

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

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**Key words:** South America, bivalves, palaeolatitudinal gradients, palaeogeography, Early Jurassic.

**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.

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## 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 well-documented 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 1<sup>1</sup>). 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 first-hand 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<sup>2</sup>) is a species list showing the distribution of 233 bivalves in thirteen areas (0–12), each with a latitudinal range of 2°, spanning a north-south 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

<sup>1</sup> See: <http://www.voluminajurassica.org/>.

<sup>2</sup> See: <http://www.voluminajurassica.org/>.

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 re-sampling 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 sub-

strate (*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

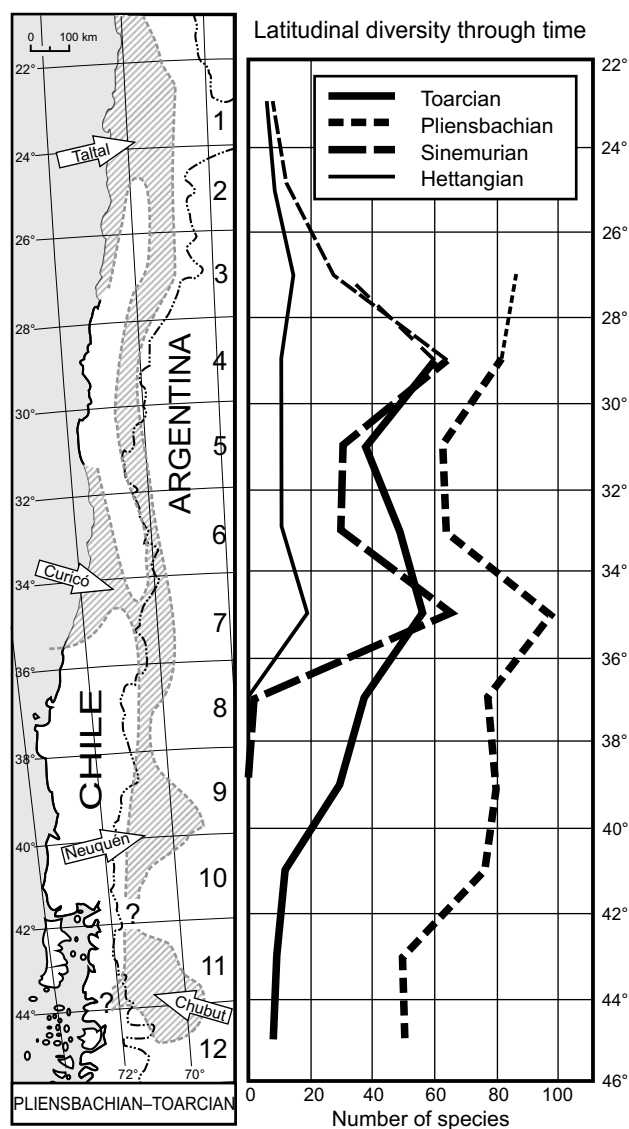


Fig. 1. Latitudinal diversity through time

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.

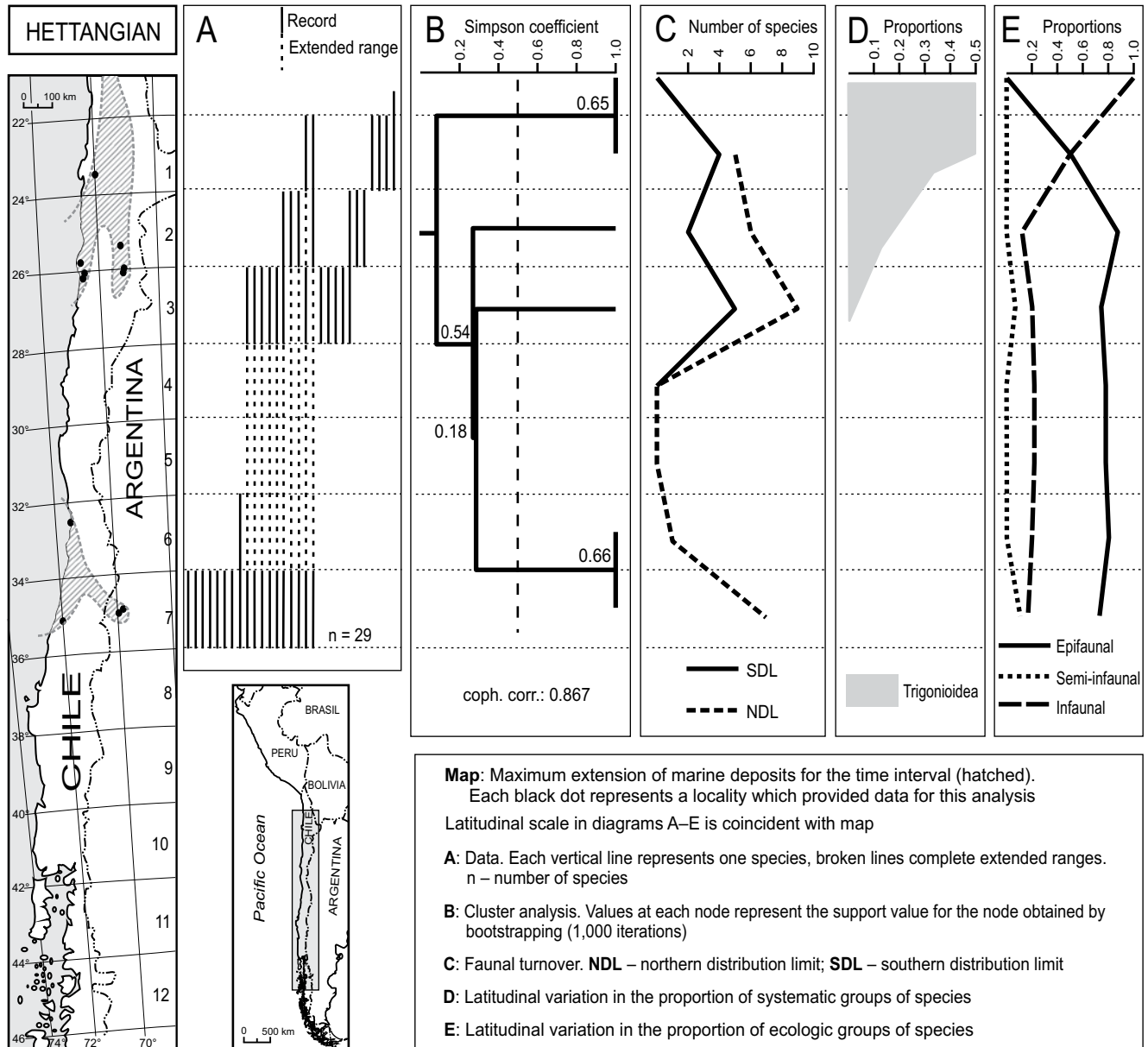


Fig. 2. Latitudinal diversity for Hettangian times

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, generalised linear model for life habits groups

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°.

## SINEMURIAN

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	Generalized linear model analysis results				Relative diversity	Comparable trends in living faunas	Comparable trends in Late Jurassic faunas
	Hettangian	Sinemurian	Pliensbachian	Toarcian			
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	decreasing towards higher latitudes	no data	
Limoidea				lp = -0.09 p = 0.048			Limidae (Crame, 2002)
Lucinoidea				lp = -0.31 p = 0.027		lucinoids (Crame, 2000a)	lucinoids (Crame, 2002)
Pholadomyoidea			lp = -0.05 p = 0.08				Pholadomyidae (Crame, 2002)
Pectinoidea				lp = 0.07 p = 0.009	decreasing towards lower latitudes	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			Nuculanidae (Roy <i>et al.</i> , 2000a) protobranchs (Crame, 2000a)	protobranchs (Crame, 2002)
Monotoidea				lp = 0.15 p = 0.001		extinct	Inoceramidae, Oxytomidae and Buchiidae (Crame, 1993, 2002)
Inoceramoidea			lp = 0.30 p = 0.042			extinct	
Arcoidea			lp = 0.06 p = 0.036				

\* Calculated excluding interval areas 1 and 2.

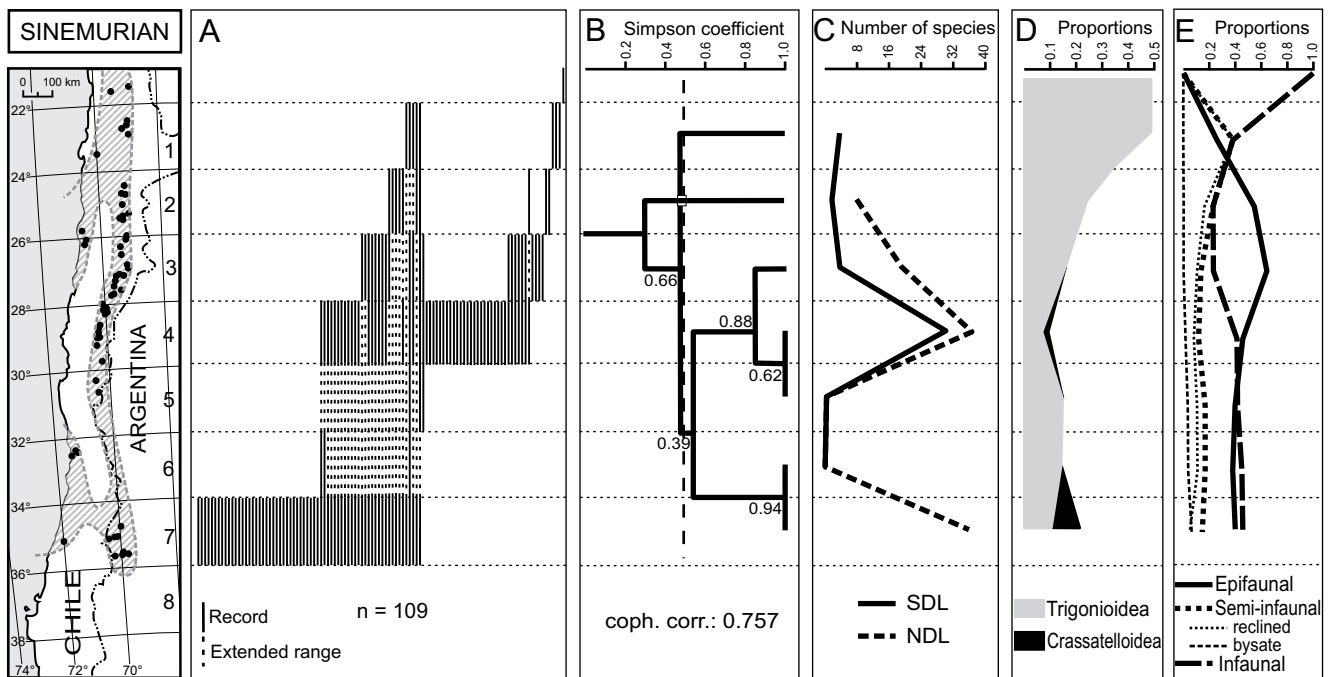


Fig. 3. Latitudinal diversity for Sinemurian times

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

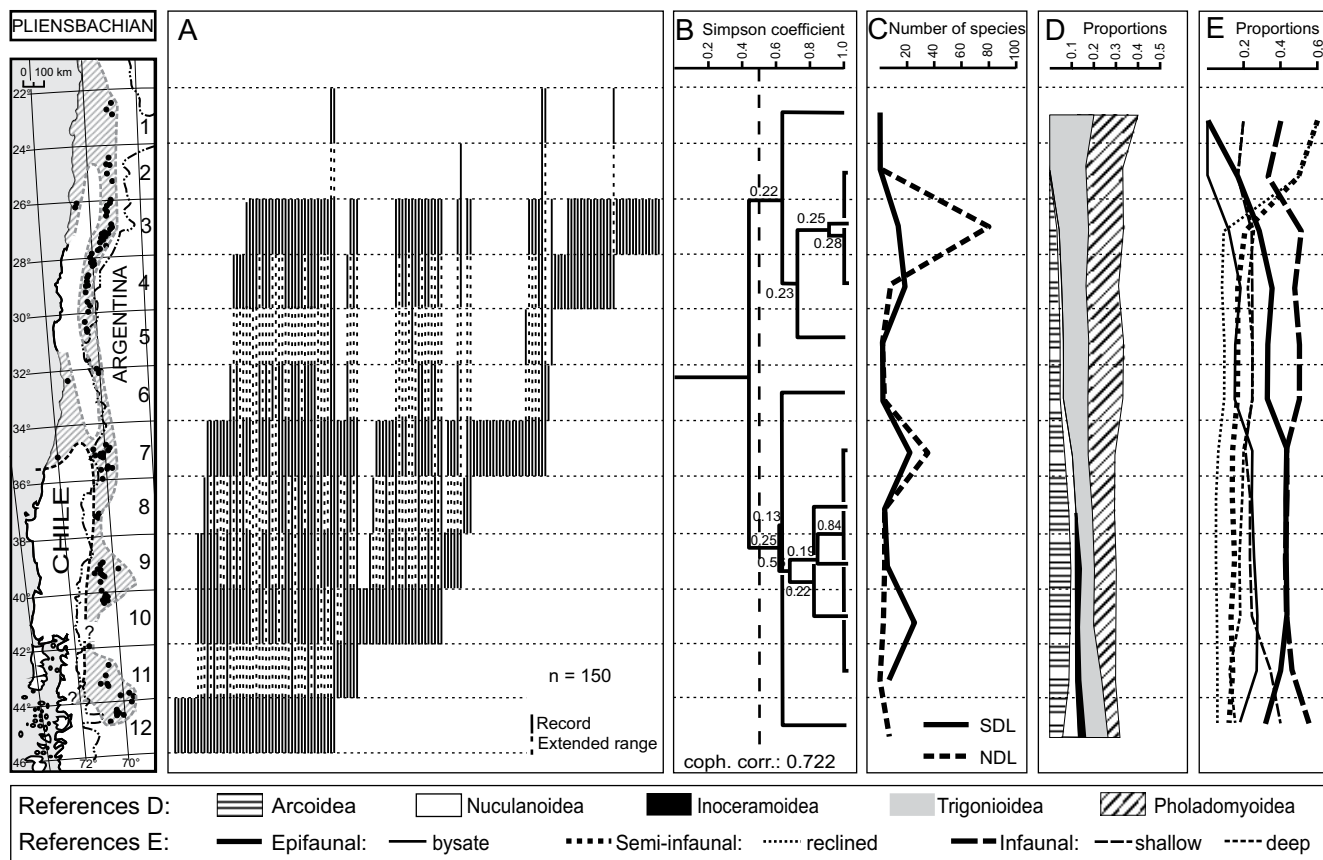
decreasing relative diversity at higher latitudes for the superfamily Trigonioidea when range extension data were used (Fig. 3D), although these results seem strongly influenced by the datum between 20 and 22°, which is a trigoniid species. On the other hand, the superfamily Crassatelloidea showed the 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°S) from southern ones (32–46°), 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



**Fig. 4. Latitudinal diversity for Pliensbachian times**

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 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 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-



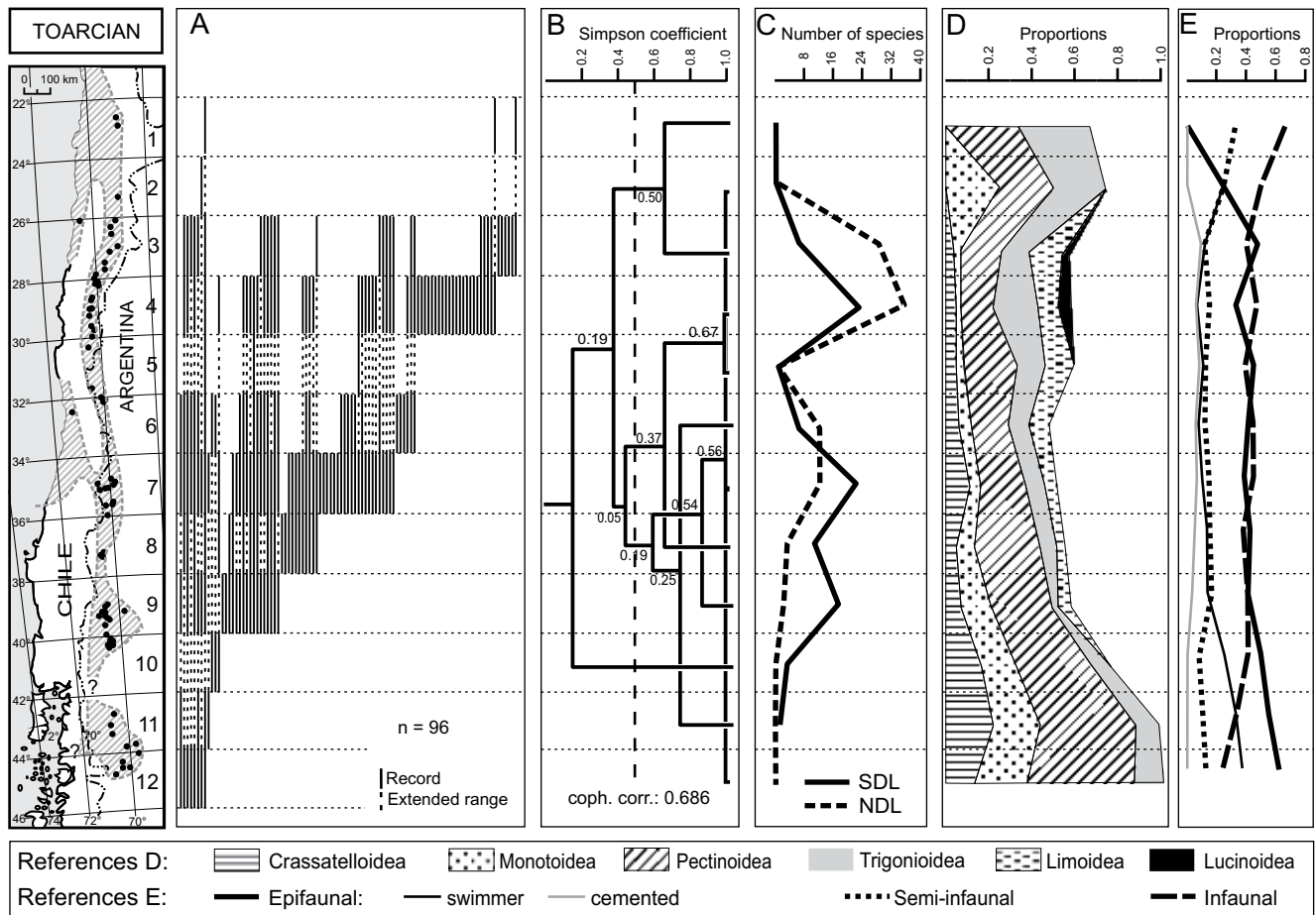
myoidea) decreased in the same direction (linear predictor:  $-0.034$ ;  $p = 0.037$ ) although they can be found up to lower latitudes than in previous stages.

### TOARCIAN

Toarcian faunas are widespread and relatively diverse (96 species), but less well known than Pliensbachian ones, especially south of  $40^\circ$  (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  $2^\circ$  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).

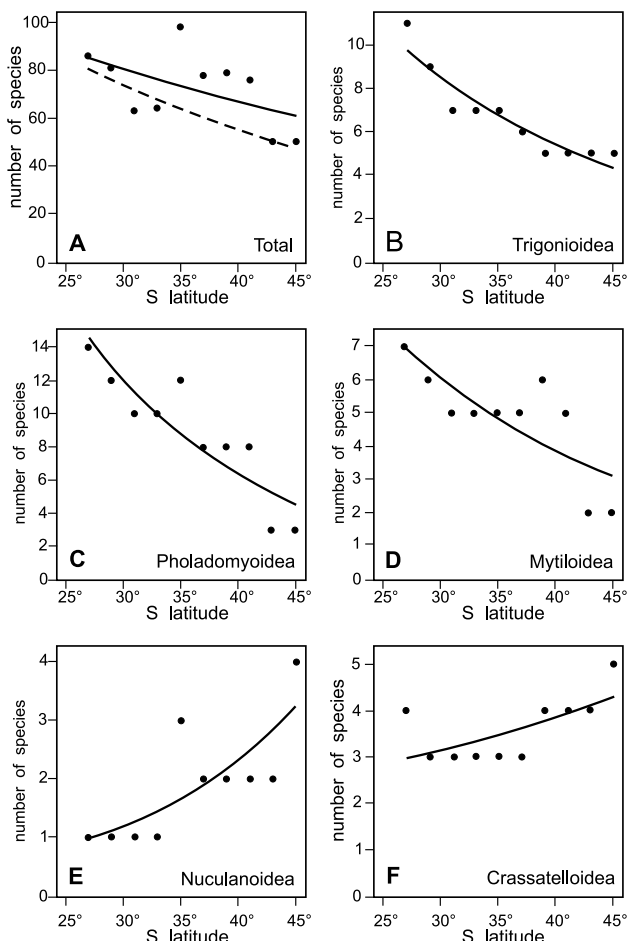
## DISCUSSION AND CONCLUSIONS

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



**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:  $0.021$ ,  $p = 0.49$ )

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 (Trigonoidea, 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, pteroids, pholadomyoids and arcoids display a steep decrease towards high latitudes (Crame, 2000a; Roy *et al.*, 2000a), also present in Late Jurassic myti-

loids (Crame, 2002). Although mytiloids and pteroids 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, pteroids 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 Trigonoidea in our study for Hettangian and Sinemurian

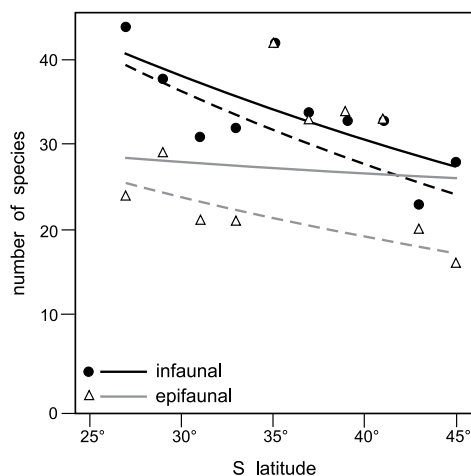
times may be related to the relatively young age of the lineage at that time, coincident with a great radiation of the group. Unfortunately, there are no comparable data about the latitudinal relative distribution of this diverse group during the Mesozoic; those from about a hundred Late Jurassic Trigoniidae 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:

- breaks in general latitudinal trends may be highly influenced by large scale geographical conditions;
- the history of relative diversity trends observed in different bivalve lineages may have been more complex and deeply rooted in time than previously thought.

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**Main localities and data sources for the latitudinal analysis along western South America.  
Data are arranged according to 13 areas with a 2<sup>o</sup> 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 <i>et al.</i> , 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; Pérez <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 Llaretta, Quebrada San Miguel, Figueroa, Río 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°	Río Manflas, Quebrada las Amolanas, La Iglesia, Río 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, Río 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, Río 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 Cucho, 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

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

Species	Geographical range		1	2	3	4	5	6	7	8	9	10	11	12	Life habit		Superfamily
															S	Bi	
<i>Modiolus lonsdalei</i> (Morris et Lycett)	<i>Pji</i>				---										S	Bi	Mytiloidea
<i>Modiolus chilensis</i> Aberhan	<i>Pji</i>			---	---										S	Bi	Mytiloidea
<i>Modiolus gerthi</i> Damborenea	<i>Pji</i>											---			S	Bi	Mytiloidea
<i>Modiolus gerthi</i> Damborenea	<i>Toa</i>			---	...	...	---	---	---	---	---				S	Bi	Mytiloidea
<i>Modiolus imbricatus</i> J. Sowerby	<i>Pji</i>			---											S	Bi	Mytiloidea
<i>Modiolus imbricatus</i> J. Sowerby	<i>Toa</i>			---	---										S	Bi	Mytiloidea
<i>Inoperna</i> ? sp.	<i>Sin</i>								.....						I	Bo?	Mytiloidea
<i>Inoperna</i> sp.	<i>Pji</i>							---							I	Bo?	Mytiloidea
<i>Lithophaga</i> ? sp.	<i>Pji</i>			---	---	...	...	---	---	---	---	---	---		I	Bo	Mytiloidea
<i>Lithophaga</i> ? sp.	<i>Toa</i>				---										I	Bo	Mytiloidea
<i>Pinna</i> cf. <i>folium</i> Young et Bird	<i>Het</i>								.....						S	Bi	Pinnoidea
<i>Pinna</i> cf. <i>folium</i> Young et Bird	<i>Sin</i>								.....						S	Bi	Pinnoidea
<i>Pinna</i> cf. <i>folium</i> Young et Bird	<i>Pji</i>							---	---	---	---	---	...	---	S	Bi	Pinnoidea
<i>Pinna</i> cf. <i>folium</i> Young et Bird	<i>Toa</i>				---	...	---	---	---	---	---				S	Bi	Pinnoidea
<i>Pinna</i> cf. <i>radiata</i> Münster	<i>Pji</i>			---	---										S	Bi	Pinnoidea
<i>Trichites</i> sp.	<i>Pji</i>								---						S	Ne	Pinnoidea
<i>Pteroperna</i> sp.	<i>Sin</i>								.....						E	Be	Pterioidea
<i>Pteroperna</i> sp.	<i>Pji</i>								---	...	---				E	Be	Pterioidea
<i>Aguirella kobyi</i> (Loriol)	<i>Sin</i>					.....									E	Be	Pterioidea
<i>Aguirella neuquensis</i> Damborenea	<i>Pji</i>											---			E	Be	Pterioidea
" <i>Pteria</i> " sp.	<i>Het</i>			.....											E	Be	Pterioidea
<i>Gervillia</i> ( <i>Cultrioipsis</i> ) sp.	<i>Sin</i>								.....						E	Be	Pterioidea
<i>Gervillia</i> ( <i>Cultrioipsis</i> ) sp.	<i>Pji</i>								---	...	---	---	---		E	Be	Pterioidea
<i>Gervillia</i> ( <i>Cultrioipsis</i> ) sp.	<i>Toa</i>							---	---	---	---	---	---		E	Be	Pterioidea
<i>Bakevillia waltoni</i> (Lycett)	<i>Sin</i>					.....									E	Be	Pterioidea
<i>Bakevillia pintadae</i> Damborenea	<i>Pji</i>			---	...	...	...	...	...	...	...	---			E	Be	Pterioidea
<i>Gervillela araucana</i> Damborenea	<i>Sin</i>					.....	.....	.....	.....						S?	Be?	Pterioidea
<i>Gervillela araucana</i> Damborenea	<i>Pji</i>			---	---	...	...	---	---	---	---	---	---		S?	Be?	Pterioidea
<i>Gervillela</i> cf. <i>aviculoides</i> (Sowerby) ?	<i>Sin</i>								.....						S?	Be?	Pterioidea
<i>Gervillaria</i> ? <i>ashcroftensis</i> (Crickmay)	<i>Pji</i>			---											S?	Re	Pterioidea
<i>Gervillaria</i> ? <i>ashcroftensis</i> (Crickmay)	<i>Toa</i>				---										S?	Re	Pterioidea
<i>Gervillaria alaeformis</i> (Sowerby)	<i>Pji</i>			---	...	...	...	---							S?	Re	Pterioidea
<i>Gervillaria alaeformis</i> (J. Sowerby)	<i>Toa</i>			---	---										S?	Re	Pterioidea
<i>Gervillaria hartmanni</i> (Münster)	<i>Sin</i>					.....									S?	Re	Pterioidea
<i>Gervillaria hartmanni</i> (Münster)	<i>Toa</i>				---										S?	Re	Pterioidea
<i>Gervillaria pallas</i> (Leanza)	<i>Sin</i>					.....	.....	.....							S?	Re	Pterioidea
<i>Gervillaria pallas</i> (Leanza)	<i>Pji</i>			---	---	...	...	---	---	---	---	---	...	---	S?	Re	Pterioidea
<i>Gervillaria pallas</i> (Leanza)	<i>Toa</i>							---							S?	Re	Pterioidea
<i>Gervilleioperna</i> ( <i>Gervilletia</i> ) <i>turgida</i> (Leanza)	<i>Sin</i>					.....									S?	Re	Pterioidea
<i>Gervilleioperna</i> ( <i>Gervilletia</i> ) <i>turgida</i> (Leanza)	<i>Pji</i>			---	---	---	...	...	...	...	---				S?	Re	Pterioidea
<i>Gervilleioperna</i> ( <i>Gervilletia</i> ) <i>turgida</i> (Leanza)	<i>Toa</i>							---							S?	Re	Pterioidea
<i>Gervilleioperna</i> ( <i>Gervilleiognoma</i> ) <i>aurita</i> A. et H.	<i>Toa</i>				---										S?	Re	Pterioidea
<i>Parainoceramus</i> ? sp.	<i>Het</i>								.....						E	Be	Inoceramoidea
<i>Parainoceramus apollo</i> (Leanza)	<i>Pji</i>										---	---	...	---	E	Be	Inoceramoidea
<i>Parainoceramus apollo</i> ? (Leanza)	<i>Sin</i>					.....									E	Be	Inoceramoidea
Inoceramidae gen. et ap. indet.	<i>Toa</i>									---					E	Be	Inoceramoidea
<i>Isognomon jupiter</i> (Leanza)	<i>Sin</i>								---						E	Be	Pterioidea
<i>Isognomon jupiter</i> (Leanza)	<i>Pji</i>				---	...	---	---	---	---	---	---	...	---	E	Be	Pterioidea
<i>Isognomon jupiter</i> (Leanza)	<i>Toa</i>				---	...	---	---	---	---	---				E	Be	Pterioidea

Species	Geographical range	1	2	3	4	5	6	7	8	9	10	11	12	Life habit	Superfamily	
<i>Hypotrema liasica</i> (Damborenea)	<i>Pli</i>							—						E	Be	Pterioidea
<i>Asoella asapha</i> (Leanza)	<i>Sin</i>							-----						E	Be	Monotoidea
<i>Asoella asapha</i> (Leanza)	<i>Pli</i>							—	...	...	—			E	Be	Monotoidea
<i>Otapiria neuquensis</i> Damborenea	<i>Sin</i>		-----											E	Be	Monotoidea
<i>Otapiria neuquensis</i> Damborenea	<i>Pli</i>							—	...	...	—			E	Be	Monotoidea
<i>Otapiria pacifica</i> Covacevich et Escobar	<i>Het</i>							-----						E	Be	Monotoidea
<i>Otapiria pacifica</i> Covacevich et Escobar	<i>Sin</i>		-----	.....	.....	.....	.....	-----						E	Be	Monotoidea
<i>Arctotis ? frenguelli</i> Damborenea	<i>Toa</i>												—	E	Be	Monotoidea
<i>Oxytoma inequivalvis</i> (J. Sowerby)	<i>Het</i>		-----											E	Be	Monotoidea
<i>Oxytoma inequivalvis</i> (J. Sowerby)	<i>Sin</i>		-----	.....	.....									E	Be	Monotoidea
<i>Oxytoma inequivalvis</i> (J. Sowerby)	<i>Pli</i>			—	...	...	...	—	—	—	—	—	—	E	Be	Monotoidea
<i>Oxytoma inequivalvis</i> (J. Sowerby)	<i>Toa</i>						—	—	...	—				E	Be	Monotoidea
<i>Palmoxytoma cf. cygnipes</i> (Young et Bird)	<i>Het</i>		-----	.....	.....	.....	.....	-----						E	Be	Monotoidea
<i>Meleagrinnella</i> sp.	<i>Toa</i>						—	—	...	—	...	—	—	E	Be	Monotoidea
<i>Bositra ornati</i> (Quenstedt)	<i>Toa</i>		—	...	...	...	...	...	...	...	...	...	—	E	Sw?	Monotoidea
<i>Ochotochlamys</i> sp.	<i>Pli</i>												—	E	Be	Pectinoidea
<i>Kolymonectes weaveri</i> Damborenea	<i>Pli</i>							—	—	—	—	—	—	E	Re-Sw	Pectinoidea
<i>Kolymonectes</i> sp.	<i>Sin</i>							-----						E	Re-Sw	Pectinoidea
<i>Parvamussium pumilum</i> (Lamarck)	<i>Toa</i>		—	—	...	—	—	—	...	...	...	...	—	E	Re-Sw	Pectinoidea
<i>Entolium cf. lunare</i> (Roemer)	<i>Het</i>		-----											E	Re-Sw	Pectinoidea
<i>Entolium cf. lunare</i> (Roemer)	<i>Sin</i>				-----	.....	.....							E	Re-Sw	Pectinoidea
<i>Entolium cf. lunare</i> (Roemer)	<i>Pli</i>			—	—	...	—	—	—	—	—	...	—	E	Re-Sw	Pectinoidea
<i>Entolium cf. lunare</i> (Roemer)	<i>Toa</i>		—	—	...	...	—							E	Re-Sw	Pectinoidea
<i>Entolium disciforme</i> (Schübler)	<i>Pli</i>							—	—	—	...	—		E	Re-Sw	Pectinoidea
<i>Entolium disciforme</i> (Schübler)	<i>Toa</i>						—	...	—					E	Re-Sw	Pectinoidea
<i>Entolium ? sp.</i>	<i>Het</i>							—						E	Re-Sw	Pectinoidea
<i>Entolium ? sp.</i>	<i>Sin</i>						—							E	Re-Sw	Pectinoidea
<i>Entolium mapuche</i> Damborenea	<i>Pli</i>							—	...	...	—			E	Re-Sw	Pectinoidea
<i>Entolium mapuche</i> Damborenea	<i>Toa</i>							—	—					E	Re Sw	Pectinoidea
<i>Posidonotis cancellata</i> (Leanza)	<i>Pli</i>		—	—	—	...	...	...	...	—				E	Re-Sw	Pectinoidea
<i>Posidonotis cancellata</i> (Leanza)	<i>Toa</i>		—	—	...	—	—	—	—	...	...	—		E	Re-Sw	Pectinoidea
<i>Lywea ? sp.</i>	<i>Het</i>		-----											S	Re	Pectinoidea
<i>Lywea unca</i> (Philippi)	<i>Sin</i>		-----	.....	.....	.....	.....	-----						S	Re	Pectinoidea
<i>Lywea unca</i> (Philippi)	<i>Pli</i>		—	...	—	—	—	—	—	—	—	...	—	S	Re	Pectinoidea
<i>Lywea unca</i> (Philippi)	<i>Toa</i>				—	...	...	—	—	—				S	Re	Pectinoidea
<i>Weyla alata angustecosta</i> (Philippi)	<i>Toa</i>		—	...	—	—	—	—	—	—	...	—	—	S	Re	Pectinoidea
<i>Weyla alata alata</i> (von Buch)	<i>Sin</i>		-----	.....	.....	.....	.....	-----						S	Re	Pectinoidea
<i>Weyla alata alata</i> (von Buch)	<i>Pli</i>		—	—	—	—	—	—	—	—	—	—	—	S	Re	Pectinoidea
<i>Weyla bodenbenderi</i> (Behrendsen)	<i>Sin</i>		-----											S	Re	Pectinoidea
<i>Weyla bodenbenderi</i> (Behrendsen)	<i>Pli</i>		—	...	—	—	—	—	—	—	—	—	—	S	Re	Pectinoidea
<i>Weyla bodenbenderi</i> (Behrendsen)	<i>Toa</i>				—	...	—	—	...	—				S	Re	Pectinoidea
<i>Weyla titan</i> (Möricke)	<i>Pli</i>			—	—									S	Re	Pectinoidea
<i>Weyla</i> sp.	<i>Sin</i>							-----						S	Re	Pectinoidea
<i>Eopecten abjectus</i> (Phillips)	<i>Pli</i>			—										E	Be	Pectinoidea
<i>Eopecten abjectus</i> (Phillips)	<i>Toa</i>				—	...	...	—	—					E	Be	Pectinoidea
<i>Eopecten hartzii</i> (Rosenkrantz)	<i>Pli</i>							—	—	—	...	—		E	Be	Pectinoidea
<i>Eopecten velatus</i> (Goldfuss)	<i>Het</i>		-----	.....	.....	.....	.....	-----						E	Be	Pectinoidea
<i>Eopecten velatus</i> (Goldfuss)	<i>Sin</i>				-----	.....	.....	-----						E	Be	Pectinoidea
<i>Eopecten velatus</i> (Goldfuss)	<i>Pli</i>				—									E	Be	Pectinoidea

Species	Geographical range	1	2	3	4	5	6	7	8	9	10	11	12	Life habit	Superfamily
<i>Camptonectes</i> ? sp.	<i>Pli</i>							—	...	...	—			E Be	Pectinoidea
<i>Camptonectes auritus</i> (Schlotheim)	<i>Pli</i>			—	...	...	...	—						E Be	Pectinoidea
<i>Camptonectes auritus</i> (Schlotheim)	<i>Toa</i>				—	...	...	—						E Be	Pectinoidea
<i>Camptonectes</i> cf. <i>subulatus</i> (Münster)	<i>Het</i>							.....						E Be	Pectinoidea
<i>Camptonectes</i> cf. <i>subulatus</i> (Münster)	<i>Sin</i>							.....						E Be	Pectinoidea
<i>Radulonectites sosneadoensis</i> (Weaver)	<i>Pli</i>			—	—	...	...	—	...	—	—	...	—	E Be	Pectinoidea
<i>Radulonectites</i> ? sp.	<i>Pli</i>							—						E Be	Pectinoidea
<i>Agerchlamys</i> ? sp.	<i>Het</i>			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	E Be	Pectinoidea
<i>Agerchlamys</i> ? sp.	<i>Sin</i>			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	E Be	Pectinoidea
<i>Agerchlamys</i> sp.	<i>Pli</i>							—						E Be	Pectinoidea
<i>Agerchlamys wunschae</i> (Marwick)	<i>Pli</i>							—	—	—	—	—	—	E Be	Pectinoidea
<i>Praechlamys</i> cf. <i>valoniensis</i> (Defrance)	<i>Het</i>			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	E Be	Pectinoidea
<i>Praechlamys</i> cf. <i>valoniensis</i> (Defrance)	<i>Sin</i>			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	E Be	Pectinoidea
<i>Praechlamys</i> cf. <i>valoniensis</i> (Defrance)	<i>Pli</i>							—						E Be	Pectinoidea
" <i>Chlamys</i> " cf. <i>tingensis</i> (Tilmann)	<i>Pli</i>			—	—									E Be	Pectinoidea
" <i>Chlamys</i> " cf. <i>tingensis</i> (Tilmann)	<i>Toa</i>			—										E Be	Pectinoidea
" <i>Chlamys</i> " <i>textoria</i> (Schlotheim)	<i>Het</i>			.....										E Be	Pectinoidea
" <i>Chlamys</i> " <i>textoria</i> (Schlotheim)	<i>Sin</i>			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	E Be	Pectinoidea
" <i>Chlamys</i> " <i>textoria</i> (Schlotheim)	<i>Pli</i>			—	—	...	—	—	—	—	—	...	—	E Be	Pectinoidea
" <i>Chlamys</i> " <i>textoria</i> (Schlotheim)	<i>Toa</i>			—	—	...	—	—	—	—	...	...	—	E Be	Pectinoidea
<i>Pseudopecten equivalvis</i> (J. Sowerby)	<i>Pli</i>			—	...	...	—	—	—	—	...	...	—	E Re	Pectinoidea
<i>Pseudopecten equivalvis</i> (J. Sowerby)	<i>Toa</i>								—					E Re	Pectinoidea
<i>Pseudopecten</i> sp.	<i>Pli</i>							—						E Re	Pectinoidea
<i>Terquemia</i> ? sp.	<i>Pli</i>							—						E Ce	Pectinoidea
<i>Terquemia</i> ? <i>andina</i> Damborenea	<i>Toa</i>							—	—	—				E Ce	Pectinoidea
<i>Plicatula</i> ( <i>P.</i> ) <i>armata</i> Goldfuss	<i>Sin</i>			.....	.....									E Ce	Plicatuloidea
<i>Harpax rapa</i> (Bayle et Coquand)	<i>Sin</i>			.....	.....									E Ce	Plicatuloidea
<i>Harpax rapa</i> (Bayle et Coquand)	<i>Pli</i>			—	—	...	...	—	—	—	—	—	—	E Ce	Plicatuloidea
<i>Harpax rapa</i> (Bayle et Coquand)	<i>Toa</i>							—						E Ce	Plicatuloidea
<i>Placunopsis</i> cf. <i>striatula</i> (Oppel)	<i>Sin</i>			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	E Ce	Plicatuloidea
<i>Placunopsis</i> cf. <i>striatula</i> (Oppel)	<i>Pli</i>			—	...	...	...	—	—	—	—	—	—	E Ce	Plicatuloidea
<i>Placunopsis</i> cf. <i>striatula</i> (Oppel)	<i>Toa</i>			—										E Ce	Plicatuloidea
<i>Atreta intusstriata</i> (Emmrich)	<i>Pli</i>												—	E Ce	Dimyioidea
<i>Actinostreon costatum</i> (J. de C. Sowerby)	<i>Sin</i>			.....	.....									E Ce	Ostreoidea
<i>Actinostreon costatum</i> (J. de C. Sowerby)	<i>Pli</i>			—										E Ce	Ostreoidea
<i>Actinostreon longistriatum</i> (Jaworski)	<i>Sin</i>			.....	.....									E Ce	Ostreoidea
<i>Actinostreon longistriatum</i> (Jaworski)	<i>Pli</i>			—	—	...	...	—	—	—	—	...	—	E Ce	Ostreoidea
<i>Actinostreon longistriatum</i> (Jaworski)	<i>Toa</i>			—	...	...	—							E Ce	Ostreoidea
<i>Actinostreon solitarium</i> (J. Sowerby)	<i>Pli</i>			—	—									E Ce	Ostreoidea
<i>Actinostreon solitarium</i> (J. Sowerby)	<i>Toa</i>			—	—	...	...	—						E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>Bilobissa</i> ) <i>latior</i> Steinmann	<i>Sin</i>			.....	.....									E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>Bilobissa</i> ) <i>latior</i> Steinmann	<i>Pli</i>			—	—									E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>Bilobissa</i> ) <i>tricarinata</i> Philippi	<i>Sin</i>			.....	.....	.....	.....							E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>G.</i> ) cf. <i>dumortieri</i> Joly	<i>Sin</i>			.....	.....									E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>G.</i> ) cf. <i>dumortieri</i> Joly	<i>Pli</i>			—	—	...	—	—	...	—	...	...	—	E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>G.</i> ) <i>darwini</i> (Forbes)	<i>Het</i>			.....	...	...	...	.....	.....	.....	.....	.....	.....	E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>G.</i> ) <i>darwini</i> (Forbes)	<i>Sin</i>			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	E Ce	Ostreoidea
<i>Gryphaea</i> aff. <i>cymbium</i>	<i>Sin</i>			.....	.....	.....	.....							E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>G.</i> ) sp. B	<i>Sin</i>			.....	.....	.....	.....							E Ce	Ostreoidea
<i>Gryphaea</i> ( <i>G.</i> ) sp. B	<i>Pli</i>							.....						E Ce	Ostreoidea

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

Species	Geographical range	1	2	3	4	5	6	7	8	9	10	11	12	Life habit	Superfamily	
<i>Frenguelliella chubutensis</i> (Feruglio)	<i>Pli</i>												---		Sb	Trigonoidea
<i>Frenguelliella inexpectata</i> (Jaworski)	<i>Pli</i>			---	...	...	...	---	...	---	---	...	---		Sb	Trigonoidea
<i>Frenguelliella poultoni</i> Leanza	<i>Sin</i>		-----	.....	.....	.....	.....	.....							Sb	Trigonoidea
<i>Frenguelliella tapiai</i> (Lambert)	<i>Sin</i>							---							Sb	Trigonoidea
<i>Frenguelliella tapiai</i> (Lambert)	<i>Pli</i>			---	...	...	...	---	---	---	---	...	---		Sb	Trigonoidea
<i>Frenguelliella tapiai</i> (Lambert)	<i>Toa</i>			---	...	...	---	---	---	---	---	---	---		Sb	Trigonoidea
<i>Trigonia</i> sp. 1 Pérez et al.	<i>Toa</i>				---										Sb	Trigonoidea
<i>Trigonia</i> sp. 2 Pérez et al.	<i>Toa</i>				---										Sb	Trigonoidea
<i>Trigonia (T.) stelzneri</i> Gottsche	<i>Toa</i>				---	...	...	---	---						Sb	Trigonoidea
<i>Trigonia (T.) stelzneri</i> Gottsche	<i>Pli</i>	---	...	...	---										Sb	Trigonoidea
<i>Quadratojaworskiella acarinata</i> Pérez et al.	<i>Het</i>		-----												Sb	Trigonoidea
<i>Quadratojaworskiella acarinata</i> Pérez et al.	<i>Sin</i>			-----											Sb	Trigonoidea
<i>Quadratojaworskiella pustulata</i> (R. et P.)	<i>Pli</i>			---											Sb	Trigonoidea
<i>Jaworskiella burckhardtii</i> (Jaworski)	<i>Pli</i>			---	---	...	...	...	...	...	---	...	---		Sb	Trigonoidea
<i>Jaworskiella burckhardtii</i> (Jaworski)	<i>Toa</i>				---	...	...	---							Sb	Trigonoidea
<i>Jaworskiella gryphitica</i> (Möricke)	<i>Sin</i>				-----	.....	.....	.....							Sb	Trigonoidea
<i>Jaworskiella gryphitica</i> (Möricke)	<i>Pli</i>			---	---										Sb	Trigonoidea
<i>Jaworskiella</i> sp. Pérez et al.	<i>Sin</i>	-----													Sb	Trigonoidea
<i>Neuquenitrigonia huenickeni</i> (Leanza et Garate)	<i>Toa</i>				---										Sb	Trigonoidea
<i>Neuquenitrigonia plazaensis</i> Pérez et al.	<i>Toa</i>				---										Sb	Trigonoidea
<i>Psilotrigonia vegaensis</i> Pérez et al.	<i>Sin</i>		-----												Sb	Trigonoidea
<i>Myophorella</i> cf. <i>araucana</i> (Leanza)	<i>Sin</i>							-----							Sb	Trigonoidea
<i>Myophorella araucana</i> (Leanza)	<i>Pli</i>			---	---	...	---	---	---	---	---	---	---		Sb	Trigonoidea
<i>Myophorella araucana</i> (Leanza)	<i>Toa</i>				---	...	---	---	---						Sb	Trigonoidea
<i>Myophorella</i> cf. <i>catenifera</i> (Hupé)	<i>Pli</i>					---	...	---							Sb	Trigonoidea
<i>Myophorella (M.) reginae</i> Pérez et al.	<i>Toa</i>			---											Sb	Trigonoidea
<i>Myophorella (M.)</i> sp. 2 Pérez et al.	<i>Pli</i>			---											Sb	Trigonoidea
<i>Scaphorella susanae</i> Pérez et al.	<i>Toa</i>			---											Sb	Trigonoidea
<i>Vaugonia substriata</i> (Burmeister et Giebel)	<i>Toa</i>				---	...	---	---							Sb	Trigonoidea
<i>Vaugonia substriata</i> (Burmeister et Giebel)	<i>Pli</i>			---	...	...	...	---	---						Sb	Trigonoidea
<i>Vaugonia hectorleanzai</i> Pérez et al.	<i>Het</i>	---													Sb	Trigonoidea
<i>Vaugonia hectorleanzai</i> Pérez et al.	<i>Toa</i>	---	...	...	---										Sb	Trigonoidea
<i>Vaugonia</i> cf. <i>gottschei</i> (Möricke)	<i>Pli</i>				---										Sb	Trigonoidea
<i>Vaugonia</i> cf. <i>gottschei</i> (Möricke)	<i>Toa</i>				---										Sb	Trigonoidea
<i>Vaugonia</i> sp. 1 Pérez et al.	<i>Toa</i>				---										Sb	Trigonoidea
<i>Vaugonia</i> sp. 2 Pérez et al.	<i>Pli</i>			---											Sb	Trigonoidea
" <i>Lucina</i> " <i>atacamensis</i> (Möricke)	<i>Toa</i>			---	---										Db?	Lucinoidea
" <i>Lucina</i> " <i>chubutensis</i> Wahnish	<i>Sin</i>				-----										Db?	Lucinoidea
" <i>Lucina</i> " <i>chubutensis</i> Wahnish	<i>Pli</i>												---		Db?	Lucinoidea
" <i>Lucina</i> " <i>feruglioi</i> Wahnish	<i>Pli</i>												---		Db?	Lucinoidea
<i>Mesomiltha</i> ? <i>payllalefi</i> Leanza	<i>Sin</i>							-----							Db?	Lucinoidea
<i>Mesomiltha</i> ? <i>payllalefi</i> Leanza	<i>Toa</i>				---										Db?	Lucinoidea
<i>Mesomiltha</i> ? <i>payllalefi</i> Leanza	<i>Pli</i>							---	...	...	---	...	---		Db?	Lucinoidea
<i>Mesomiltha</i> cf. <i>bellona</i> (d'Orbigny)	<i>Sin</i>				-----										Db?	Lucinoidea
<i>Mesomiltha</i> cf. <i>bellona</i> (d'Orbigny)	<i>Toa</i>				---										Db?	Lucinoidea
<i>Mesomiltha</i> cf. <i>bellona</i> (d'Orbigny)	<i>Pli</i>			---	---										Db?	Lucinoidea
<i>Mesomiltha huayquimili</i> (Leanza)	<i>Pli</i>			---	...	...	...	...	...	...	---	...	---		Db?	Lucinoidea
<i>Mesomiltha huayquimili</i> Leanza	<i>Toa</i>				---										Db?	Lucinoidea
<i>Mactromya</i> ? sp.	<i>Pli</i>							---							Db?	Lucinoidea
<i>Shaeriola</i> ? cf. <i>leedae</i> Marwick	<i>Pli</i>							---	...	---					Db?	Lucinoidea



Species	Geographical range													Life habit		Superfamily		
		1	2	3	4	5	6	7	8	9	10	11	12					
<i>Unicardium</i> sp.	<i>Sin</i>				.....	.....	.....	.....								I	Db?	Lucinoidea
<i>Unicardium</i> sp.	<i>Pli</i>			---	...	...	...	---	---							I	Db?	Lucinoidea
<i>Kalentera</i> n. sp.	<i>Het</i>							.....								S?	Sb	Modiomorpoidea
<i>Kalentera</i> ? sp.	<i>Sin</i>			.....	.....	.....	.....	.....								S?	Sb	Modiomorpoidea
<i>Kalentera riccardii</i> Damborenea	<i>Pli</i>							---	...	---						S?	Sb	Modiomorpoidea
<i>Palaeopharus</i> ? sp.	<i>Sin</i>							.....								S?	Sb	Modiomorpoidea
<i>Palaeopharus</i> ? sp.	<i>Pli</i>			---												S?	Sb	Modiomorpoidea
<i>Myoconcha neuquena</i> Leanza	<i>Toa</i>															S?	Sb	Modiomorpoidea
<i>Myoconcha neuquena</i> Leanza	<i>Pli</i>			---	---	...	...	---	...	---	...	---	...	---		S?	Sb	Modiomorpoidea
<i>Myoconcha</i> sp.	<i>Sin</i>							.....								S?	Sb	Modiomorpoidea
<i>Cardinia andium</i> (Giebel)	<i>Sin</i>				.....			?								I	Sb	Crassatelloidea
<i>Cardinia andium</i> (Giebel)	<i>Toa</i>							---	---							I	Sb	Crassatelloidea
<i>Cardinia andium</i> (Giebel)	<i>Pli</i>			---	---	...	---	---	---	---	---	---	---	---		I	Sb	Crassatelloidea
<i>Cardinia</i> cf. <i>listeri</i> (J. Sowerby)	<i>Sin</i>							.....								I	Sb	Crassatelloidea
<i>Cardinia multilamellosa</i> Jaworski	<i>Pli</i>			---	...	...	---	---	---	---	---	---	---	---		I	Sb	Crassatelloidea
<i>Coelastarte fuersichi</i> Aberhan	<i>Pli</i>			---												I	Sb	Crassatelloidea
<i>Neocrassina aureliae</i> (Feruglio)	<i>Pli</i>			---	---	...	...	---	---	---	---	---	---	---		I	Sb	Crassatelloidea
<i>Neocrassina aureliae</i> (Feruglio)	<i>Toa</i>				---	---	...	---								I	Sb	Crassatelloidea
<i>Neocrassina</i> cf. <i>andium</i> (Gottsche)	<i>Toa</i>			---	...	...	---	---	---	---	---	---	---	---		I	Sb	Crassatelloidea
<i>Neocrassina</i> sp.	<i>Sin</i>							.....								I	Sb	Crassatelloidea
" <i>Astarte</i> " <i>chubutensis</i> (Wahnish)	<i>Pli</i>											---	---	...	---	I	Sb	Crassatelloidea
" <i>Astarte</i> " <i>keideli</i> Wahnish	<i>Pli</i>														---	I	Sb	Crassatelloidea
<i>Astartidae</i> indet. 1	<i>Het</i>							.....								I	Sb	Crassatelloidea
<i>Astartidae</i> indet. 1	<i>Sin</i>							.....								I	Sb	Crassatelloidea
<i>Astartidae</i> indet. 2	<i>Sin</i>							.....								I	Sb	Crassatelloidea
<i>Praeconia</i> ? sp.	<i>Toa</i>							---								I	Sb	Crassatelloidea
<i>Trigonastarte</i> ? sp.	<i>Toa</i>							---								I	Sb	Crassatelloidea
<i>Opis</i> sp.	<i>Toa</i>							---	...	...	...	---	---			I	Sb	Crassatelloidea
<i>Opisoma</i> cf. <i>excavatum</i> Boehm	<i>Toa</i>											?				E	Re	Crassatelloidea
<i>Cardinioidea lanesae</i> Damborenea	<i>Sin</i>							.....								I	Sb	Unionoidea
<i>Protocardia</i> sp.	<i>Sin</i>				.....	.....	.....	.....								I	Sb	Cardioidea
<i>Protocardia</i> sp.	<i>Pli</i>			---	...	...	---	---	---	---	---	---	---	---		I	Sb	Cardioidea
<i>Protocardia</i> sp.	<i>Toa</i>							---	---							I	Sb	Cardioidea
<i>Protocardia striatula</i> (Sowerby)	<i>Pli</i>			---	---											I	Sb	Cardioidea
<i>Protocardia striatula</i> (Sowerby)	<i>Toa</i>				---											I	Sb	Cardioidea
<i>Tancredia</i> sp.	<i>Sin</i>							.....								I	Db	Tellinoidea
<i>Quenstedtia</i> ? sp.	<i>Sin</i>				.....											I	Db	Tellinoidea
<i>Quenstedtia</i> ? sp.	<i>Pli</i>			---												I	Db	Tellinoidea
<i>Corbicellopsis</i> ? sp.	<i>Sin</i>				.....											I	Db	Tellinoidea
Arcticoidea indet.	<i>Sin</i>							.....								I	Sb	Arcticoidea
<i>Anisocardia</i> sp.	<i>Sin</i>				.....											I	Db	Arcticoidea
<i>Anisocardia</i> sp.	<i>Pli</i>			---	---	...	...	...	...	...	...	...	...	---		I	Db	Arcticoidea
<i>Isocyprina ancatrui</i> (Leanza)	<i>Sin</i>				.....											I	Sb	Arcticoidea
<i>Isocyprina ancatrui</i> (Leanza)	<i>Pli</i>				---	...	...	---	---	---	---	---	---	---		I	Sb	Arcticoidea
<i>Isocyprina</i> sp.	<i>Toa</i>			---												I	Sb	Arcticoidea
Arcticoidea gen. et ap. nov. Aberhan	<i>Pli</i>			---	---											I	Sb	Arcticoidea
<i>Pseudisocardia</i> ? <i>liasina</i> (Wahnish)	<i>Pli</i>			---	---	...	...	...	...	...	...	---	---			I	Sb	Glossoida
<i>Pseudisocardia</i> ? <i>liasina</i> (Wahnish)	<i>Toa</i>							---								I	Sb	Glossoida
<i>Pseudisocardia</i> sp.	<i>Pli</i>							---								I	Sb	Glossoida

Species	Geographical range	1	2	3	4	5	6	7	8	9	10	11	12	Life habit	Superfamily
<i>Pholadomya cf. oretiensis</i> Campbell et G-M.	Het			—	.....	.....	.....	—						Db	Pholadomyoidea
<i>Pholadomya cf. oretiensis</i> Campbell et G-M.	Sin				—	.....	.....	—						Db	Pholadomyoidea
<i>Pholadomya cf. oretiensis</i> Campbell et G-M.	Pli							—						Db	Pholadomyoidea
<i>Pholadomya aff. favrina</i> Agassiz	Sin				.....									Db	Pholadomyoidea
<i>Pholadomya aff. favrina</i> Agassiz	Pli			—	...	...	...	—						Db	Pholadomyoidea
<i>Pholadomya cf. abbreviata</i> Hupé	Pli			—										Db	Pholadomyoidea
<i>Pholadomya corrugata</i> Koch et Dunker	Sin			.....	.....	.....	.....	.....						Db	Pholadomyoidea
<i>Pholadomya corrugata</i> Koch et Dunker	Pli			—	—	...	—	—	—	—	—	—	—	Db	Pholadomyoidea
<i>Pholadomya corrugata</i> Koch et Dunker	Toa			—	—	...	—	—	—	—	—	—	—	Db	Pholadomyoidea
<i>Pholadomya fidicula</i> Sowerby	Sin				.....									Db	Pholadomyoidea
<i>Pholadomya fidicula</i> Sowerby	Pli			—	—	...	...	—	—	—	—	...	—	Db	Pholadomyoidea
<i>Pholadomya fidicula</i> Sowerby	Toa			—	—	...	...	—	—	—	—	—	—	Db	Pholadomyoidea
<i>Pholadomya multilineata</i> Gabb	Pli			—	—									Db	Pholadomyoidea
<i>Pholadomya cf. decorata</i>	Sin							.....						Db	Pholadomyoidea
<i>Pholadomya cf. decorata</i>	Pli							.....						Db	Pholadomyoidea
<i>Pholadomya hemicardia</i> Roemer	Sin				.....									Db	Pholadomyoidea
<i>Pholadomyocardia</i> sp.	Pli			—										Db	Pholadomyoidea
<i>Homomya neuquena</i> Leanza	Pli			—	—	...	...	—	...	—	—	—	—	Db	Pholadomyoidea
<i>Homomya neuquena</i> Leanza	Toa									—				Db	Pholadomyoidea
<i>Pachymya rotundocaudata</i> (Leanza)	Sin				.....	.....	.....	—						Db	Pholadomyoidea
<i>Pachymya rotundocaudata</i> (Leanza)	Pli			—	—	...	...	—	...	...	...	—	—	Db	Pholadomyoidea
<i>Pachymya</i> sp.	Toa						—							Db	Pholadomyoidea
<i>Goniomya cachinensis</i> Aberhan	Het			.....										Db	Pholadomyoidea
<i>Goniomya asientosensis</i> Aberhan	Pli			—	—									Db	Pholadomyoidea
<i>Goniomya cf. proboscidea</i> (Agassiz)	Sin							.....						Db	Pholadomyoidea
<i>Goniomya cf. proboscidea</i> (Agassiz)	Pli			—	—	...	—	—	...	...	...	...	—	Db	Pholadomyoidea
<i>Goniomya cf. proboscidea</i> (Agassiz)	Toa				—	—	—	—	—	—	—	—	—	Db	Pholadomyoidea
<i>Osteomya cf. dilata</i> (Phillips)	Sin				.....									Db	Pholadomyoidea
<i>Gresslya</i> sp. A Aberhan	Sin			.....	.....	.....	.....	.....						Db	Pholadomyoidea
<i>Gresslya cf. peregrina</i> (Phillips)	Pli			—	...	...	—	—	...	...	...	—	—	Db	Pholadomyoidea
<i>Gresslya cf. peregrina</i> (Phillips)	Toa				—	...	—	—	—	—	—	—	—	Db	Pholadomyoidea
<i>Pteromya</i> sp.	Sin							.....						Db	Pholadomyoidea
<i>Pteromya</i> sp.	Pli		—	...	...	...	—	—						Db	Pholadomyoidea
<i>Pteromya</i> sp.	Toa						—	—						Db	Pholadomyoidea
<i>Pleuromya galathea</i> Agassiz	Het			.....	...	...	...	.....						Db	Pholadomyoidea
<i>Pleuromya uniformis</i> (J. Sowerby)	Sin				.....	.....	.....	.....						Db	Pholadomyoidea
<i>Pleuromya uniformis</i> (J. Sowerby)	Pli			—	—	...	—	—	—	—	—	—	—	Db	Pholadomyoidea
<i>Pleuromya uniformis</i> (Sowerby)	Toa			—	—	...	—	—	—	—	—	—	—	Db	Pholadomyoidea
<i>Ceratomya</i> ? sp.	Sin						—							Db	Pholadomyoidea
<i>Ceratomya</i> sp.	Pli			—	...	...	—	...	—	—	—	—	—	Db	Pholadomyoidea
<i>Ceratomya</i> sp.	Toa						—	—						Db	Pholadomyoidea
<i>Thracia</i> ? sp.	Toa						—	—						Db	Thracioidea
<i>Cercomya</i> sp.	Sin				.....	.....	.....	.....						Db	Thracioidea
<i>Cercomya peruviana</i> Cox	Pli			—	...	...	—	—	...	...	—	—	—	Db	Thracioidea
<i>Cercomya undulata</i> (Sowerby)	Toa			—	—	...	—	—	...	—	—	—	—	Db	Thracioidea
<i>Platymyoidea</i> ? cf. <i>longa</i> (Buvignier)	Pli			—										Db	Thracioidea
Gen. et sp. indet. Leanza	Pli			—	...	...	...	...	...	...	...	—	—	Db	Cuspidarioidea ?