

Jurassic evolution of Southern Hemisphere marine palaeobiogeographic units based on benthonic bivalves

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Abstract

The distribution of benthonic Jurassic bivalve genera in the Southern Hemisphere is analysed here. For this region, palaeobiogeographic units (biochoremas) are quantitatively characterized according to their biologic contents (mainly levels of endemism). Their evolution through time is followed from the latest Triassic to the earliest Cretaceous. The Tethyan Realm is undoubtedly the most mature and persistent through time, with three subordinate units: an Australian unit restricted to the Late Triassic, a North Andean unit, which appears sporadically as an endemic centre, and an East African unit which is recognisable from Bajocian times onwards. From Late Triassic times, a South Pacific Realm has been recognised, with a Maorian Province mostly based on the distribution of monotoid genera. A South Andean unit is also recognisable through most of the Jurassic, and its reference either to the South Pacific unit or to the Tethyan Realm is a matter of debate. Being a transitional biogeographic setting between Tethyan and South Pacific first-order units, it is included in the South Pacific unit due to the common presence of antitropical (didemic) genera. The East African unit is included within the Tethyan Realm during the Jurassic, but during Early Cretaceous times, it splits into two units, one of which was regarded as part of the “South Temperate Realm” by Kauffman. The rank of all these units changed with time. Throughout the Jurassic, the ecotone between South Pacific and Tethyan palaeobiogeographic units fluctuated in position with time. The approximate latitudinal location of the ecotonal boundary area and its shift through time are recognised on the basis of faunal composition along the Andean region. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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1. Introduction

The history of large-scale biogeographic patterns is increasingly attracting the attention of biologists, since it is evident that many biogeographic phenomena develop over long periods of time. Thus, the origin, establishment and evolution of palaeobiogeographic units of any rank or biochoremas (biochores in the sense of Makridin, 1973, and Westermann, 2000a) are of special interest. These units are dynamic and change in range and rank through time. Those based on benthonic faunas do not necessarily have a coincident history with those based on pelagic taxa. These aspects are clearly exemplified by the history and evolution

of Southern Hemisphere biogeographic units during Jurassic times.

Mainly as a consequence of the unevenness of land mass distribution on the Earth, the northern–southern asymmetry in some aspects of marine fauna distribution patterns is well known at different times (see discussion in Crame, 1996b, 2000). Nevertheless, three major biogeographic units based on benthonic invertebrates (one low-latitude and two high-latitude) are recognised for Permian (see Shi and Grunt, 2000, and references therein), Triassic (e.g. Stevens, 1980), Cretaceous (e.g. Fleming, 1963; Kauffman, 1973; Sohl, 1987; Stevens, 1980) and Cainozoic times (e.g. Fleming, 1963; Hayami, 1989). In contrast, the hemispherical asymmetry of biogeographic units during most of the Mesozoic has led many authors to recognise only two first order palaeobiogeographic units for the Jurassic, mainly on the basis of the distribution of ammonites: the Boreal and Tethyan Realms (Hallam, 1969, 1971, 1977; Stevens, 1980,

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1990; Doyle, 1987; Challinor et al., 1992; Hillebrandt et al., 1992; and many others, see discussion and references in Westermann, 2000a,b). As Kauffmann (1973) aptly expressed, “poor knowledge of south temperate [*bivalve*] faunas has led many authors to assume no “anti-Boreal” Realm existed south of Tethys during the Mesozoic” and he demonstrated that this is clearly not true for the Cretaceous, although he admitted that “this was possibly true in the Early Jurassic”. In fact, lack of data and proper analysis for the Southern Hemisphere pervades also studies of other fossil groups (see, for instance, Dommergues et al., 2001).

This twofold division hinders the determination of the possible role that the austral regions may have had in the origin and diversification of the biota (see Crame, 1997) during the Jurassic. Widespread phenomena like austral endemism or antitropicality are either ignored or their relative importance is disregarded. Some authors who work on Southern Hemisphere faunas (especially bivalves) have challenged this twofold division (see Stevens, 1980, and references therein; Crame, 1986, 1987, 1992, 1993; Damborenea, 1993, 1996; Enay and Cariou, 1997, and references therein), but their attempts were dismissed by some authors (Hallam, 1994a, b; Westermann, 2000a, b), while others adhered to a threefold division, at least for some periods of time within the Jurassic. In fact, several marine palaeobiogeographic units of low rank have been proposed for the Southern Hemisphere Jurassic on the basis of the known distribution of different marine organisms. The relationships, rank and history of these units were recently reviewed by Enay and Cariou (1997) and Westermann (2000b).

This paper is an attempt to recognise the development and evolution of biochoremas based on benthonic bivalve endemism in the Southern Hemisphere. There is no space here to discuss in detail either the processes involved or the possible causes of the observed diversification of the recognised biogeographic units, or the complexities of nomenclature involved, and thus all these issues are deliberately avoided or only mentioned without further discussion. The paper is then mainly limited within the first rationale of those listed by Rosen (1992), i.e. the determination of palaeobiogeographical patterns with delimitation of provinces and realms, as a starting point for further discussion.

Global studies on the distribution of Mesozoic bivalves have largely been based on data from Cox et al. (1969) (for instance, Kauffman, 1973; Hallam, 1977). Those databases had a poor coverage of the Southern Hemisphere, but there is now a wealth of recently published information from this region which certainly adds substantial evidence and can be used in this context. Palaeobiogeographic provinces based on bivalves were recently analysed quantitatively for the European Tethyan and Proto-Atlantic (Liu, 1995; Liu et al., 1998). In contrast, there are no updated comprehensive palaeobiogeographic analyses based on bivalves for the Southern Hemisphere, although several contributions related to palaeobiogeographic issues using these organisms are available for the South Pacific (Stevens, 1967, 1977,

1980, 1989, 1990; Hayami, 1984, 1987; Grant-Mackie et al., 2000), Antarctica (Crame, 1987, 1992, 1996a, b) and the South American margin of the Pacific (Damborenea and Manceñido, 1979, 1988; Hillebrandt, 1981; Hallam, 1983; Damborenea, 1993, 1996).

2. Database

Occurrences of Jurassic bivalve species were compiled from various published sources as well as the author’s own data, and plotted stage by stage. To frame the analysis, data from latest Triassic and earliest Cretaceous were added. The study area is restricted to the palaeo-Southern Hemisphere, but the database was compiled on a global scale, not only to provide the necessary framework for the detailed analysis of southern regions, but also to adequately recognise patterns of general distribution and endemism.

Data were then gathered within wide areas, each containing a large variety of habitats. Eleven such areas were chosen for the present analysis (located in Fig. 1). On the whole, they represent a wide coverage of the Southern Hemisphere Jurassic seas, but some important gaps still exist, limited by the availability of data (Table 1). A brief description and list of main data sources are given in Appendix A.

Both the amount and quality of data are, unsurprisingly, very uneven, but although this precludes serious detailed quantitative analysis at the moment, the database provides enough information to obtain a broad framework. The species’ distribution data compiled were systematically and stratigraphically updated as far as possible and dubious records were excluded. For this analysis, data were processed at the genus-group level and according to the

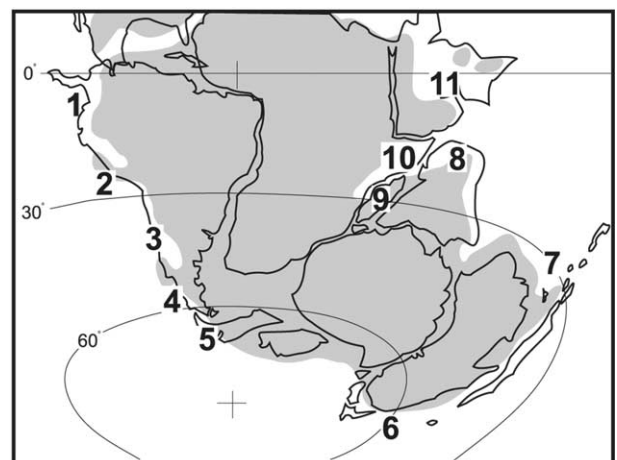


Fig. 1. Location of the geographic units used in this study. 1, NW South America; 2, Perú and northernmost Chile; 3, Central Argentina and Chile; 4, Southern Argentina and Chile; 5, Antarctica; 6, New Zealand–New Caledonia; 7, Western Australia; 8, Western India; 9, Madagascar; 10, Mozambique and eastern Africa; 11, Arabia and Iran. Base map for the Early Jurassic, continent palaeopositions based on Smith and Briden (1977) and Scotese (1991, 1997), palaeogeography compiled from many sources.

Table 1
Overview of the Norian to Berriasian bivalve data from the study areas. Total number of genus-level taxa are given for each time-interval and each region.

Regions	NE South America (1)	Perú and northern Chile (2)	Central Argentina and Chile (3)	Southern Argentina and Chile (4)	Antarctica (5)	New Zealand–New Caledonia (6)	W Australia–New Guinea (7)	Western India (8)	Madagascar (9)	Mozambique and E Africa (10)	Arabia and Iran (11)
Tithonian–Berriasian	16		74	27	27	11		14			
Oxfordian–Kimmeridgian		5	9		31	24	6	31	9	64	6
Bathonian–Callovian			31			23		120	35	57	10
Aalenian–Bajocian		33	69		16	44	24	8	4	26	10
Pliensbachian–Toarcian	5	66	97	33		25	5		16	17	27
Hettangian–Sinemurian	15	54	70		5	6					
Norian–Rhaetian	12	47	11			23	17				11

following seven time-intervals: Norian–Rhaetian, Hettangian–Sinemurian, Pliensbachian–Toarcian, Aalenian–Bajocian, Bathonian–Callovian, Oxfordian–Kimmeridgian and Tithonian–Berriasian. Admittedly, this implies a loss of detail in the information for some regions, but on the other hand, it allows the use of some occurrences with uncertain stratigraphic provenance. The age slice including Tithonian and Berriasian has the extra drawback that in this way any fact related to the Jurassic–Cretaceous boundary may be not noticed in this study. Within the general aims of this paper, though, this arrangement is satisfactory and gives enough information to recognise biogeographic units and describe their overall trends through time.

3. Methods

From the many methods that can be used to recognise palaeobiogeographic units, a traditional approach based on endemism has been followed, using the set of rules for their definition, rank and nomenclature proposed by [Westermann \(2000a\)](#). Bivalve genera were classified according to their palaeobiogeographic affinities, following basically [Kauffman \(1973\)](#), [Stevens \(1980\)](#) and [Damborenea \(1993\)](#), as follows (see examples in [Fig. 2](#)):

- **Pandemic:** Widespread bivalves, truly cosmopolitan forms. It is interesting to note that many genera traditionally referred to as “cosmopolitan” have not been reported from the Southern Hemisphere during the time-interval considered. These include, for instance, *Atrina*, *Cirtopinna*, *Ctenoides*, *Limopsis*, *Linotrigonia*, *Malletia*, *Martesia*, *Megalodon*, *Mytiloides*, *Palaomya*, *Paratancredia*, *Procardia*, *Septifer*. Other so-called “cosmopolitan” genera are present only in the northern regions of the Southern Hemisphere (1, 2, 8, 9, 10, and 11 of this study) but are not known from the southernmost areas. Examples are *Hippopodium*,

Neomegalodon, *Pinguistarte* and *Rollieria*. All the genera mentioned with such distributions were excluded from the list of “cosmopolitan” taxa for this analysis.

- **Endemic:** These are the key elements to recognise and characterise biogeographic units. For this study, only true endemics (from each region compared at the global scale) were counted as such.
- **Low-latitude or Tethyan.**
- **High-latitude:**
 - Austral (= Maorian or palaeoaustral).
 - Boreal.
 - Didemic, antitropical or bipolar, restricted to high-latitudes and present in both hemispheres, being absent from the low-latitude intervening areas ([Crame, 1993](#); [Damborenea, 1993](#); [Sha, 1996](#)).
- **Trans-temperate** ([Kauffman, 1973](#)): This category includes taxa common in temperate regions, but with a distribution not latitudinally limited, and at the same time, not pandemic. For instance, bivalves with the so-called “Pacific” distribution, i.e. along the margins of the palaeo-Pacific ocean both in low and medium (sometimes even high) palaeolatitudes, absent from other areas.

Only pandemic and endemic taxa can be objectively defined, reference of some genera to either of the other categories is necessarily a matter of debate. This is not a serious drawback in this context, however, since these last categories are only accessory elements in this study. From the nearly 500 bivalve genera known from this time-interval, 52% are here regarded as low-latitude, 21% as high-latitude, 6% as trans-temperate and 21% as pandemic ([Fig. 3](#)).

Since geographic ranges of taxa change through time, sometimes this results in a different categorization for the same taxon. For instance, a genus may be endemic to a certain region during a stage and then become widespread.

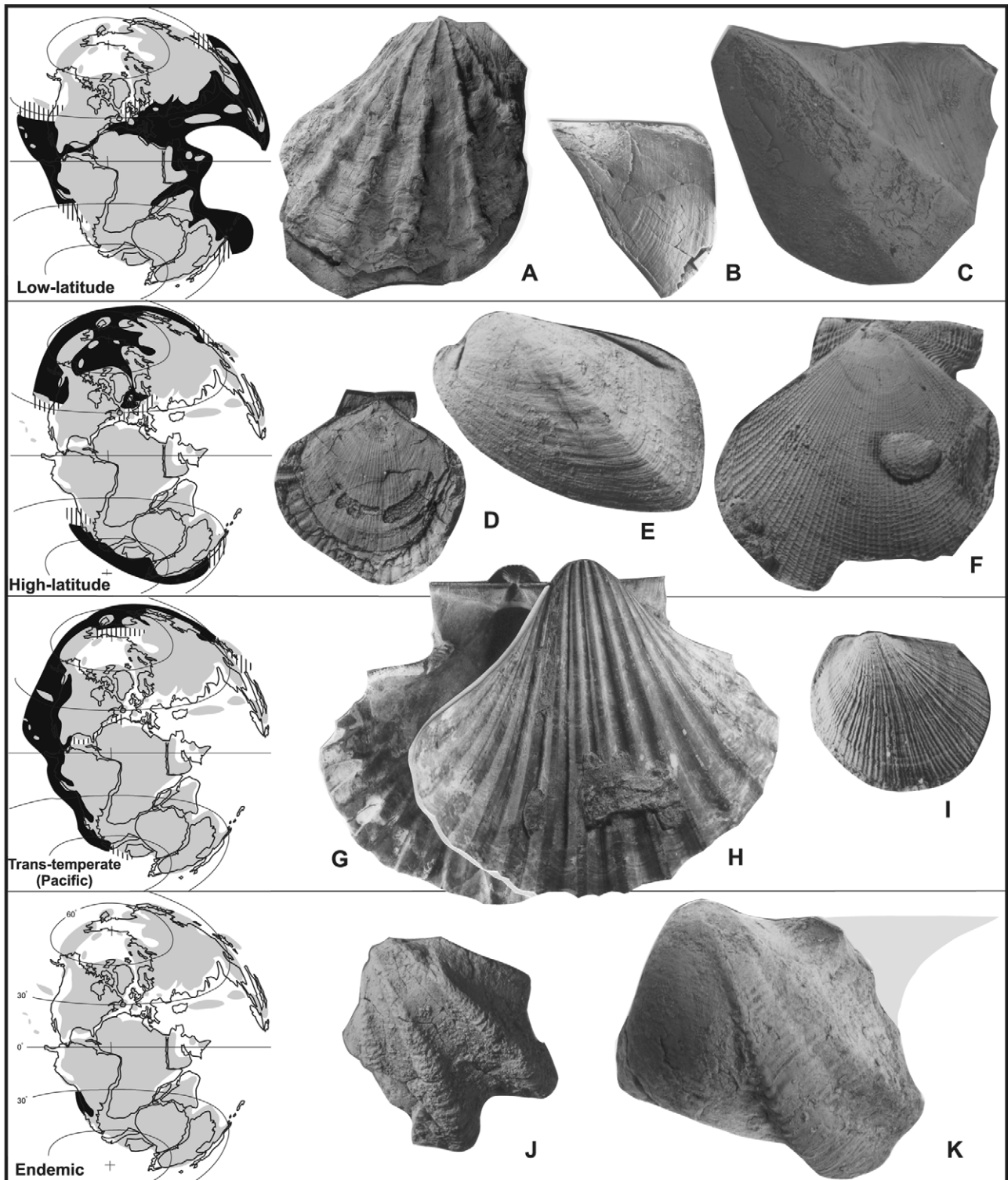


Fig. 2. Some examples of Early Jurassic bivalves from the Central Argentina region (3) according to generic palaeobiogeographic affinities. Specimens housed at La Plata Natural Sciences Museum (MLP) and National Geological Survey, Argentina (DNGM). (A)–(C) Low-latitude; (A) *Ctenostreon raricostatum* (BAYLE AND COQUAND), MLP 28428, Pliensbachian, Piedra Pintada, $\times 0.44$; (B) *Lycettia hypertrigona* DAMBORENEA, MLP 16308, Pliensbachian, Piedra Pintada, $\times 0.7$; (C) *Gervillaria pallas* (LEANZA), MLP 19079, Pliensbachian, Nueva Lubecka, $\times 0.8$. (D)–(F) High-latitude; (D) *Kolymonectes weaveri* DAMBORENEA, MLP 23804a, Pliensbachian, Chacay Melehue, $\times 1$; (E) *Kalentera* nov. sp., MLP 24294, Early Pliensbachian, Atuel river, $\times 1$; (F) *Agerchlamys wunschae* (MARWICK) and epizoic *Harpax rapa* (BAYLE AND COQUAND), MLP 23658, Pliensbachian, arroyo Ñireco, $\times 1$. (G)–(I) Trans-temperate (Pacific); (G), (H) *Weyla alata angustecostata* (PHILIPPI), internal and external views of right valve, MLP 19076, Early Toarcian? Sierra de Agnia, $\times 0.34$; (I) *Otapiria neuquensis* DAMBORENEA, MLP 16480, Pliensbachian, Piedra Pintada, $\times 2$. (J)–(K) Endemic, J, *Groebrella neuquensis* (GROEBER), DNGM 7340, Pliensbachian, Nueva Lubecka, $\times 1$; (K) *Gervilletia turgida* (LEANZA), MLP 6260, Pliensbachian, Piedra Pintada, $\times 0.6$.

An example is *Kalentera*, which was endemic to the Maorian Province in Late Triassic times but became antitropical during the Early Jurassic. Similarly, *Gryphaea* was restricted to high-latitudes during the Triassic but later became pandemic. Conversely, a previously widespread taxon may have a temporarily restricted distribution. The recognition of these subtle changes is highly dependent on a very detailed knowledge of recorded distributions, and is thus not always easy to establish in the fossil record. Nevertheless, these changes were herein recognised and taken into account as far as possible.

4. Biogeographic units and their evolution

The percentage of cosmopolitan bivalve genera, even restricted as mentioned above, was high worldwide during most of the Jurassic (about 21% for the whole Jurassic), leaving only a few endemic taxa (16%) as diagnostic of palaeobiogeographic units. It is interesting to note here that for the whole Jurassic endemic genera are proportionately equally abundant in high-latitude and in low-latitude regions.

For the following analysis, percentage of endemism was calculated excluding cosmopolitan forms (see [Kauffman, 1973](#)) and including only strictly endemic taxa. In the following discussion, all the percentages quoted are calculated over total minus cosmopolitan genera. At different times through the Jurassic, endemism within the different areas of the Southern Hemisphere varied, and was used here to recognise palaeobiogeographic units.

A summary of the results regarding the percentage of endemic genera in each of the units is presented in [Table 2](#). These percentages are low according to normalised scales based on species' distribution (see discussion in [Westermann, 2000a](#)), but are of the same order as those used by other authors to define palaeobiogeographic units on the basis of bivalve genera (e.g. [Kauffman, 1973](#)), and they allow the recognition of units of different rank. Nevertheless, taking into account the nature of the database, no attempt is made here to establish a table of minimum values for each rank. It is interesting to note that the distinction between Tethyan and Boreal Realms based on bivalves in the Northern Hemisphere rests on only a few taxa. According to [Liu \(1995\)](#), for instance, for the Pliensbachian, only the presence of *Hippodidium* and *Meleagrinnella* is characteristic of the Boreal Realm and *Weyla* and *Lithiotis* of the Tethyan Realm in Europe (note that these taxa were not even endemic).

Five basic biochoremas and two of higher rank can be recognised according to the distribution and percentage of endemic taxa ([Fig. 4](#)). Some of the basic units are here regarded as belonging to the Tethyan Realm, while others can be grouped in another high rank unit which, following [Westermann's \(2000b\)](#) recommendations, is called South Pacific ([Challinor, 1991](#) = Austral Realm in [Damborenea, 1993](#)). Overall endemism for this high rank unit is over 60% during the latest Triassic, between 15% and 30% for the Early Jurassic, and over 30% for Middle and Late Jurassic. These fluctuations suggest its change in rank through time.

All units are further characterised by other aspects, such as the presence and relative abundance of high-latitude or strictly low-latitude taxa ([Table 2](#)), overall diversity, and the presence/absence of certain higher rank taxonomic groups. Antitropical (or didemic) taxa were also common within monotoids, pectinoids, inoceramoids and other bivalve groups and add character to some of these units.

On a worldwide scale, this implies the presence of three first order units during the Jurassic based on bivalve data:

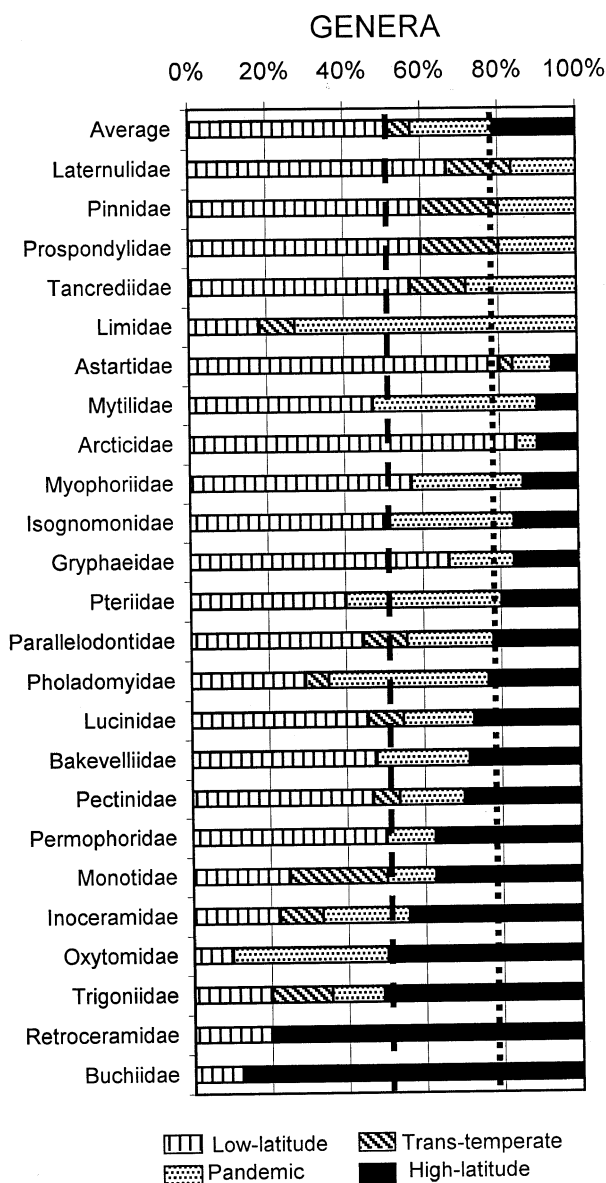


Fig. 3. Percentage of genera with different palaeobiogeographic affinities in selected bivalve families. Average composition for the whole time-interval at the top, broken lines indicate average percentage of low-latitude (long dashes) and high-latitude (short dashes) genera.

Table 2

Percentages of endemic, low-latitude, high-latitude and trans-temperate genera and subgenera (calculated excluding cosmopolitan taxa) for the palaeobiogeographic units recognised here for each time-slice. Units not recognizable at a given time are indicated by 0 in the endemic portion of the table (lack of endemic taxa) or no figures (insufficient data).

Taxa	Endemic					Low-latitude					High-latitude					Trans-temperate				
	Tethyan			South Pacific		Tethyan			South Pacific		Tethyan			South Pacific		Tethyan			South Pacific	
	East African	Australian	North Andean	South Andean	Maorian	East African	Australian	North Andean	South Andean	Maorian	East African	Australian	North Andean	South Andean	Maorian	East African	Australian	North Andean	South Andean	Maorian
Tithonian–Berriasian	14		0	14	8	72			72	50	14			3	17	0			11	25
Oxfordian–Kimmeridgian	13	0	0	50	13	73			50	43	7			0	31	7			0	13
Bathonian–Callovian	8			18	20	88			55	40	0			27	20	4			0	20
Aalenian–Bajocian	17	0	9	15	17	66		82	56	44	0		9	19	28	17		0	11	11
Pliensbachian–Toarcian	0	0	9	7	22		53		46	0			19	27	44			19	20	33
Hettangian–Sinemurian			0	14	0				52					24					10	
Norian–Rhaetian		50	14	0	47		50	52		6		0	24		29		0	10		18

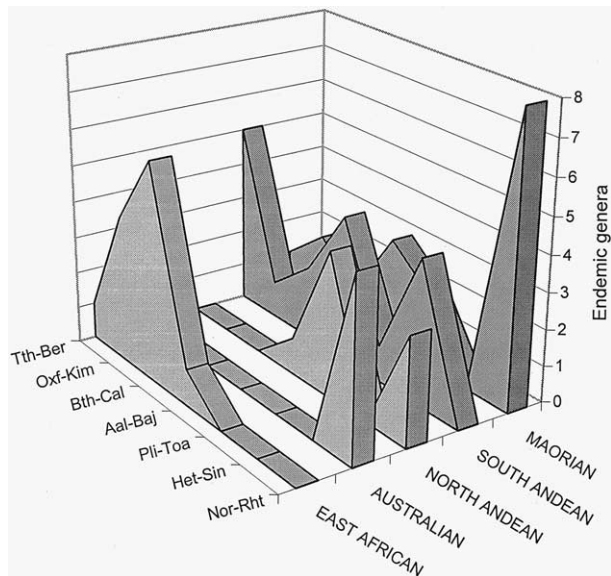


Fig. 4. Number of endemic genera through time in the recognised palaeobiogeographical units.

Boreal, Tethyan and South Pacific. The distribution of bivalves and the corresponding proposed palaeobiogeographic zonation is evidently not symmetrical to the palaeo-equator. In fact, in view of the unbalanced distribution of land/water masses and the related uneven oceanic current patterns (which are mostly hypothetical at this stage), such a palaeobiogeographic asymmetry is only to be expected. The data analysed here do not support the alternative of overstressing this asymmetry to the point of reducing the palaeobiogeographic zonation for the Jurassic to only two first order units.

At the family level, all the three first order palaeobiogeographic units are well characterised. During the Jurassic and Early Cretaceous, most genera of Anomiidae, Burmesiididae, Ceratomyopsidae, Cuspidariidae [Dattidae], Diceratidae, Dicerocardiidae, Isoarcidae, Lithiotidae, Mactromyidae,

Malleidae, Megalodontidae, Myalinidae, Myopholadidae, Myophoricardiidae, Mysidiellidae, Ostreidae, Pergamidiidae, Protocardiidae, Ptychomyidae, Pulvinitidae, Requienuidae, Sowerbyidae and Unicardiopsidae are restricted to low-latitudes and characterise the Tethyan Realm. To these, a group of families with more than average low-latitude taxa (Fig. 3) should be added: Laternulidae, Pinnidae, Prospondylidae, Tancrediidae, Astartidae, Arcticidae, Myophoridae and Gryphaeidae. The first four of these have no high-latitude taxa, and the others contain less than average high-latitude genera.

Families strictly restricted to high-latitudes in the Jurassic are fewer; among them Asoellidae, Minetrigoniidae and Palaeopharidae are present in both Boreal and South Pacific Realms whereas Sportellidae and Yoldiidae are known only from the Boreal Realm. There is a consistent group of families which have more than average high-latitude taxa and at the same time less than average low-latitude genera (Fig. 3), all of them diverse and abundant in both Boreal and South Pacific Realms: Monotidae, Inoceramidae, Oxytomidae, Trigoniidae, Retroceramidae and Buchidae. It should be pointed out here that updated systematic knowledge of bivalve faunas is still very uneven in the Southern Hemisphere and that future revisions are likely to alter this picture slightly.

As these basic units change with time in rank, geographic spread and even realm to which they are assigned, the discussion below will follow a stratigraphic order (Figs. 5 and 6) and will be restricted to the Southern Hemisphere.

4.1. Late Triassic

Three basic units can be recognised: the South Pacific Realm contains the Maorian Province, whilst all the other regions belong to the Tethyan Realm, with an Australian Province and a North Andean endemic centre (Fig. 5(A)).

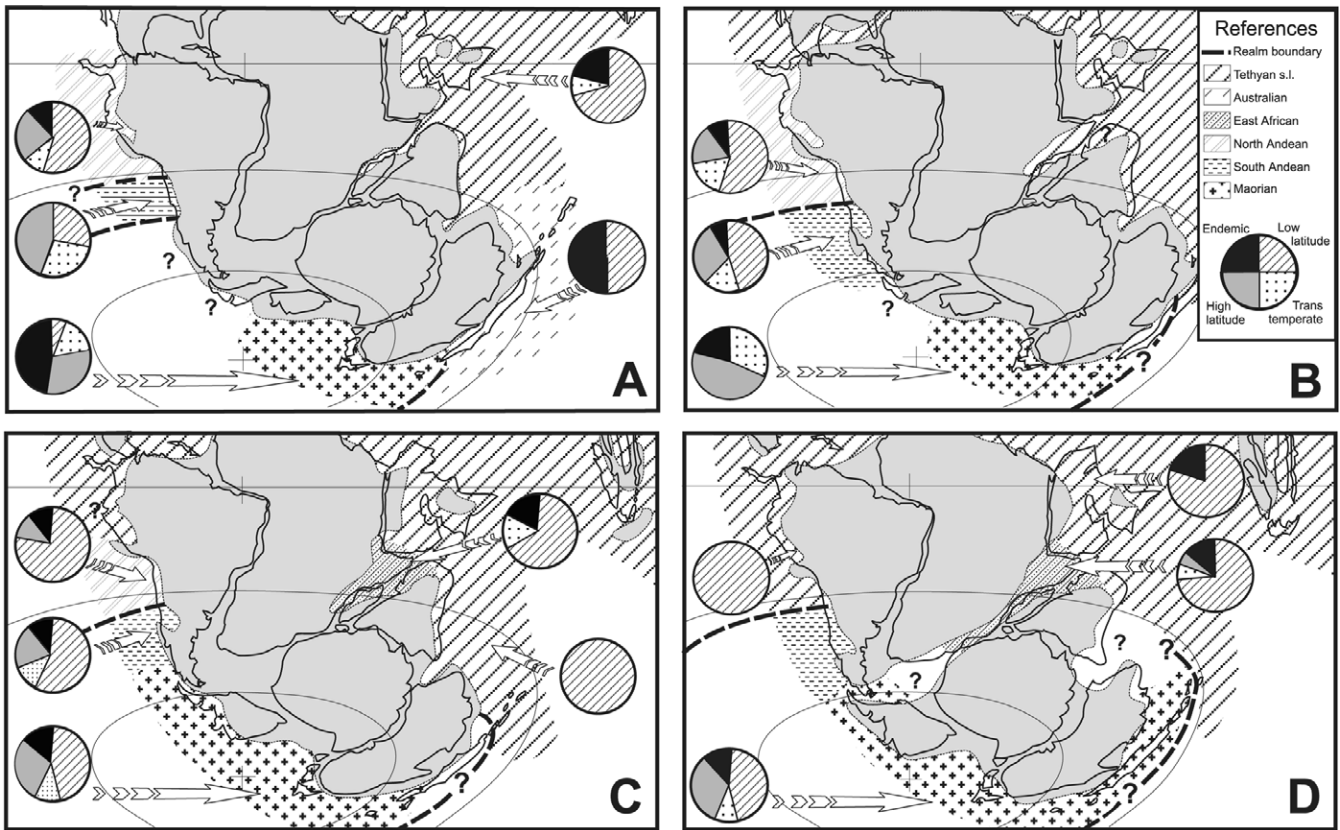


Fig. 5. Palaeobiogeographic maps for four time-slices: (A) latest Triassic; (B) Toarcian; (C) Bajocian and (D) Oxfordian. Thick broken lines show the approximate position of ecotone between Tethyan and South Pacific Realms for each time-slice. Pie diagrams represent percentage of genera according to palaeobiogeographic affinities. Base maps for the Late Triassic, Early, Middle and Late Jurassic, continent palaeopositions based on Smith and Briden (1977) and Scotese (1991, 1997), palaeogeography compiled from many sources.

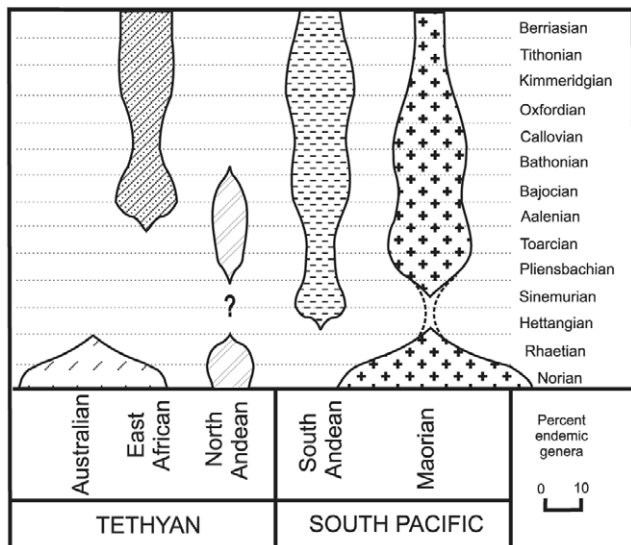


Fig. 6. A summary of the evolution of the biogeographic units here recognised according to their percentage of endemism.

The Maorian Province (Diener, 1916) presents very high endemism: the genera *Caledogonia*, *Heslingtonia*, *Hokonuia*, *Kalentera*, *Maorimonotis*, *Ouamouia*, *Torastarte* and *Triaphorus* are endemic to New Zealand–New Caledonia (region 6 here) during this time. This province is very

well characterised during the Middle and Late Triassic, not only by the percentage of endemics (47%), but also by the abundance (29%) of genera with antitropical or austral distribution, such as *Eomonotis*, *Inflatomonotis*, *Maoritrigonia*, *Minetrigonia* and *Phaenodesmia*. Strictly low-latitude genera are very few (6%).

An Australian Province is also well characterised by several endemic genera (50%), such as *Gervillancea*, *Guineana*, *Krumbeckiella*, *Prosogyrotrigonia* and *Somareoides*. Low-latitude genera are equally numerous, but high-latitude and trans-temperate forms are absent.

A North Andean endemic centre extends along the Andes from Venezuela to northern Chile. The endemic genera *Isopristes*, *Perugonia* and *Schizocardita* are abundant elements of the Late Triassic fauna from Peru and northern Chile (totalling 14%), and some genera with high-latitude distribution are also present (24%).

The central Argentina–Chile area represents a transitional zone, with no endemic taxa but with a high percentage (43%) of high-latitude genera, including *Gryphaea*, *Liostrea* and *Phaenodesmia*. The abundance of trans-temperate taxa (28%) is mainly due to genera distributed along the eastern margins of the palaeo-Pacific in both the hemispheres. Reference of this transitional area to the Tethyan or the South Pacific Realm is still doubtful.

Extensive areas without Late Triassic outcrops or reliable palaeontologic data in the key regions prevent adequate discussion of the boundary between realms at this time.

4.2. Early Jurassic

At the beginning of the Jurassic, the percentage of endemism is low for all the regions. This is not restricted to the Southern Hemisphere, but is also true at a global scale: Liu (1995) concluded that provinciality in the Northern Hemisphere during Hettangian, Sinemurian and Toarcian was unrecognisable. Although it is difficult to point a definite cause, this situation is probably a consequence of the end-Triassic extinction. Some authors have indicated that endemic bivalve taxa were relatively more vulnerable to mass extinction events (Hallam and Miller, 1988). Our data clearly show this pattern for the end Triassic extinction, and it is also evident that the biota and endemic centres took some time to recover (see discussion in Hallam, 1996). For instance, the lack of endemic genera makes the Maorian unit difficult to recognise during Hettangian and Sinemurian times, when, possibly apart from *Torastarte*, no endemic bivalves are present in New Zealand–New Caledonia. It is interesting to note that, based on the available data, the low-latitude regions of the Southern Hemisphere also contain no endemic genera. On the other hand, in transitional zones, such as the South Andean areas (2 and 3 here), an endemic centre appeared during Sinemurian times, with a few endemic genera (14%), such as *Gervilletia* (Fig. 2(K)), *Groeberella*, *Lywea* and *Quadratojaworskiella*. This endemic centre is regarded here as part of the South Pacific Realm despite the relatively high proportion of low-latitude taxa, due to the common occurrence of genera with anti-tropical or austral distributions (24%), such as *Agerchlamys* (Fig. 2(F)), *Asoella*, *Harpax*, *Kalentera* (Fig. 2(E)), *Palaeopharus* and *Kolymonectes* (Damborenea, 1998, 2002).

By Pliensbachian–Toarcian times (Fig. 5(B)), the Maorian unit (= South West Pacific Province in Hallam, 1977) had recovered, having 22% of endemic genera, including *Torastarte* and *Pseudauccella* (Grant-Mackie et al., 2000) and 44% of high-latitude genera. A South Andean endemic centre persists (see Fig. 6) with a low percentage of endemics (7%), including *Groeberella* (Fig. 2(J)) but with a high percentage of high-latitude taxa (27%), which include *Asoella*, *Harpax*, *Kolymonectes* (Fig. 2(D)), *Palaeopharus*, *Ochotochlamys*, *Praebuchia?* and *Radulonectites* (Damborenea and Manceñido, 1992; Damborenea, 1993, 2002). This interval is characterised by the highest percentages of high-latitude taxa for the whole Jurassic in this region and also the highest levels of trans-temperate (mainly east Pacific) taxa (see Table 2). A North Andean endemic centre within the Tethyan Realm is again discernible (9% of endemic genera), with its southern limit extending farther south than earlier in the Lower Jurassic (see discussion below and Fig. 7). The peculiar genera *Lithiotis* and

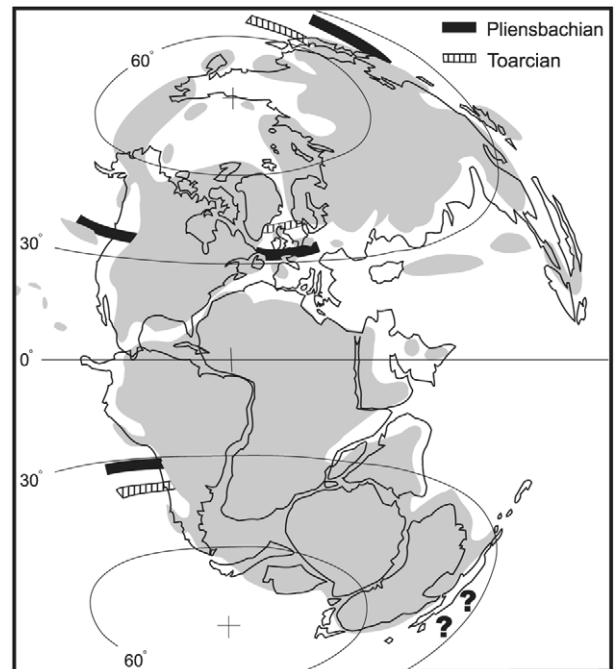


Fig. 7. Shift of the ecotone between the Tethyan and high-latitude units based on bivalves during the Early Jurassic (Pliensbachian–Toarcian) in a global context. Data from Smith and Tipper (1986), Smith (1989) and Aberhan (1998, 1999) for western North America; Hayami (1990) for northeastern Asia; Liu (1995) and Lui et al. (1998) for Europe; Damborenea (1996) for South America. Base map for the Early Jurassic, continent palaeopositions based on Smith and Briden (1977) and Scotese (1991, 1997), palaeogeography compiled from many sources.

Opisoma, characteristic of the Jurassic tropics during Pliensbachian times (see discussions in Geyer, 1977; Hillebrandt, 1981; Hayami, 1984; Nauss and Smith, 1988; Aberhan and Hillebrandt, 1999), extended to northern Chile during the Toarcian, but are absent further south in the South Andean unit.

Cox (1965) mentioned that the presence of the species *Weyla ambongoensis* (THEVENIN) in Toarcian beds of eastern Africa: “affords a somewhat meagre evidence that a faunal subprovince comprising the western part of the present Indian Ocean region and extending over northern Africa had come into existence”. Nevertheless, data from this area are scarce, and no endemic bivalve genera have been reported so far for the Early Jurassic.

4.3. Middle Jurassic

During Middle Jurassic (Fig. 5(C)) and early Late Jurassic times, the Southern Hemisphere bivalve benthonic faunas maintain their high proportion of cosmopolitan genera, always above 60% of all the taxa, but still some endemic and high-latitude genera are present.

The two South Pacific subunits maintain their level of endemism between 15% and 20% for the whole Middle Jurassic (see Table 2), although at the same time they experienced the proportional increase of low-latitude taxa. The influx of low-latitude genera reaches 44% for the

Maorian and 56% for the South Andean units, and is only exceeded during the Tithonian–Berriasian. Based on this evidence, many authors (see Grant-Mackie et al., 2000) concluded that the Maorian Province ceased to exist in the early Middle Jurassic. Nevertheless, a palaeogeographic unit is here still recognised (though probably with lower rank) throughout the Middle Jurassic. There are two alternatives to name this unit for Middle and Late Jurassic times: it can either be regarded as an extension of the Maorian Province, or it can be called Austral as the origin of the Austral Province recognized by Kauffman (1973) for Early Cretaceous times. The first alternative is followed here, but regardless of how we choose to call it, the continuity of an austral biogeographic unit from Triassic (Maorian Province) to Cretaceous (Austral Province) is evident from the results of this study. This unit is recognised on the basis of the following endemic genera: *Haastina* (Bajocian), *Malagasitrigonia* (Aalenian–Bajocian), *Kanakimya* (Aalenian–Bajocian?) and *Moewakamya* (Bathonian–Oxfordian). Endemic genera include *Anditrigonia* (Bajocian–Tithonian), *Andivaugonia* (Bajocian–Callovian), *Eoanditrigonia* (Bajocian–Callovian), *Neuquenitrigonia* (Bajocian), *Lambertrigonia* (Callovian) for the South Andean unit. High-latitude taxa in these two units are proportionately fewer; they include *Retroceramus* (Bajocian–Oxfordian) and *Scaphogonia* (Bajocian–Tithonian) for both units, *Praebuchia?* (Aalenian) for the South Andean, and *Fractoceramus* (Bajocian) and *Hijitrigonia* (Bajocian) for the Maorian unit. Again, probably as a consequence of the end Pliensbachian extinction event, endemism in the Maorian unit drops from 22% at the late Early Jurassic to 17% at the early Middle Jurassic. In this connection, Aberhan and Fürsich (2000) have pointed out that the Pliensbachian–Toarcian extinction event affected the endemic bivalve species more than others in the Andean region.

A new East African unit (= Provincia Etiopico-Indo-Malgascia in Ficarelli, 1968; Ethiopian Province in Hallam, 1977) appears to be recognisable from Bajocian times on the basis of its endemic genera: *Indolucina* (Bajocian–Oxfordian), *Agrawalimya* (Bathonian–Callovian), *Indocorbula* (Bathonian–Callovian), *Indomya* (Bathonian–Callovian), *Indoweyla* (Bathonian–Callovian), and *Venilicyprina* (Bathonian–Callovian). This unit contains, however, a high percentage of strictly low-latitude genera (66% for Aalenian–Bajocian and 88% for Bathonian–Callovian times) and lacks high-latitude genera. For these reasons, it is here regarded as part of the Tethyan Realm at this time.

The North Andean endemic centre is still faintly discernible during the Aalenian, with the presence of the endemic *Gervilleiognoma*. Species of *Heterostrea*, a genus strictly restricted to low-latitude areas in both hemispheres, extend not only to southern Perú but also to northern Chile, pushing further south the boundary between Tethyan and South Pacific units. Published data from younger times are very scarce and incomplete, not allowing their use in this context.

4.4. Late Jurassic

The general situation observed for Bathonian–Callovian times is generally maintained for the Late Jurassic (Fig. 5(D)). The Maorian unit is extended geographically to include the Antarctic and South Atlantic Plateau regions, and even some western Pacific localities (Timor, Sula, Buru, Ceram; see Hayami, 1984), but is somewhat less strongly recognisable, and its rank should be lowered, since its overall endemism at the generic level diminishes to 13% during Oxfordian–Kimmeridgian and to only 8% during Tithonian–Berriasian times. Endemic genera include *Moewakamya* (Oxfordian), *Jeletzkiella* (Oxfordian–Kimmeridgian) and *Praeaucellina* (Tithonian–Berriasian), whilst *Malayomaorica* (Oxfordian–Kimmeridgian) has an austral distribution reaching Australia–New Guinea. *Retroceramus*, *Scaphogonia*, *Lyapinella?* and *Anopaea* are high-latitude genera, mostly didemic in distribution.

On the other hand, the South Andean unit maintains its levels of endemism. The apparently very high percentage of endemism for the Oxfordian–Kimmeridgian is due to the small number of taxa reported so far and this figure is not statistically significant. Endemic genera include the trigonoideans *Anditrigonia* (Bajocian–Tithonian), *Antutrigonia* (Tithonian–Berriasian), *Notoscabrotrigonia* (Tithonian) and *Splenditrigonia* (Tithonian–Berriasian), and *Retroceramus* and *Scaphogonia* represent the high-latitude taxa.

The East African unit maintains a percentage of endemic taxa between 13% and 14%, including *Africomiodon* and *Eoseebachia* (Oxfordian–Kimmeridgian), with a very high percentage (over 70%) of low-latitude taxa. It is interesting to note here that the influence of high-latitude taxa in this area steadily increases towards the end of the Jurassic.

4.5. Early Cretaceous

By the end of the Jurassic and beginning of the Cretaceous, the situation changes and antitropical bivalve genera are again well established at least within inoceramoids and monotoids (Crame, 1986, 1993). According to Kauffman (1973), recognition of a relatively mature “South Temperate Realm” is clear, with well-defined “Austral” and “East African” Provinces as subordinate biogeographic units by the beginning of the Cretaceous. The change of the East African unit from the Tethyan (during most of the Jurassic) to the South Pacific Realm is indicated by the relatively high percentage (14%) of high-latitude taxa during Tithonian–Berriasian times, possibly as a direct consequence of the opening of the Mozambique channel. Kauffman (1973) includes the East African Province within the Indo-Pacific Region in the Early Cretaceous, according to its content of southern Pacific bivalve lineages, but with a geographic range now restricted to southern Africa, Madagascar and Mozambique. To the north, a transition zone developed (India, Arabia, NE Africa) with strong Tethyan influence (the north Indian Ocean Subprovince in Kauffman, 1973).

During the Early Cretaceous (Berriasian), the South Andean unit contains a few endemic trigoniodeans, such as *Antutrigonia*, *Splenditrigonia*, and *Transitrigonia*. *Anopaea* is a genus with didemic distribution, and during the Berriasian, it is present in New Zealand and Antarctica, whilst the endemic *Praeaucellina* lingers from Tithonian times in the Maorian unit. According to Kauffman (1973), the Austral Province of the Indo-Pacific Region (South Temperate Realm) was strongly developed at the beginning of the Cretaceous, including Australia, New Zealand and New Guinea.

From Middle Cretaceous time onwards, the North Andean unit is clearly recognisable as a Caribbean Subprovince/Province (Kauffman, 1973), and an Austral Realm was proposed by Fleming (1963) on the basis of bivalve and gastropod distribution.

5. Transitional zones

Transitional zones occurred between the Tethyan and South Pacific first order units. To study the evolution of these ecotones requires a very detailed set of data and is outside the scope of this paper. Nevertheless, some broad features will be pointed out, since it is interesting to compare them with the evolution of Boreal/Tethyan ecotones. The evolution of the boundary between Tethyan and Boreal Realms has been the subject of many contributions, most of them based on the distribution of ammonite taxa (e.g. Imlay, 1965; Hallam, 1969, 1981; Fürsich and Sykes, 1977; Hayami, 1990; Dommergues and Meister, 1991; Hillebrandt et al., 1992; Hallam, 1994b), and on the basis of bivalve distribution was recently followed in Europe by Liu (1995). All the data indicate that a northward migration from Pliensbachian to Bathonian times took place, and that the Bathonian can be recognised as the time of the greatest Tethyan spread during the Jurassic. The boundary then shifted southwards during the Callovian, when the distinctiveness of the Boreal bivalve fauna strongly increased and was maximum at the Oxfordian (Liu, 1995). The Callovian and Early Oxfordian marked the widest spread of the Boreal Realm according to Hallam (1971).

From the possible transitional zones located in palaeotemperate regions of the Southern Hemisphere, the relationship between Maorian-type and other faunas in the western Pacific was studied by Hayami (1984). In the eastern Pacific, the South Andean ecotone has been recognised for Early Jurassic times (Fig. 7) and described in detail (Damborenea, 1996). Based on species' distribution along the eastern palaeo-Pacific margin, a southward shift of this boundary of about 8–10° latitude has been proposed for the Hettangian–Toarcian interval. It is interesting to compare these observations with the evolution of the boundary areas between Tethyan and Boreal Realms in the Jurassic. To make this comparison, the boundary areas proposed on the basis of bivalve distribution (Hayami, 1984; Smith and

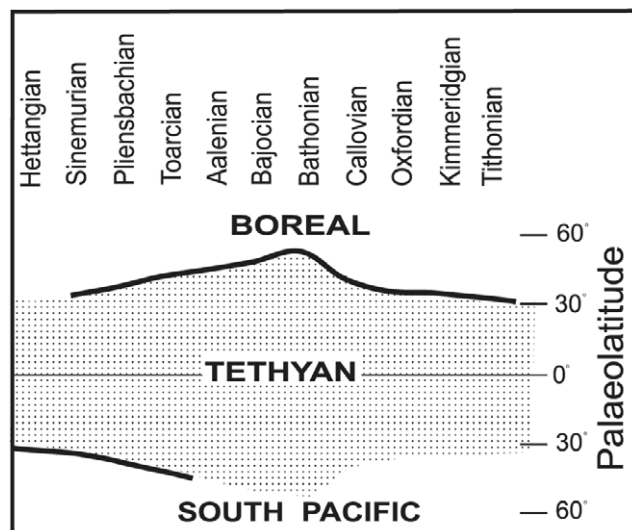


Fig. 8. Approximate palaeolatitude variation of the Tethyan/Boreal and Tethyan/South Pacific ecotones through the Jurassic, indicating possibly symmetrical expansion of Tethyan Realm during Middle Jurassic. Data compiled from various sources (see discussion in text). Solid lines: average positions proposed by different authors on the basis of bivalve distribution.

Tipper, 1986; Smith, 1989; Hayami, 1990; Liu, 1995; Damborenea, 1996; Liu et al., 1998; Aberhan, 1998, 1999), which are not always coincident with the limits proposed on the basis of ammonites, have been plotted in Fig. 7 for the Pliensbachian and Toarcian. The results show a high congruence between the behaviour of the boundary in both hemispheres during the Early Jurassic: the southward shift in the Southern Hemisphere is matched by an equivalent northward shift in the Northern Hemisphere (Fig. 8). There are not yet detailed enough data from the Southern Hemisphere to follow this comparison for later Jurassic times. It is interesting to point out, though, that the greatest expansion of low-latitude bivalve faunas in the Southern Hemisphere occurred during Middle Jurassic times (see also Grant-Mackie, 2000), and that the northward shift of the Maorian/Tethyan boundary during Late Jurassic times in western Pacific regions, albeit somewhat complicated by the tectonic history of the area (Hayami, 1984, 1987), roughly corresponds with the widest expansion of the Boreal Realm in the Northern Hemisphere. These coincidences suggest that the main faunal shifts are related in their origin.

6. Brief comparison with data from other organisms

Since this analysis is only based on one group of organisms, it is interesting to compare the results with those obtained using other groups, with the aim of meaningfully evaluating the evolution of palaeobiogeographic patterns during the Jurassic. Nevertheless, most other benthonic invertebrate groups (gastropods, corals and echinoderms) are still insufficiently known to be used in palaeobiogeography for the Jurassic at a global scale. From the scattered available data, it is evident that some groups of restricted

tropical affinities, such as reef building corals and certain sponges like *Stylothalamia*, are completely absent from the Southern Hemisphere low-latitude areas belonging to the South Pacific palaeobiogeographic unit as understood in this paper (Hillebrandt, 1981; Crame, 1987; Beauvais, 1992). Gastropods have been used to recognise palaeobiogeographic units for the Cretaceous (Sohl, 1987), but are poorly known on a global scale from Jurassic and Triassic. Within these limitations, Tong and Erwin (2001) noted that the relationships between Triassic Tethyan and American gastropods are weak, even at the generic level. Brachiopods from austral regions do show a considerable degree of endemism which supports the recognition of a Maorian Province during the Late Triassic and Early Jurassic (MacFarlan, 1992; Manceñido and Dagys, 1992); the endemism extends during Middle and Late Jurassic in New Zealand–New Caledonia (MacFarlan in Grant-Mackie et al., 2000).

As expected (see discussion in Masse, 1992), there are important differences between the results obtained in this study and the palaeobiogeographic units recognised on the basis of pelagic organisms. One of the most interesting questions that needs further discussion is the observed differences in the first order palaeobiogeographic units for the Southern Hemisphere between those based on bivalves as here described and those based on ammonites. According to the pattern of ammonite distribution, most authors consistently recognise only two realms (Boreal and Tethyan) for the Jurassic (see references in Cecca, 1999; Westermann, 2000b; Grant-Mackie et al., 2000). Hillebrandt (1981) and Hillebrandt et al. (1992) distinguished an Eastern Pacific and an Indo-SW Pacific Subrealm during some lapses of time within the Early and Middle Jurassic, but they admit that for the Late Jurassic, lack of data severely constrains the discussion of ammonite provincialism in circum-Pacific regions. Dommergues et al. (2001) recently reviewed the distribution of Early Jurassic ammonoids trying to match different morphologic sets previously recognised with analytical distribution patterns, defined by considering the distribution and abundance of species, but they did not use data from the southern high-palaeolatitude regions. In fact, a different picture seems to be emerging as new data are known. Riccardi (1991) found a nearly continuous presence of endemic ammonites from Pliensbachian to Oxfordian in South America, with a sharp increase during Aalenian, and almost no endemics during Kimmeridgian–Berriasian. Westermann (1996) recognised a high proportion of endemic taxa for the Bajocian of New Zealand, with a marked increase in Andean affinities for the Bathonian–Callovian (see Grant-Mackie et al., 2000, for references). According to Enay and Cariou (1997), an austral ammonite fauna of low diversity became progressively better established around east and south Gondwana from Oxfordian times.

Knowledge of Jurassic radiolarians from the Southern Hemisphere is just emerging (see Kiessling and Scasso, 1996; Aita et al. in Grant-Mackie et al., 2000), but clearly

points to non-Tethyan affinities for the Late Jurassic faunas from Antarctica and the Waipapa Terrane (New Zealand). These data support a palaeolatitudinal zonation for Late Jurassic radiolarian faunas in the Southern Hemisphere, with a distinct austral palaeobiogeographic unit (which is not symmetrical with the boreal one), characterised by low endemism and dominated by *Parvicingula*–*Praeparvicingula* (Kiessling and Scasso, 1996).

Only Boreal and Tethyan Realms are also recognised on the basis of the belemnite distribution (Stevens, 1973) but according to Challinor et al. (1992) a South Pacific Province (referred to the Tethyan Realm) may be distinguished in the Jurassic. Belemnitina (which define the Boreal Realm) are dominant in Boreal regions throughout the Jurassic but are also known in South America–New Zealand–New Caledonia up to the Middle Jurassic (Challinor et al., 1992; Doyle et al., 1997).

Brief references to palaeoclimate and palaeogeography can be made to explain these differences. According to Golonka and Ford (2000), greenhouse conditions prevailed during the Sinemurian–Toarcian, with a warm, humid environment, and moderate temperatures into high-latitudes with no evidence of significant continental glaciation. Based on several evidences, Price (1999) concluded that the extent of polar ice during the Mesozoic was probably only one-third the size of the present-day. Kiessling and Scasso (1996) suggested that Antarctic surface waters may have been warmer on average than those in equivalent northern high-latitudes, according to the distribution of Pantanelliidae radiolarians. During the Jurassic, climates are said to have been milder, temperatures more equable across latitude, but with some seasonality due to the different day lengths through the year. This may have been a particularly important factor affecting marine benthonic biota at high-latitudes. Pelagic taxa are probably less affected by seasonality than benthonic inhabitants of littoral environments, such as bivalves. But apart from climate, purely geographic factors, affecting the ocean circulation patterns, may have had considerable influence. For instance, the distribution of land and sea during the Jurassic in high-latitude regions; whilst in boreal regions there was a polar ocean, nearly completely surrounded by land or shallow seas, the austral regions were part of the proto-Pacific ocean, which was continuous with the eastern Tethys. Enay and Cariou (1997) emphasized that the lack of such geographical trap in austral regions explains why the austral ammonite faunas were never as distinct from the Tethyan as the Boreal ones. In addition, an important migration route for benthonic organisms since the Early Jurassic, the Hispanic Corridor (Damborenea and Manceñido, 1979; Smith, 1989; Boomer and Ballent, 1996; etc.), remained as a barrier for most pelagic animals until Late Middle or even Late Jurassic times (Elmi, 1993; Damborenea, 2000; Aberhan, 2001).

Regarding the evidence from terrestrial organisms, Balme (in Grant-Mackie et al., 2000) indicated that there is general agreement that latitudinal zonations based on

megafossil plant distribution existed in the Jurassic, but these do not support the existence of substantial climatic barriers.

7. Conclusions

A preliminary, hierarchical, palaeobiogeographic framework is proposed for the Southern Hemisphere Jurassic based on the distribution of bivalve genera. Two first order palaeobiogeographic units (Realms or Subrealms) are recognised for this region:

- *Tethyan Realm*
- *South Pacific Realm/Subrealm*: This unit, though not symmetrical with the Boreal Realm of the Northern Hemisphere, is clearly recognisable according to bivalve data.

The following five basic units are characterised according to the content of endemic genera and subgenera:

- *North Andean* [Endemic centre]: Though data are very few, it is distinctive sporadically as an endemic centre during the Late Triassic and Pliensbachian–Bajocian. The geographic range varies also with time, but roughly includes areas 1 and 2 of the present study during the Norian–Rhaetian and Pliensbachian–Toarcian, but only area 2 (due to lack of data) for Aalenian–Bajocian.
- *East African* [Endemic centre → Subprovince → Province]: Includes Madagascar, Mozambique and western India (areas 8, 9 and 10 here) during the Jurassic. On the basis of bivalve endemic genera, it begins to be recognisable as an endemic centre by Middle Jurassic times (Bathonian–Callovian), forming the origin of the East African Province, well established at the beginning of the Cretaceous.
- *Australian* [Province → vanishes]: Includes Australia, New Guinea and surrounding areas (area 7 here). Well characterised during the Late Triassic, it is not recognisable during the Jurassic.
- *Maorian* [Province → Subprovince]: Very well characterised during the Late Triassic, it is almost not recognisable at the beginning of the Jurassic, but recovers quickly (though never attains the same levels of endemism) and from Pliensbachian times maintains an almost steady amount of endemic taxa, declining again at the end of the Jurassic. In the Early Cretaceous, it is known as Austral Province. The geographic range varies, apart from New Zealand–New Caledonia (area 6) it included Antarctica (area 5) at some intervals.
- *South Andean* [Endemic centre → Subprovince]: From the Hettangian it is recognisable as an endemic centre, from Middle Jurassic (Bajocian) onwards, it maintains a moderate level of endemism and can be regarded as a subprovince. It includes areas 3 and 4.

The North Andean and Australian units are included within the Tethyan Realm, whilst the Maorian and South

Andean units are grouped together in the South Pacific first order unit. The East African units begins to develop as part of the Tethyan Realm, but near the end of the Jurassic, it begins to experience the increasing influence of South Pacific faunas, especially in its southernmost areas (southern Africa and Madagascar)

Although significant progress has been made on understanding the distribution of Southern Hemisphere bivalves during the Jurassic, many unsolved questions still remain. This paper is a contribution to Southern Hemisphere bivalve palaeobiogeography, to be complemented (and hopefully integrated) with Northern Hemisphere schemes.

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Appendix A

A.1 Brief description of regions and data sources

1 *NW South America* (Venezuela, Colombia, northernmost Perú) (Geyer, 1973, 1979; Guzmán, 1984, and references therein): Though rich faunas are known to occur, the published information from this region is very scarce and cannot be compared with the other data sets, being confined to Norian to Toarcian and Tithonian–Berriasian.

2 *Perú and Northern Chile*: Comprises most of Perú and the northernmost regions of Chile (up to about 26° S present-day latitude) References: listed in Damborenea (1996); and Jaworski (1915, 1922), Körner (1937), Cox (1949, 1956), Harrington (1961), Pérez and Reyes (1977, 1983, 1985, 1986, 1991), Hayami et al. (1977), Westermann et al. (1980), Chong and Hillebrandt (1985), Riccardi et al. (1990a, b), Pérez et al. (1987), Romero et al. (1995), Aberhan and Hillebrandt (1996, 1999), Rubilar (1998).

3 *Central Argentina and Chile*: Comprises what is regionally known as the Neuquén basin. References: listed in Damborenea (1996); and Burckhardt (1900a, b, 1903), Haupt (1907), Jaworski (1914, 1915), Stehn (1923), Fuenzalida Villegas (1937), Leanza (1941), Lambert (1944), Sokolov (1946), Levy (1967), Thiele Cartagena (1967), Cecioni and Westermann (1968), Hallam et al. (1986), Damborenea (1990), Leanza and Garate-Zubillaga (1987),

Riccardi (1988), Riccardi et al. (1990a, b, c, 1997), Lo Forte (1988), Damborenea et al. (1992), Leanza (1993), Malchus and Aberhan (1998), Rubilar (1998), Damborenea (2002) and unpublished data. Well documented for the whole time-interval of the present study.

4 *Southern Argentina and Chile*: References: listed in Damborenea (1996); and Feruglio (1936), Leanza (1968), Riccardi (1977), Olivero (1988) and unpublished data. Very few data known, only from Pliensbachian–Toarcian and Tithonian–Berriasian, Damborenea (2002).

5 *Western Antarctica*: References: Stevens (1967), Thomson and Willey (1972), Thomson (1975a, b, 1981, 1982), Willey (1975a, b, c), Jones and Plafker (1976), Quilty (1978, 1982, 1983), Edwards (1980), Crame (1981, 1982a, b, 1983, 1984, 1985, 1996a), Jeletzky (1983), Medina and Ramos (1983), Thomson and Tranter (1986), Riccardi et al. (1990c), Doyle et al. (1990), Thomson and Damborenea (1993), Crame et al. (1993), Crame and Kelly (1995), Kelly (1995). This region comprises mainly the Antarctic Peninsula and adjacent areas. The few data available from the Falkland Plateau have been included here.

6 *New Zealand–New Caledonia*: References: Trechmann (1918, 1923), Marwick (1935, 1953, 1956), Avias (1953), Fleming (1959, 1962, 1964, 1987), Grant-Mackie (1960, 1976a, b, 1978a, b, c, d, 1980a, b), Speden (1970), Stevens (1978), Freneix et al. (1974), Speden and Keyes (1981), Begg and Campbell (1985), Crampton (1988), Grant-Mackie and Silberling (1990), Damborenea and Manceñido (1992), Damborenea (1993) and unpublished data (in Hudson, 1999). Very well documented for the whole time-interval of the present study.

7 *Western Australia, New Guinea and Sula Islands*: References: Etheridge (1910), Whitehouse (1924), Teichert (1940), Skwarko (1967, 1973, 1974, 1981a, b, 1983), Coleman and Skwarko (1967), Skwarko et al. (1976), Sato et al. (1978), Grant-Mackie (1994).

8 *Western India*: References: Kitchin (1903), Cox (1935b, 1937a, 1940, 1952), Agrawal (1956a, b), Kanjilal and Singh (1973, 1980), Singh and Kanjilal (1974, 1977, 1982), Agrawal and Rai (1978), Kanjilal (1979a, b, 1980a, b, 1981), Singh and Rai (1980), Singh et al. (1982), Jaitly and Singh (1983), Pandey and Agrawal (1984), Jaitly (1986a, b, c, 1988, 1989, 1992), Jaitly et al. (1995), Pandey et al. (1996), Fürsich and Heinze (1998), Fürsich et al. (2000). No data for Late Triassic and Early Jurassic are available.

9 *Madagascar*: References: Newton (1889, 1895), Douvillé (1904), Thevenin (1908), Barrabé (1929), Besairie (1930), Nicolai (1950–1951). Reliable data only from Pliensbachian times onwards.

10 *Mozambique and eastern Africa*: References: Weir (1930, 1938), Cox (1935a), and references therein, (1937a, b), Venzo (1949), Jaboli (1952), Desio et al. (1960), Cox (1965), Ficcarelli (1968), Jordan (1971). Reliable data only from Pliensbachian times onwards.

11 *Arabia and Iran*: References: Fischer (1915), Cox (1936), Arkell (1956), Fantini-Sestini (1966), Kalantari (1981), Lewy (1982), Hautmann (2001). Data are few and very uneven, bivalves from this region are in need of revision.

References to Appendix A

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