this stage (Fig. 4E) epifaunal species increased in proportional diversity with higher latitude (linear predictor: 0.029; p = 0.030), particularly epibyssates (linear predictor: 0.045; p = 0.006) like Inoceramoidea. Semi-infaunal bivalves show the opposite trend (linear predictor: -0.044; p = 0.015), particularly the reclining ones (linear predictor: -0.072; p = 0.005). Among infaunal species, shallow burrowers increased in proportional diversity with latitude (linear predictor: 0.047; p = 0.014), while deep burrowers (like Pholado-

TOARCIAN

Toarcian faunas are widespread and relatively diverse (96 species), but less well known than Pliensbachian ones, especially south of 40° (Fig. 5). Consequently, the results for the Toarcian seem a little unclear, at least for the ordination methods. The cluster analysis (Fig. 5B) shows no clear pat-

tern, while the graphics for the limits of distribution displays several peaks (Fig. 5C).

For the Toarcian (Fig. 5D; Table 1) the superfamilies Lucinoidea, Limoidea and Trigonioidea decreased southwards in relative number of species, while Monotoidea, Pectinoidea and Crassatelloidea tended to increase their relative diversity in that same direction. These results were obtained using extended ranges. When actual records were used the linear predictor values changed but the trends were maintained and were still significant, except for Crassatelloidea and Trigonioidea.



Fig. 5. Latitudinal diversity for Toarcian times

Left hand map shows the localities with bivalves and the inferred extension of marine deposits for the Toarcian along the study area (compiled from several sources). **A.** Latitudinal occurrences of bivalve species along the study area. **B.** Cluster analysis, hierarchical clustering of the observed presence-absence of bivalve species in 2° latitudinal bands, using Simpson's similarity coefficient and paired group algorithm. **C.** Faunal turnover analysis scale: diversity in number of species, using extended ranges. **D.** Latitudinal variation in the proportion of species, generalised linear model for Crassatelloidea, Monotoidea, Pectinoidea, Trigonioidea, Limoidea and Lucinoidea, see linear predictor values in Table 1. **E.** Latitudinal variation in the proportion of species, generalised linear model for life habits groups. Other references in Figure 2

Among epifaunal bivalves, facultative swimmers tended to proportionally increase towards higher latitudes (linear predictor: 0.089; p = 0.011) whilst cementing species seem to have reduced their proportional diversity southwards (linear predictor: -0.10; p = 0.076), but this trend is not significant when compared to all life habits (linear predictor: -0.068; p = 0.197) (Fig. 5E).



Fig. 6. Absolute diversity latitudinal gradients between 26 and 46° present-day S latitude, Pliensbachian

The GLM model fitted is based on Poisson's distribution. **A.** Latitudinal trend for the whole data set (linear predictor: -0.019, p = 0.12); continuous line based on the whole data set; broken line excluding the data from the Neuquén Basin. **B.** Latitudinal trend for Trigonioidea (linear predictor: -0.045, p = 0.04). **C.** Latitudinal trend for Pholadomyoidea (linear predictor: -0.064, p <<0.01). **D.** Latitudinal trend for Mytiloidea (linear predictor: -0.045, p = 0.08). **E.** Latitudinal trend for Nuculanoidea (linear predictor: 0.067, p = 0.11). **F.** Latitudinal trend for Crassatelloidea (linear predictor: 0.021, p = 0.49)

DISCUSSION AND CONCLUSIONS

The results just presented undoubtedly have regional significance, but they may also be relevant to the comprehensive discussion of bivalve distribution patterns, especially concerning breaks in general latitudinal trends, as well as the origin and history of the latitudinal proportional trends observed in different bivalve lineages and life habit types.

SPECIES DIVERSITY

When all available data are plotted, there is a very slightly decreasing tendency of overall diversity towards higher latitudes (Fig. 1), but the analysis performed on Pliensbachian data show that this gradient is not statistically significant (Fig. 6A). This trend is punctuated (Pliensbachian and Toarcian times) by a sudden increase in diversity at 34-36°S lat., and high values are present to about 42°S lat. This coincides with the location of the Curicó connection with the open Palaeo-Pacific Ocean and the establishment of the Neuquén Basin in western Argentina. Latitudinal species ranges could be sensitive to the variety of physical conditions displayed through the stretch of coast, including water current systems, geomorphology of the coast, input of freshwater and nutrients, local oxygenation conditions, and so on. Some of these factors (freshwater input, oxygenation) can be disregarded on account of the nature of our data, which span several habitats and local environmental conditions. We suggest that this local increase may be mostly due to the establishment of favourable conditions and an increased variety of habitats within the extensive Neuquén Basin, which at that time was a quasi-isolated shallow water epeiric sea. The geomorphology to the north was a narrow trans-arc strip instead. Comparable distribution breaks were reported for living cephalopods along a similar latitudinal range along modern Chilean coasts (Ibáñez et al., 2009), and were attributed to physical factors other than temperature. Furthermore, when data from the Neuquén basin are omitted, the general diversity gradient becomes statistically significant (Fig. 6A).

To try to assess how the different systematic groups contributed to the general diversity trend, the gross diversity (number of species) within each superfamily was analysed along latitudes for the Pliensbachian, since bivalve faunas from this stage are the best known within this data set. The results were not statistically significant for most superfamilies, except for Trigonioidea, Pholadomyoidea, and probably also Mytiloidea, which follow the general decreasing gradient towards higher latitudes (Fig. 6B–D). Some superfamilies do not reveal any gradient, but interestingly enough there are some which show an increase in general diversity towards higher latitude, such as Nuculanoidea and Crassatelloidea (Fig. 6E–F), and probably also Inoceramoidea and Arcoidea; these are particularly noteworthy since they oppose the general decreasing trend in overall diversity towards higher latitudes.

PROPORTIONAL DIVERSITY OF SUPERFAMILIES

In view of the trends just mentioned, based on count data, it is relevant to discuss now our results concerning the gradational proportional distribution of superfamilies and compare them with those known in living bivalve faunas. This study shows (Table 1) that already in the Early Jurassic we can distinguish between groups which significantly tend to increase their relative diversity towards lower latitudes (Trigonioidea, Limoidea, Lucinoidea, Pholadomyoidea) from those with the opposite trend (Pectinoidea, Crassatelloidea, Nuculanoidea, Monotoidea, Inoceramoidea). The relative latitudinal distributions of members of the first group agree with the general gradient on species number, whilst those of the second group not necessarily reflect an actual inverse latitudinal gradient. Considering the general reduction in species number with higher latitudes, a relative (i.e. proportional) increase in that same direction may be due to either a relatively less steep normal gradient or to the lack of any gradient. This is clear when analyzing the number of species within the different superfamilies for the Pliensbachian; the superfamily Inoceramoidea for example, was represented by only one species recorded south of 38°, but due to the general reduction in diversity towards the south, it becomes one of the superfamilies with significant increasing proportion towards higher latitudes (Table 1). Other superfamilies, on the other hand, truly increased their diversity towards higher latitudes (e.g., Nuculanoidea, Fig. 6E).

Knowledge of the latitudinal distribution of living bivalves (Crame, 1996a, b, 2000a, b, 2001, 2002; Roy *et al.*, 2000a, b) shows that some of the superfamilies mentioned are nowadays latitudinally limited in their distribution, or have very steep diversity gradients towards the poles.

Living protobranchs show no significant latitudinal gradient (Crame, 2002) or a slight tendency for diversity to increase with latitude (Crame, 2000a), which translates into a relative diversity increase when analysed as proportional composition of faunas (Roy *et al.*, 2000a, fig. 3). Our results show that Pliensbachian southern hemisphere nuculanoids were significantly more diverse towards higher latitudes (Table 1; see also Damborenea *et al.*, 2012, fig. 4.17).

Extant mytiloids, pterioids, pholadomyoids and arcoids display a steep decrease towards high latitudes (Crame, 2000a; Roy *et al.*, 2000a), also present in Late Jurassic mytiloids (Crame, 2002). Although mytiloids and pterioids did not show significant proportional trends in our present analysis, at a limited regional scale in western Argentina, a general comparison of the Late Pliensbachian-Early Toarcian faunas from Mendoza/Neuquén with those from Chubut (Damborenea et al., 2010) shows that some superfamilies (notably mytiloids, pterioids and pholadomyoids) were more diverse in the northern region (Damborenea et al., 2012, fig. 4.17). Due to the limited time-span of the Chubut extensive marine deposits, these trends can only be noticed in this particular time-slice. Anomalodesmata are peculiar in this context, since nowadays they lack a diversity maximum in the tropics (Krug et al., 2007), and appear to display two maxima in temperate northern and southern hemispheres. Our results show that already in the Pliensbachian pholadomyoids were proportionally more diverse towards lower latitudes (Table 1), agreeing with the Late Jurassic results (Crame, 2002, fig. 8). The relative diversity pattern for the superfamily Arcoidea resulting from our analysis shows that during the Pliensbachian they were proportionally more diverse in the Neuquén Basin and decreased towards both north and south (Fig. 4D; Table 1). Within this superfamily, living Arcidae are clearly more diverse towards lower latitudes (Roy et al., 2000a), but our results are not strictly comparable since the Early Jurassic arcoids from the study area do not belong to that family but to Parallelodontidae and Cucullaeidae instead.

Also South American Toarcian Lucinoidea show a significant trend to the proportional increase in diversity towards lower latitudes (Table 1), agreeing with a slight tendency in the same direction for living faunas from both hemispheres (Crame, 2000a). On the other hand, living Limidae do not show a statistically significant trend (Crame, 2000a), and thus cannot be compared with our results, which show a northwards proportional increase during the Toarcian for limoids (Table 1).

Evidently, the pattern emerging from our analysis suggests that at least some of these particular trends may be considerably older than previously thought. Crame (2000a) argued that the steepest latitudinal biodiversity gradients for bivalve groups are related to the youngest clades. Thus, the present-day latitudinal gradient in marine bivalve groups is influenced by a tropical and low latitude concentration of infaunal taxa (mainly heteroconchs), whilst the gradient in the much older clade of epifaunal pteriomorphs is far less marked. These results were compared with a similar analysis of Late Jurassic bivalve distribution (Crame, 2002), and the differences observed were attributed to a large Cenozoic heteroconch diversification, which caused a steepening of the latitudinal gradient, more evident in the Northern Hemisphere. In this context, the steep gradient observed for the Trigonioidea in our study for Hettangian and Sinemurian times may be related to the relatively young age of the lineage at that time, coincident with a great radiation of the group. Unfortunately, there are no comparable data about the latitudinal relative distribution of this diverse group during the Mesozoic; those from about a hundred Late Jurassic Trigoniidae species were combined informally into "heteroconchs" (Crame, 2002) and when pooled with the Astartidae exhibit a concentration in low- to mid-latitude regions.

It is also interesting to note that the Jurassic was characterized by temperature gradients less evident than at the present, and even so, some of these selective diversity gradients were revealed in this study. Proportional trends of increasing diversity towards higher latitudes are thus particularly remarkable, and, apart from the already discussed Nuculanoidea, have been confirmed for the South American Early Jurassic Pectinoidea and Crassatelloidea (Table 1), suggesting that similar tendencies observed in living faunas (Roy et al., 2000a) may have a very long history. Within Crassatelloidea, the family Astartidae is nowadays almost restricted to both polar regions (see Crame, 1996b), but although it had a wider distribution in the Jurassic, in South America its relative distribution was already significantly more diverse towards the south during Sinemurian times (Table 1). Analogous relative decreases in diversity towards lower latitudes in extinct groups, such as Monotoidea and Inoceramoidea (Table 1), had been also noticed before, especially in the context of bipolar distributions and the origin of high latitude Jurassic faunas (Damborenea, 1993, 2002; Crame, 1993, 1996b, 2002), and appear to represent long-lasting patterns as well.

PROPORTIONAL DIVERSITY OF ECOLOGICAL TYPES

Concerning ecological types, latitudinal diversity gradients in living marine bivalves are also evident for both infauna and epifauna, and for most major functional groups (Roy *et al.*, 2000b), except for the deposit feeders. Our results show that epifaunal bivalves were dominant during the Hettangian (Fig. 2E), while later on they were as frequent (Sinemurian, Fig. 3E) and eventually became even less common (Pliensbachian-Toarcian, Figs 4E, 5E) than infaunal ones. Semi-infaunal species remained in low diversities during the whole time interval studied here. This change in dominance from epifaunal to infaunal life habits during the Lower Jurassic is in agreement with global scale data (Ros, Echevarría, 2011).

When the species number of each main life habit type are analysed, both epifaunal and infaunal Pliensbachian bivalves tend to decrease in diversity towards higher latitudes (Fig. 7). Nevertheless, whilst the reduction in the number of infaunal



Fig. 7. Relationships between main life habits and latitude, Pliensbachian

The lines are the expected values according to a GLM fitted to the data, based on Poisson's distribution; continuous lines represent the models based on the whole data set between 26 and 46° (for infaunal bivalves it is a significantly decreasing trend, linear predictor: -0.022, p = 0.021); broken lines represent the models excluding the data from the Neuquén Basin (between 34 and 42°).

species is statistically significant, the less steep reduction of epifaunal species is not. Epifaunal bivalves (especially epibyssates and swimmers) increased in proportional diversity towards higher latitudes during the Pliensbachian and Toarcian (Figs 4E, 5E). It is remarkable how infaunal bivalves are more diverse than epifaunal ones through the whole latitudinal range, except between 34 and 42°, where both life habits show the same number of species; it seems that although both groups benefited from the development of the Neuquén Basin, the epifauna took more advantage of it. The tendency observed among Tithonian infaunal bivalves (Crame, 1996a) is not confirmed by our analysis.

Regarding major feeding types, deposit feeders (represented by nuculanoids in our study) do show a clear relative increase in diversity (both absolute and proportional) towards higher latitudes according to our results (Table 1, Figs 4D, 6E), in agreement with the already mentioned tendencies observed in living faunas (Roy *et al.*, 2000a; Crame, 2000a).

This study provides at least two conclusions which may add to the global discussion of bivalve distribution patterns:

a) breaks in general latitudinal trends may be highly influenced by large scale geographical conditions;

b) the history of relative diversity trends observed in different bivalve lineages may have been more complex and deeply rooted in time than previously thought. Acknowledgements. Many colleagues provided bibliography and facilitated access to collections housed in museums from Chile and Argentina, they are all greatly acknowledged. Dr. M. Manceñido discussed some aspects of this research and critically read an earlier version of the manuscript. Research for this paper was partly financed by grants from CONICET: PIP 112-200801-01567 and 112-201101-01088.

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Appendix 1

Main localities and data sources for the latitudinal analysis along western South America. Data are arranged according to 13 areas with a 2º latitudinal range each

Region	Present-day latitude range	Main localities	Sources of data
0	20–22°	Socosani, Longacho, Pampa Soledad, Quillagua	Pérez, Reyes, 1994; Pérez et al., 2008
1	22–24°	Cerritos Bayos, Cerros de Moctezuma, Sierra de Limón Verde, SSE de Calama, Caracoles, Cerros de Cuevita[s] en Sierra del Tigre, Oficina Cochrane-Azabache	Steinmann, 1881; Möricke, 1894; Pérez, Levi, 1961; Harrington, 1961; Pérez, Reyes, 1977, 1994; Hillebrandt, 1990; Aberhan, 1994; Perez <i>et al.</i> , 2008
2	24–26°	Cordillera Domeyko, Alto Varas, Quebrada Bonita, Quebrada Chaco Sur, Sierra Candeleros, Incahuasi, Posada de los Tres Hidalgos, Quebrada Oreganito, Quebrada de los Burros, Sierra Áspera, Quebrada del Profeta, Sierra Argomedo, Quebrada de las Mulas-Paposo, Sierra Vaquillas Altas, Quebrada Carreta[s], Quebrada Cachina	Hillebrandt, 1971, 1973, 1977, 1980, 2000; Pérez, Reyes, 1977, 1994; Covacevich, Escobar, 1979; Chong, Hillebrandt, 1985; Hillebrandt <i>et al.</i> , 1986; Quinzio, 1987; Aberhan, 1994; Pérez <i>et al.</i> , 2008
3	26–28°	Quebrada Doña Inés Chica, Sierra Minillas, Quebrada Pan de Azúcar, Salar de Pedernales, Portezuelo de Pedernales, Quebrada San Juan, Quebrada Asientos, Quebrada Caballo Muerto-Tamberías, Quebrada El Peñón, La Chaucha, Quebrada de Paipote-Redonda, Quebrada El Bolito, Quebrada El Patón, Quebrada El Carbón, Quebrada Cortaderita, Sierra de La Ternera, Quebrada Potrerillos-Vaca Muerta, Quebrada Yerbas Buenas, Quebrada San Pedrito, Quebrada Larga-Noria, Quebrada Llareta, Quebrada San Miguel, Figueroa, Rio Jorquera, Majada del Carrizo, La Guardia, Quebrada Calquis, Quebrada Los Eucaliptus, Quebrada de Las Vizcachas, Quebrada Las Trancas	Möricke, 1894; Philippi, 1899; Hillebrandt, 1973; Pérez, Reyes, 1977; Hillebrandt, Schmidt-Effing, 1981; Mercado, 1982; Sepúlveda, Naranjo, 1982; Chong, Hillebrandt, 1985; Hillebrandt, Westermann, 1985; Hillebrandt <i>et al.</i> , 1986; Quinzio, 1987; Hillebrandt, 1990, 2000; Aberhan, 1992, 1993, 1994, 2004; Pérez <i>et al.</i> , 1995, 2008; Aberhan, Hillebrandt, 1996
4	28–30°	Rio Manflas, Quebrada las Amolanas, La Iglesia, Rio Pulido, Quebrada de la Iglesia, Juntas del Tolar, Cerro Salto del Toro, El Tránsito, Quebrada El Corral, La Totora, Quebrada Chanchoquín, Paitepén, Quebrada Plaza, Tatul, Las Pircas, Quebrada Pinte, Quebrada Las Pircas, Picudo, Quebrada La Plata, Quebrada La Papa, Los Cuartitos, Calabocito, Cordillera de La Punilla, Cordillera de Doña Ana, Elqui	Bayle, Coquand, 1851; Burmeister, Giebel, 1861; Möricke, 1894; Philippi, 1899; Groeber, 1953; Thiele, 1964; Hillebrandt, 1971, 1973, 1977, 2002; Pérez, Reyes, 1977; Hillebrandt, Westermann, 1985; Aberhan, 1992, 1994, 2004; Pérez <i>et al.</i> , 1995, 2008; Aberhan, Hillebrandt, 1996, 1999
5	30–32°	Matahuaico, Quebrada Tres Cruces, Rio Mostazal y Los Molles, Mina Los Pingos (Cordillera de Ovalle), Los Erizos, El Pachón	Bayle, Coquand, 1851; Conrad, 1855; Philippi, 1899; Dediós, 1967; Mpodozis <i>et al.</i> , 1973; Pérez, Reyes, 1977; Ramos <i>et al.</i> , 1993; Aberhan, 1994, 2004; own data
6	32–34°	Las Flores, Quebrada Honda, Los Molles, Arroyo La Laguna, Cerro 738 (La Ligua), Quebrada del Pobre	Rigal, 1930; Thomas, 1958; Cecioni, Westermann, 1968; Pérez, Reyes, 1977; Volkheimer <i>et al.</i> , 1978; Damborenea, 1987a, b, 2002; Ramos <i>et al.</i> , 1993; Pérez <i>et al.</i> , 2008; own data
7	34–36°	Arroyo La Manga, Arroyo Malo-Alumbre, La Horqueta, Tinguiririca, Arroyo Blanco, Arroyo El Pedrero, Quebrada Los Caballos, Arroyo Las Chilcas, Puesto Araya, Cerro La Brea, Arroyo La Bajada, Curepto, Portezuelo Ancho, Arroyo del Portezuelo Ancho, Arroyo del Deshecho, Arroyo Santa Elena, Rio Salado, Troncoso, El Infiernillo, Arroyo Serrucho, Cerro Puchenque, Cerro Tricolor, Barda Blanca, Arroyo Chacayco, Arroyo Poti-Malal, Cañada Colorada	Behrendsen, 1891; Philippi, 1899; Jaworski, 1925; Groeber, 1953; Damborenea, 1987a, b, 2002, 2004; Riccardi <i>et al.</i> , 1988, 1991; Pérez <i>et al.</i> , 1995; Damborenea, Lanés, 2007; own data
8	36–38°	Los Baños, Tocuyo, Arroyo Ñiraico, Estación Rajapalo, Arroyo Chacay Melehue, Perfil, Arroyo Lista Blanca	Damborenea, 1987a, b, 2002; own data

Region	Present-day latitude range	Main localities	Sources of data
9	38–40°	Arroyo Del Gringo, Arroyo Los Toldos, Arroyo Ñireco, Pichi Picún Leufú, Cerro Granito, Puruvé Pehuén, Vuta Picún Leufú, Arroyo Lonqueo, Mallín de Ibáñez, Espinazo del Zorro, Llao-Llao, Aluminé, Arroyo Lapa, Estancia Charahuilla, Cerro Keli Mahuida, Los Molles, Picún Leufú, Arroyo La Jardinera, Catán Lil, Estancia Santa Isabel	Weaver, 1931; Groeber, 1953; Damborenea, 1987a, b, 2002; Pérez <i>et al.</i> , 1995; own data
10	40–42°	Carrán Cura, Salitral Grande, N de Sañicó, Subida a Sañicó, Arroyo Los Chilenos, Arroyo Los Pantanos, Cerro Roth, Cerro Mesa, Cañadón La Pintada, Cerro del Vasco, Cerro Corona, Cerro Piltri quitrón	Leanza, 1942; Manceñido, Damborenea, 1984; Damborenea, 1987a, b, 2002; Pérez <i>et al.</i> , 1995; own data
11	42–44°	Gualjaina, Arroyo Pescado, Cerro Cuche, Puesto Peña, La Carlota, Pampa de Agnia, Puesto Currumil, Nahuelquir, Chapingo, Cerro Carnerero, Loma de Plate, Lomas Chatas, El Córdoba	Piatnitzky, 1936; Robbiano, 1971; Lesta <i>et al.</i> , 1980; Lage, 1982; Nullo, 1983; Benito, Chernicoff, 1986; Vizán, 1988; Massaferro, 2001; own data
12	44–46°	Cañadón Puelman, Cerro Negro, Altamiran, Piedra Shotle, Puesto Parra, Lomas de Betancourt, Cerro La Trampa, Nueva Lubecka, Aguada Loca, Estancia Ferrarotti, Loncopán, Salazar, Guadal, Colorado	Piatnitzky, 1933, 1936; Feruglio, 1934; Wahnish, 1942; Robbiano, 1971; Malumián, Ploszkiewicz, 1976; Blasco <i>et al.</i> , 1980; Lesta <i>et al.</i> , 1980; Nullo, 1983; Cortiñas, 1984; Pérez <i>et al.</i> , 1995; Damborenea, 2002; Pagani <i>et al.</i> , 2012; own data

APPENDIX REFERENCES

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Appendix 2

Distribution in time and space of the taxa

Geographical ranges as in Appendix 1 and Figs 1–5. Long dash – record, broken line – inferred presence. Het – Hettangian, Sin – Sinemurian, Pli – Pliensbachian, Toa – Toarcian.

Life habits: I - infaunal, E - epifaunal, S - semi-infaunal, Sb - shallow burrower, Db - deep burrower, Be - epibyssate, Bi - endobyssate, Re – resting, Ce – cemented, Ne – nestler, Sw – swimmer, Bo – borer.

Species Geographica	I range	1	2	3	4	5	6	7	8	9	10	11	12	Lif	e habit	Superfamily
Palaeonucula cuevitana Aberhan	Het													Ι	Sb	Nuculoidea
Palaeonucula n. sp.	Pli							000000						Ι	Sb	Nuculoidea
Palaeoneilo patagonidica (Leanza)	Pli							800000		000000	000000	000000	-	I	Sb	Nuculanoidea
<i>Malletia</i> ? sp.	Pli													Ι	Sb	Nuculanoidea
<i>Ryderia</i> n. sp.	Pli												000000	I	Sb	Nuculanoidea
Nuculana ovum (J. de C. Sowerby)	Pli			600000			000000				000000		000000	I	Sb	Nuculanoidea
Nuculana ovum (J. de C. Sowerby)	Тоа			60300				00000	00000					Ι	Sb	Nuculanoidea
Solemya cf. waikaensis (Marwick)	Pli										000000			I	Db	Solemyoidea
Parallelodon aff. groeberi Damborenea	Het	-												Е	Ne?	Arcoidea
Parallelodon groeberi Damborenea	Pli			000000	000000			000000		000000	000000			Е	Ne?	Arcoidea
Parallelodon hirsonensis (d'Archiac)	Sin													Е	Ne?	Arcoidea
Parallelodon hirsonensis (d'Archiac)	Pli			000000				000000		000000				Е	Ne?	Arcoidea
Parallelodon riccardii Damborenea	Pli									000000	000000			Е	Ne	Arcoidea
Grammatodon cf. toyorensis Hayami	Pli								000000		000000			Ι	Sb	Arcoidea
Grammatodon concinnus (Phillips)	Sin													Ι	Sb	Arcoidea
Grammatodon concinnus (Phillips)	Pli													Ι	Sb	Arcoidea
Grammatodon concinnus (Phillips)	Тоа													Ι	Sb	Arcoidea
Grammatodon costulatus (Leanza)	Pli										000000			Ι	Sb	Arcoidea
Grammatodon sulcatus Aberhan	Sin													Ι	Sb	Arcoidea
Cosmetodon sp.	Sin													Ι	Sb	Arcoidea
Idonearca cf. rothi (Leanza)	Pli			000000				00000	000000		000000	000000		I	Sb	Arcoidea
Idonearca cf. rothi (Leanza)	Toa							65555	60000					Ι	Sb	Arcoidea
Idonearca rothi (Leanza)	Pli							000000		000000	000000			I	Sb	Arcoidea
Idonearca rothi (Leanza)	Тоа						-				00000			Ι	Sb	Arcoidea
Ashcroftia jaworskii (Leanza)	Pli							800000		600000	000000		-	S?	Sb	Arcoidea
Lycettia hypertrigona Damborenea	Sin													Е	Be	Mytiloidea
Lycettia hypertrigona Damborenea	Pli									000000				Е	Be	Mytiloidea
Lycettia hypertrigona Damborenea	Тоа						60000							Е	Be	Mytiloidea
Falcimytilus ? gigantoides (Leanza)	Sin													Е	Be	Mytiloidea
Falcimytilus ? gigantoides (Leanza)	Pli				000000						000000		-	Е	Be	Mytiloidea
Falcimytilus ? gigantoides (Leanza)	Тоа				00000			00000						Е	Be	Mytiloidea
<i>Modiolus baylei</i> (Philippi)	Sin													S	Bi	Mytiloidea
<i>Modiolus baylei</i> (Philippi)	Pli			600000			000000	600000	000000		8680680		-	S	Bi	Mytiloidea
<i>Modiolus baylei</i> (Philippi)	Тоа				00000		00000	00000	00000					S	Bi	Mytiloidea
Modiolus cf. scalprum Sowerby	Pli			000000	000000	000000								S	Bi	Mytiloidea
Modiolus cf. scalprum J. Sowerby	Toa				60000									S	Bi	Mytiloidea
Modiolus cf. thiollierei (Dumortier)	Sin													S	Bi	Mytiloidea
Modiolus cf. thiollierei (Dumortier)	Pli			600000	000000			-			000000			S	Bi	Mytiloidea
Modiolus cf. thiollierei (Dumortier)	Toa							00000	00000					S	Bi	Mytiloidea

Species Geographical ra	ange	1	2	3	4	5	6	7	8	9	10	11	12	Lif	e habit	Superfamily
Modiolus lonsdalei (Morris et Lycett)	Pli													S	Bi	Mytiloidea
Modiolus chilensis Aberhan	Pli				000000									S	Bi	Mytiloidea
Modiolus gerthi Damborenea	Pli									000000				S	Bi	Mytiloidea
Modiolus gerthi Damborenea	Тоа													S	Bi	Mytiloidea
Modiolus imbricatus J. Sowerby	Pli													S	Bi	Mytiloidea
Modiolus imbricatus J. Sowerby	Тоа				00000									S	Bi	Mytiloidea
Inoperna ? sp.	Sin													1	Bo?	Mytiloidea
Inoperna sp.	Pli													I	Bo?	Mytiloidea
Lithophaga ? sp.	Pli			000000							000000			1	Во	Mytiloidea
Lithophaga ? sp.	Тоа				00000									1	Во	Mytiloidea
Pinna cf. folium Young et Bird	Het													S	Bi	Pinnoidea
Pinna cf. folium Young et Bird	Sin													S	Bi	Pinnoidea
Pinna cf. folium Young et Bird	Pli													S	Bi	Pinnoidea
Pinna cf. folium Young et Bird	Toa													S	Bi	Pinnoidea
Pinna cf. radiata Münster	Pli				10000		0.000	00000	COLORD	00000				S	Bi	Pinnoidea
Trichites sp.	Pli			CCCCCC	PORTON O									S	Ne	Pinnoidea
Pteroperna sp.	Sin							000000						F	Be	Pterioidea
Pteroperna sp.	Pli								•					F	Be	Pterioidea
Aquirerella kobvi (Loriol)	Sin							000000						F	Be	Pterioidea
Aquilerella neuquensis Damborenea	Dii													F	Be	Pterioidea
"Pteria" sp	, " Hot										000000			F	Be	Pterioidea
Gervillia (Cultriopsis) sp.	Sin				•									F	Be	Pterioidea
Gervillia (Cultriopsis) sp.	Dii								•					F	Be	Pterioidea
Gervillia (Cultriopsis) sp.	, " Toa							000000	••••	600000	00000	000000		F	Be	Pterioidea
Bakevellia waltoni (Lycett)	Sin						00000	••••	•••	••••	00000			F	Be	Pterioidea
Bakevellia pintadae Damborenea	Dii					•								F	Be	Pterioidea
Gervillela araucana Damborenea	Sin			00000	•••		••••	••••		••••	000000			S2	Be?	Pterioidea
Gervillela araucana Damborenea	Dii								•					S2	Be?	Pterioidea
Gervillella cf. aviculoides (Sowerby) ?	Sin			000000	600000		••••	000000			000000	000000		S2	Be?	Pterioidea
Gervillaria ? ashcroftensis (Crickmay)	Dii								•					S2	Re	Pterioidea
Gervillaria ? ashcroftensis (Crickmay)	, " Top													\$2	Re	Ptorioidea
Gervillaria alaeformis (Sowerby)	Pli				00000									S2	Re	Pterioidea
Gervillaria alaeformis (J. Sowerby)	, " Toa						••••	Eccation						S2	Re	Pterioidea
Genvillaria bartmanni (Münster)	Sin			00000	nencei									S2	Re	Pterioidea
Genvillaria hartmanni (Münster)	5/// Top													S2	Re	Pterioidea
Genvillaria pallas (Leanza)	Sin				nonce									S2	Re	Pterioidea
Gervillaria pallas (Leanza)	Dii													S2	Re	Pterioidea
Genvillaria pallas (Leanza)	г <i>II</i> Тор			000000	000000	••••	•••	000000	•••	600600	000000		000000	S2	Re	Pterioidea
Gervilleioperna (Gervilletia) turgida (Leanza)	Sin							00000						S2	Re	Pterioidea
Genvilleioperna (Genvilletia) turgida (Leanza)	511													<u>6</u> 2	Do	Pterioidea
Genvilleioperna (Genvilletia) turgida (Leanza)	г <i>і</i> і Тоо				000000		••••	••••	••••	••••				S2	Po	Btorioidea
Genvilleionerna (Genvilleionnoma) aurita A et H	Toa													62	Po	Dterioidea
Parainoceramus 2 sp	liet				00000									5:	Po	Plenoidea
Parainoceramus anollo (Leanza)	nei								•						Be	Inoceramoidea
Parainoceramus apollo 2 (Leanza)	Pli									600000	800000		600000		Be	Inoceramoidea
	SIN Te -				•										De Do	Inoceramoidea
Inoceramidae gen. et ap. indet.	i oa								66606						De Ro	Dtaricida
	sin Di:														Bo	Pterioidea
	г"! Т											•••			Pc	Pterioldea
(Leanza)	roa	1		000000			000000	000000							Бе	Pterioidea

percente

1 2 3 4 5 6 7 8

Species

Hypotrema liasica (Damborenea)

Asoella asapha (Leanza)

Geographical range

Pli

Sin

9	10	11	12	Lif	e habit	Superfamily
				Е	Be	Pterioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
				Е	Be	Monotioidea
		000000		Е	Be	Monotioidea

Asoella asapha (Leanza)	Pli		E	Be	Monotioidea
Otapiria neuquensis Damborenea	Sin		Е	Be	Monotioidea
Otapiria neuquensis Damborenea	Pli		Е	Be	Monotioidea
Otapiria pacifica Covacevich et Escobar	Het		Е	Be	Monotioidea
Otapiria pacifica Covacevich et Escobar	Sin		Е	Be	Monotioidea
Arctotis ? frenguellii Damborenea	Toa	_	Е	Be	Monotioidea
Oxytoma inequivalvis (J. Sowerby)	Het		Е	Be	Monotioidea
Oxytoma inequivalvis (J. Sowerby)	Sin		Е	Be	Monotioidea
Oxytoma inequivalvis (J. Sowerby)	Pli		Е	Be	Monotioidea
Oxytoma inequivalvis (J. Sowerby)	Toa		Е	Be	Monotioidea
Palmoxytoma cf. cygnipes (Young et Bird)	Het		Е	Be	Monotioidea
Meleagrinella sp.	Toa		Е	Be	Monotioidea
Bositra ornati (Quenstedt)	Тоа		Е	Sw?	Monotioidea
Ochotochlamys sp.	Pli	_	Е	Be	Pectinoidea
Kolymonectes weaveri Damborenea	Pli		Е	Re-Sw	Pectinoidea
Kolymonectes sp.	Sin		Е	Re-Sw	Pectinoidea
Parvamussium pumilum (Lamarck)	Toa		Е	Re-Sw	Pectinoidea
Entolium cf. lunare (Roemer)	Het		Е	Re-Sw	Pectinoidea
Entolium cf. lunare (Roemer)	Sin		Е	Re-Sw	Pectinoidea
Entolium cf. lunare (Roemer)	Pli		Е	Re-Sw	Pectinoidea
Entolium cf. lunare (Roemer)	Toa		Е	Re-Sw	Pectinoidea
Entolium disciforme (Schübler)	Pli		Е	Re-Sw	Pectinoidea
Entolium disciforme (Schübler)	Тоа		Е	Re-Sw	Pectinoidea
Entolium ? sp.	Het	_	Е	Re-Sw	Pectinoidea
Entolium ? sp.	Sin	_	Е	Re-Sw	Pectinoidea
Entolium mapuche Damborenea	Pli		Е	Re-Sw	Pectinoidea
Entolium mapuche Damborenea	Тоа		Е	Re Sw	Pectinoidea
Posidonotis cancellata (Leanza)	Pli		Е	Re-Sw	Pectinoidea
Posidonotis cancellata (Leanza)	Тоа		Е	Re-Sw	Pectinoidea
<i>Lywea</i> ? sp.	Het		S	Re	Pectinoidea
<i>Lywea unca</i> (Philippi)	Sin		S	Re	Pectinoidea
<i>Lywea unca</i> (Philippi)	Pli		S	Re	Pectinoidea
<i>Lywea unca</i> (Philippi)	Toa		S	Re	Pectinoidea
Weyla alata angustecosta (Philippi)	Тоа		S	Re	Pectinoidea
Weyla alata alata (von Buch)	Sin		S	Re	Pectinoidea
Weyla alata alata (von Buch)	Pli		S	Re	Pectinoidea
Weyla bodenbenderi (Behrendsen)	Sin		S	Re	Pectinoidea
Weyla bodenbenderi (Behrendsen)	Pli		S	Re	Pectinoidea
Weyla bodenbenderi (Behrendsen)	Toa		S	Re	Pectinoidea
Weyla titan (Möricke)	Pli		S	Re	Pectinoidea
Weyla sp.	Sin		S	Re	Pectinoidea
Eopecten abjectus (Phillips)	Pli	_	Е	Be	Pectinoidea
Eopecten abjectus (Phillips)	Toa		Е	Be	Pectinoidea
Eopecten hartzi (Rosenkrantz)	Pli		Е	Be	Pectinoidea
Eopecten velatus (Goldfuss)	Het		Е	Be	Pectinoidea
Eopecten velatus (Goldfuss)	Sin		Е	Be	Pectinoidea
Eopecten velatus (Goldfuss)	Pli	_	Е	Be	Pectinoidea

Species Geographical r	ange	1	2	3	4	5	6	7	8	9	10	11	12	Lif	e habit	Superfamily
Camptonectes ? sp.	Pli							0000000						Е	Be	Pectinoidea
Camptonectes auritus (Schlotheim)	Pli													Е	Be	Pectinoidea
Camptonectes auritus (Schlotheim)	Тоа				00000									Е	Be	Pectinoidea
Camptonectes cf. subulatus (Münster)	Het													Е	Be	Pectinoidea
Camptonectes cf. subulatus (Münster)	Sin													Е	Be	Pectinoidea
Radulonectites sosneadoensis (Weaver)	Pli				_									E	Be	Pectinoidea
Radulonectites? sp.	Pli													Е	Be	Pectinoidea
Agerchlamys ? sp.	Het													Е	Be	Pectinoidea
Agerchlamys ? sp.	Sin													Е	Be	Pectinoidea
Agerchlamys sp.	Pli								-					F	Be	Pectinoidea
Agerchlamys wunschae (Marwick)	Pli											_		F	Be	Pectinoidea
Praechlamys cf. valoniensis (Defrance)	Het										Contracts			F	Be	Pectinoidea
Praechlamys cf. valoniensis (Defrance)	Sin													F	Be	Pectinoidea
Praechlamys of valoniensis (Defrance)	Dii								•					F	Be	Poctinoidea
"Chlamys" of tingensis (Tilmann)	r II Dli													F	Be	Pectinoidea
"Chlamys" cf. tingensis (Tilmann)	г II Тор													F	Be	Pectinoidea
"Chlamys" textoria (Schlotheim)	Het			66556										F	Be	Pectinoidea
"Chlamys" textoria (Schlotheim)	Sin													E	Be	Pectinoidea
"Chlamys" textoria (Schlotheim)	Pli													E	Be	Pectinoidea
"Chlamys" textoria (Schlotheim)	Тоа													Е	Be	Pectinoidea
Pseudopecten equivalvis (J. Sowerby)	Pli													Е	Re	Pectinoidea
Pseudopecten equivalvis (J. Sowerby)	Тоа													Е	Re	Pectinoidea
Pseudopecten sp.	Pli													F	Re	Pectinoidea
Terquemia ? sp.	Pli								_					F	Ce	Pectinoidea
Terguemia ? andina Damborenea	Toa							_						F	Ce	Pectinoidea
Plicatula (P.) armata Goldfuss	Sin													F	Ce	Plicatuloidea
Harpax rapa (Bayle et Coquand)	Sin													F	Ce	Plicatuloidea
Harpax rapa (Bayle et Coguand)	Dli													F	Ce	Plicatuloidea
Harpax rapa (Bayle et Coquand)	Toa				000000	•••	••••		000000	600600				F	Ce	Plicatuloidea
Placunopsis cf. striatula (Oppel)	Sin													E	Ce	Plicatuloidea
Placunopsis cf. striatula (Oppel)	Pli													E	Ce	Plicatuloidea
Placunopsis cf. striatula (Oppel)	Toa													F	Ce	Plicatuloidea
Atreta intusstriata (Emmrich)	Pli													F	Ce	Dimvoidea
Actinostreon costatum (J. de C. Sowerby)	Sin													F	Ce	Ostreoidea
Actinostreon costatum (J. de C. Sowerby)						•								F		Ostrooidea
Actinostreon longistriatum (Jaworski)	Sin															Ostreoidea
Actinostreon longistriatum (laworski)	5111					•									Ce	Ostreoidea
Actinostreon longistriatum (Jaworski)	Р11 Таа				600600		••••		000000	650650			0000000		Ce	Ostreoidea
Actinostreen politarium (L. Sowerby)	TUa Dii														Ce	Ostreoidea
Actinostreon solitarium (J. Sowerby)	<i>Р</i> т				-										Ce	Ostreoidea
Actinostreon solitarium (J. Sowerby)	Toa					•••	•••								Ce	Ostreoidea
Gryphaea (Bilobissa) lation Steinmann	Sin					•								E	Ce	Ostreoidea
Gryphaea (Bilobissa) latior Steinmann	Pli				000000									E	Ce	Ostreoidea
Gryphaea (Bilobissa) tricarinata Philippi	Sin						•							E	Ce	Ostreoidea
Gryphaea (G.) cf. dumortieri Joly	Sin					•								E	Ce	Ostreoidea
Gryphaea (G.) cf. dumortieri Joly	Pli						000000	000000	•••					E	Се	Ostreoidea
Gryphaea (G.) darwini (Forbes)	Het			••••		•••	•••							E	Ce	Ostreoidea
Gryphaea (G.) darwini (Forbes)	Sin													E	Ce	Ostreoidea
Gryphaea aff. cymbium	Sin													E	Ce	Ostreoidea
<i>Gryphaea (G.)</i> sp. B	Sin													Е	Ce	Ostreoidea
Gryphaea (G.) sp. B	Pli													E	Ce	Ostreoidea

Species Geographical ra	ange	1 2 3 4 5 6 7 8 9 10 11 12	Lif	e habit	Superfamily
Gryphaea (G.) sp. C	Sin		Е	Ce	Ostreoidea
Gryphaea (G.) sp. C	Pli		Е	Ce	Ostreoidea
Liostrea aff. hissingeri	Sin		Е	Ce	Ostreoidea
Liostrea aff. hissingeri	Pli		Е	Ce	Ostreoidea
Gryphaea (G.) sp.	Тоа		Е	Ce	Ostreoidea
<i>Exogyra (E.)</i> sp.	Sin		Е	Ce	Ostreoidea
<i>Exogyra (E.)</i> sp.	Pli		Е	Ce	Ostreoidea
<i>Exogyra (E.)</i> sp.	Тоа		Е	Ce	Ostreoidea
<i>Lithiotis</i> sp.	Тоа	_	Е	Ce	Pterioidea
Antiquilima cf. nagatoensis Hayami	Sin		Е	Be	Limoidea
Antiquilima succincta	Het		Е	Be	Limoidea
Antiquilima succincta	Sin		Е	Be	Limoidea
Antiquilima succincta	Pli		Е	Be	Limoidea
<i>Antiquilima</i> n. sp.	Sin		Е	Ne	Limoidea
<i>Antiquilima</i> n. sp.	Pli		Е	Ne	Limoidea
Antiquilima sp.	Pli		Е	Be	Limoidea
Antiquilima sp. Aberhan	Het		Е	Be	Limoidea
Plagiostoma giganteum J. Sowerby	Pli		Е	Be	Limoidea
Plagiostoma giganteum J. Sowerby	Тоа		Е	Be	Limoidea
Plagiostoma punctatum J. Sowerby	Sin		Е	Be	Limoidea
Plagiostoma punctatum J. Sowerby	Pli		Е	Be	Limoidea
Plagiostoma sp. A Aberhan	Het		Е	Be	Limoidea
Plagiostoma sp. A Aberhan	Sin		Е	Be	Limoidea
Plagiostoma sp. A Aberhan	Pli		Е	Be	Limoidea
Plagiostoma sp. A Aberhan	Тоа		Е	Be	Limoidea
Plagiostoma sp. B Aberhan	Sin		Е	Be	Limoidea
Plagiostoma sp. B Aberhan	Toa		Е	Be	Limoidea
Plagiostoma sp. B Aberhan	Pli		Е	Be	Limoidea
Plagiostoma sp. C Aberhan	Sin		Е	Be	Limoidea
Pseudolimea cf. roemeri (Brauns)	Pli	_	Е	Be	Limoidea
Pseudolimea cf. roemeri (Brauns)	Toa		Е	Be	Limoidea
Pseudolimea duplicata (J. de C. Sowerby)	Sin		Е	Be	Limoidea
Pseudolimea duplicata (J. de C. Sowerby)	Pli		Е	Be	Limoidea
Pseudolimea duplicata (J. de C. Sowerby)	Toa		Е	Be	Limoidea
Pseudolimea hettangiensis (Terquem)	Het		Е	Be	Limoidea
Pseudolimea hettangiensis (Terquem)	Sin		Е	Be	Limoidea
Ctenostreon cf. rugosum (Smith)	Pli	_	Е	Ne	Limoidea
Ctenostreon cf. rugosum (Smith)	Тоа		Е	Ne	Limoidea
Ctenostreon raricostatum (Bayle et Coquand)	Sin		Е	Ne	Limoidea
Ctenostreon raricostatum (Bayle et Coquand)	Pli		Е	Ne	Limoidea
Ctenostreon raricostatum (Bayle et Coquand)	Toa		Е	Ne	Limoidea
Groeberella neuquensis (Groeber)	Sin		I	Sb	Trigonioidea
Groeberella neuquensis (Groeber)	Pli		I	Sb	Trigonioidea
Groeberella neuquensis (Groeber)	Toa	_	Ι	Sb	Trigonioidea
Groeberella sp.	Sin		I	Sb	Trigonioidea
Prosogyrotrigonia tenuis Perez et al.	Het		Ι	Sb	Trigonioidea
Prosogyrotrigonia tenuis Perez et al.	Sin		Ι	Sb	Trigonioidea
Prosogyrotrigonia sp. 1 Pérez et al.	Sin		Ι	Sb	Trigonioidea
Prosogyrotrigonia sp. 2 Pérez et al.	Sin		Ι	Sb	Trigonioidea
Prosogyrotrigonia sp. 3 Pérez et al.	Sin		I	Sb	Trigonioidea

Species Geographical r	ango	1	2	3	4	5	6	7	8	٩	10	11	12	l if	o hahit	Superfamily
Erenquelliella chubutensis (Eeruglio)		•	-	5	-	5		-		5	10		12		Sh	Trigonioidoa
Frenquelliella inevsnectata (Jaworski)	rıı Di												000000		Sb	Trigonioidea
Frenquelliella poultoni Leanza	F II Sin			000000	••••	•••		000000		00000	00000		000000		Sh	Trigonioidea
Frenquelliella taniai (Lambert)	Sin														Sh	Trigonioidea
Frenquelliella tapiai (Lambert)	Dii													-	Sh	Trigonioidea
Frenquelliella tapiai (Lambert)	Too			ecoceas	••••			000000	600000	DECOED					Sh	Trigonioidea
Trigonia sp. 1 Pérez et al.	Toa			00000	••••		00000	00000	•••	60000		00000	00000	· ·	Sh	Trigonioidea
Trigonia sp. 2 Pérez et al.	Toa				00000										Sh	Trigonioidea
Trigonia (T.) stelzneri Gottsche	Toa				80880										Sh	Trigonioidea
Trigonia (T.) stelzneri Gottsche	Pli				00000	••••		00000	00000					· ·	Sh	Trigonioidea
Quadratojaworskiella acarinata Pérez et al.	Het	CONSCR			DOCIDION										Sh	Trigonioidea
Quadratojaworskiella acarinata Pérez et al.	Sin													· ·	Sh	Trigonioidea
Quadratojaworskiella pustulata (R. et P.)	Dli														Sh	Trigonioidea
Jaworskiella burckhardti (Jaworski)	Pli			000000											Sh	Trigonioidea
Jaworskiella burckhardti (Jaworski)	Toa										000000				Sh	Trigonioidea
Jaworskiella gryphitica (Möricke)	Sin				80000										Sh	Trigonioidea
Jaworskiella gryphitica (Möricke)	Pli								•					· ·	Sh	Trigonioidea
Jaworskiella sp. Pérez et al.	Sin				000000										Sh	Trigonioidea
Neuquenitrigonia huenickeni (Leanza et Garate)	Toa													· ·	Sh	Trigonioidea
Neuquenitrigonia plazaensis Pérez et al.	Toa														Sh	Trigonioidea
Psilotrigonia vegaensis Pérez et al.	Sin														Sh	Trigonioidea
Myophorella cf. araucana (Leanza)	Sin														Sb	Trigonioidea
Myophorella araucana (Leanza)	Pli														Sb	Trigonioidea
Myophorella araucana (Leanza)	Toa												00000		Sb	Trigonioidea
Myophorella cf. catenifera (Hupé)	Pli														Sb	Trigonioidea
Myophorella (M.) reginae Pérez et al.	Toa													I	Sb	Trigonioidea
Myophorella (M.) sp. 2 Pérez et al.	Pli														Sb	Trigonioidea
Scaphorella susanae Pérez et al.	Тоа													1	Sb	Trigonioidea
Vaugonia substriata (Burmeister et Giebel)	Тоа													1	Sb	Trigonioidea
Vaugonia substriata (Burmeister et Giebel)	Pli			000000										Ι	Sb	Trigonioidea
Vaugonia hectorleanzai Pérez et al.	Het													1	Sb	Trigonioidea
Vaugonia hectorleanzai Pérez et al.	Тоа													Ι	Sb	Trigonioidea
Vaugonia cf. gottschei (Möricke)	Pli													Ι	Sb	Trigonioidea
Vaugonia cf. gottschei (Möricke)	Тоа													Ι	Sb	Trigonioidea
Vaugonia sp. 1 Pérez et al.	Тоа													Ι	Sb	Trigonioidea
Vaugonia sp. 2 Pérez et al.	Pli			00000										Ι	Sb	Trigonioidea
"Lucina" atacamensis (Möricke)	Тоа			00000	85500									Ι	Db?	Lucinoidea
<i>"Lucina" chubutensis</i> Wahnish	Sin													Ι	Db?	Lucinoidea
<i>"Lucina" chubutensis</i> Wahnish	Pli													Ι	Db?	Lucinoidea
<i>"Lucina" feruglioi</i> Wahnish	Pli													Ι	Db?	Lucinoidea
Mesomiltha ? payllalefi Leanza	Sin													Ι	Db?	Lucinoidea
Mesomiltha ? payllalefi Leanza	Тоа													Ι	Db?	Lucinoidea
Mesomiltha ? payllalefi Leanza	Pli							000000			000000		000000	Ι	Db?	Lucinoidea
Mesomiltha cf. bellona (d'Orbigny)	Sin													Ι	Db?	Lucinoidea
Mesomiltha cf. bellona (d'Orbigny)	Тоа													Ι	Db?	Lucinoidea
Mesomiltha cf. bellona (d'Orbigny)	Pli			DOCTOR	000000									Ι	Db?	Lucinoidea
Mesomiltha huayquimili (Leanza)	Pli													Ι	Db?	Lucinoidea
Mesomiltha huayquimili Leanza	Toa													Ι	Db?	Lucinoidea
Mactromya ? sp.	Pli													Ι	Db?	Lucinoidea
Shaeriola? cf. leedae Marwick	Pli							600600						Ι	Db?	Lucinoidea

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Species Geographical ra	inge	1	2	3	4	5	6	7	8	9	10	11	12	Lif	e habit	Superfamily
Unicardium sp.	Sin													Т	Db?	Lucinoidea
<i>Unicardium</i> sp.	Pli			000000				000000						Ι	Db?	Lucinoidea
Kalentera n. sp.	Het													S?	Sb	Modiomorphoidea
Kalentera ? sp.	Sin													S?	Sb	Modiomorphoidea
Kalentera riccardii Damborenea	Pli							010102		000000				S?	Sb	Modiomorphoidea
Palaeopharus ? sp.	Sin													S?	Sb	Modiomorphoidea
Palaeopharus ? sp.	Pli													S?	Sb	Modiomorphoidea
Myoconcha neuquena Leanza	Тоа							00000						S?	Sb	Modiomorphoidea
Myoconcha neuquena Leanza	Pli			000000							000000			S?	Sb	Modiomorphoidea
Myoconcha sp.	Sin													S?	Sb	Modiomorphoidea
Cardinia andium (Giebel)	Sin					-		?							Sb	Crassatelloidea
Cardinia andium (Giebel)	Toa					-								1	Sb	Crassatelloidea
Cardinia andium (Giebel)	Pli													· 	Sb	Crassatelloidea
Cardinia cf. listeri (J. Sowerby)	Sin			600000			000000	00000		00000	COCCUS	DOCODO		· 1	Sh	Crassatelloidea
Cardinia multilamellosa Jaworski	Dii													· ·	Sh	Crassatelloidea
Coelastarte fuersichi Aberban	r II Dli			000000	•••	•••	666666	808088		600000	000000		400008	-	Sh	Crassatelloidea
	רוו חוי			000000										-	Sb	Crassatelloidea
	<i>Р</i> Т			000000	000000	••••	••••	000000	•••	000000	000000	••••	000000	-	30 Ch	Crassatelioidea
Neocrassina durenae (Ferugilo)	Toa				80008	00000	•••							-	SD	Crassatelloidea
	Toa			00000	•••	•••	00000	0000	•••	•••	•••	•••	80000	-	SD	Crassatelloidea
Neocrassina sp.	Sin													1	SD	Crassatelloidea
"Astarte" keideli Wahnish	PII Dii									000000	000000	•••		1	Sb	Crassatelloidea
Astartidae indet 1	r II Hot													-	Sh	Crassatelloidea
Astartidae indet. 1	Sin													<u> </u>	Sb	Crassatelloidea
Astartidae indet. 2	Sin														Sb	Crassatelloidea
Praeconia ? sp.	Тоа													I	Sb	Crassatelloidea
Trigonastarte ? sp.	Тоа							00000						Ι	Sb	Crassatelloidea
<i>Opis</i> sp.	Тоа							00000						Ι	Sb	Crassatelloidea
<i>Opisoma</i> cf. <i>excavatum</i> Boehm	Тоа				80008						?			Е	Re	Crassatelloidea
Cardinioides lanesae Damborenea	Sin													Ι	Sb	Unionoidea
Protocardia sp.	Sin													Т	Sb	Cardioidea
Protocardia sp.	Pli													· 	Sb	Cardioidea
Protocardia sp.	Тоа														Sb	Cardioidea
Protocardia striatula (Sowerby)	Pli			000000	000000									Ι	Sb	Cardioidea
Protocardia striatula (Sowerby)	Тоа													1	Sb	Cardioidea
Tancredia sp.	Sin													I	Db	Tellinoidea
Quenstedtia ? sp.	Sin					_								Т	Db	Tellinoidea
Quenstedtia ? sp.	Pli					-								· 	Db	Tellinoidea
Corbicellopsis ? sp.	Sin														Db	Tellinoidea
Arcticoidea indet	Sin					-									Sb	Arcticoidea
Anisocardia sp.	Sin														Dh	Arcticoidea
Anisocardia sp						•									Db	Arcticoidea
Isocyprina apcatruzi (Leanza)	Sin			000000	000000	•••	•••		•••	•••	•••		00000	· ·	Sh	Arcticoidea
Isocyprina ancatruzi (Leanza)	3111 Dii					•								-	Sh	Arcticoidea
	г II Тоо				800000	•••		000000			00000				Sh	Arcticoldea
	nua Dii			60300										1	Ch	Arctionidan
Alculude gen. et ap. nov. Abernan	г II DI;			000000	000000										50 Sh	Clossoides
Pseudisocardia 2 liasina (Wahilish)	г II Та -			000000		•••	•••	•••	•••	•••	•••				SU Ch	Giussoidea
	i oa							00000							30 05	Giossoidea
	PII	L						000000						1	SD	Giossoldea

Species Geographical ra	nde	1 2 3 4 5 6 7 8 9 10 11 12	l if	e habit	Superfamily
Pholadomya of orationsis Campbell et G-M	Lint Lint			Dh	Pholodomyoidoo
Pholadomya cf. oretiensis Campbell et C-M.	ne. Sim		-	Db	Pholadomyoidea
Pholadomya cf. oretiensis Campbell et C.M.	SITI		-	Db	Pholadomyoidea
Pholadomya off favrina Agassiz	PII	886		Db	Pholadomyoidea
Pholadomya all. lavina Agassiz	SITI		-	Db	Pholadomyoidea
Pholodomyo of obbroviate Huné	PII	00000 000 000 000 000		Db	Pholadomyoidea
Pholodomya Ci. abbreviata Hupe	PII			Db	Pholadomyoidea
Pholodomyo corrugata Koch et Dunker	Sin		÷	Db	Pholadomyoidea
Pholadomya conugata Koch et Dunker	Pli			Db	Pholadomyoidea
Pholadomya conugata Roch et Dunker	Toa		-		Pholadomyoidea
Pholadomya fidicula Sowerby	Sin		-	Db	Pholadomyoidea
Pholadomya fidicula Sowerby	Pli			Db	Pholadomyoidea
	Тоа			Db	Pholadomyoidea
Pholadomya multilineata Gabb	Pli			Db	Pholadomyoidea
Pholadomya cf. decorata	Sin			Db	Pholadomyoidea
Pholadomya cf. decorata	Pli			Db	Pholadomyoidea
Pholadomya hemicardia Roemer	Sin		Ι	Db	Pholadomyoidea
Pholadomyocardia sp.	Pli	8000	Ι	Db	Pholadomyoidea
Homomya neuquena Leanza	Pli		Ι	Db	Pholadomyoidea
Homomya neuquena Leanza	Тоа	_	1	Db	Pholadomyoidea
Pachymya rotundocaudata (Leanza)	Sin	······ ···· ···· ····	Ι	Db	Pholadomyoidea
Pachymya rotundocaudata (Leanza)	Pli		1	Db	Pholadomyoidea
Pachymya sp.	Тоа	_	Ι	Db	Pholadomyoidea
Goniomya cachinensis Aberhan	Het		Ι	Db	Pholadomyoidea
Goniomya asientosensis Aberhan	Pli		Ι	Db	Pholadomyoidea
Goniomya cf. proboscidea (Agassiz)	Sin		Ι	Db	Pholadomyoidea
Goniomya cf. proboscidea (Agassiz)	Pli		Ι	Db	Pholadomyoidea
Goniomya cf. proboscidea (Agassiz)	Тоа		Ι	Db	Pholadomyoidea
Osteomya cf. dilata (Phillips)	Sin		Ι	Db	Pholadomyoidea
Gresslya sp. A Aberhan	Sin		Ι	Db	Pholadomyoidea
Gresslya cf. peregrina (Phillips)	Pli		Ι	Db	Pholadomyoidea
Gresslya cf. peregrina (Phillips)	Тоа		Ι	Db	Pholadomyoidea
Pteromya sp.	Sin		Ι	Db	Pholadomyoidea
Pteromya sp.	Pli		Ι	Db	Pholadomyoidea
Pteromya sp.	Тоа		Ι	Db	Pholadomyoidea
Pleuromya galathea Agassiz	Het		Ι	Db	Pholadomyoidea
Pleuromya uniformis (J. Sowerby)	Sin			Db	Pholadomvoidea
Pleuromya uniformis (J. Sowerby)	Pli			Db	Pholadomvoidea
Pleuromya uniformis (Sowerby)	Тоа			Db	Pholadomvoidea
Ceratomya ? sp.	Sin			Db	Pholadomvoidea
Ceratomya sp.	Pli			Db	Pholadomyoidea
Ceratomya sp.	Тоа		Ì	Db	Pholadomyoidea
Thracia ? sp.	Toa		i	Db	Thracioidea
Cercomya sp.	Sin		i	Db	Thracioidea
Cercomva peruviana Cox	Pli		$\left \frac{1}{1} \right $	Dh	Thracioidea
Cercomya undulata (Sowerbv)	Toa		+	Dh	Thracioidea
Platymyoidea ? cf. longa (Buyignier)	, oa Dli		$\left \frac{1}{1} \right $	Dh	Thracioidea
Cen et sp indet Leanza	, " Dii		$\left \frac{1}{1} \right $	Dh	Cuspidarioidea 2
Gen. et sp. indet. Leanza	ГIÍ		1	00	Suspidariolued ?