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Early Jurassic South American pectinaceans and circum-Pacific palaeobiogeography

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ABSTRACT

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In the light of new data from South America high-latitude southern bivalve faunas are now recognized for the Early Jurassic. It is proposed that an Austral Realm was in continuous existence throughout Jurassic times. Some bivalve genera (*Palmoxytoma, Kolymonectes, Radulonectites, Agerchlamys* n. gen.) and groups of species of *Plicatula (Harpax)* show a bipolar distribution suggesting climatic control. In the Early Jurassic, a distinctive group of high-latitude bivalves included Monotidae, Kalenteridae, Oxytomidae and some Pectinidae and Plicatulidae. Based on the pectinacean (s.l.) bivalves, the east–west faunal differentiation was weaker than the latitudinal one in the Early Jurassic Pacific. The southern Andes were situated in a transitional area between the Tethyan and Austral realms, as shown by the mixed influence of the local bivalve faunas.

Introduction

"It is often commented that there was no southern counterpart" of the Boreal Realm, but certain invertebrates do seem to be "restricted to that region" (Ager, 1975, p. 17).

Mesozoic palaeogeographic studies have always been hampered by the lack of reliable data from South America. This has not prevented the presentation of global syntheses, but careful reading of most of them soon discloses that there have been far fewer detailed palaeontological investigations at high latitudes in the Southern Hemisphere than in the rest of the world. But scarcity of data has not been the only source of bias. During the course of the historical development of palaeontology in South America, Tethyan affinities were the only ones recognized and stressed from the beginning.

The purpose of this paper is to evaluate new data of some groups of South American bivalve mollusks from a palaeobiogeographical point of view. This analysis has been focused on the Early Jurassic and on the "pectinaceans" (used in a very wide sense, including Pectinacea, Plicatulacea and Monotacea). These have been chosen for several reasons: they are benthonic animals with restricted dispersion capabilities, they cover a wide range of lithofacies, they are fairly abundant everywhere and their distribution and affinities are relatively well known. Pectinaceans (s.l.) have been used in the Northern Hemisphere to recognize palaeogeographic units in the Early Jurassic. A comprehensive revision of South American Early Jurassic bivalve faunas has shown that, if the relationships of each taxon are adequately evaluated, several pectinaceans have "Boreal" affinities (Damborenea, 1987a,b, 1989, 1991). As this revision is still in progress, most of the information contained in this paper is based on unpublished work and thus a quantitative approach would be meaningless at present. An updated biostratigraphic frame for this study has been provided by Riccardi et al. (1990),

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Damborenea (in press a) and Damborenea et al. (in press).

No formal palaeobiogeographic units below the level of Realm will be discussed in this paper, largely for the reasons so lucidly exposed by Ager (1971, p. 96).

In the following discussion, palaeolatitudes are referred to broadly as low (< 30°), middle (30–60°) and high (> 60°) according to the palaeogeographical reconstruction used in Figs. 1 and 2.

Discussion

Jurassic marine palaeobiogeography was mostly based on ammonites (cf. Arkell, 1956; Cariou, 1973; Westermann and Riccardi, 1976; Enay, 1980; Westermann, 1981; Riccardi, 1991). Bivalves have sometimes been mentioned to support the resultant palaeogeographic picture and some attempts have been made to analyze them in their own right (e.g. Hayami, 1961, 1984, 1987; Hallam, 1977; Crame, 1986, 1987, 1991).

Doyle (1987) adequately summarized prevailing ideas about the causes of provinciality. It is generally agreed that an equable climate prevailed during the Early Jurassic, with low provinciality as a direct consequence. However, two realms based on "Tethyan" and "Boreal" ammonite faunas are universally recognized (see references in Arkell, 1956; Hallam, 1975; and Hölder, 1979), with the addition of an East Pacific Realm initially defined for the Middle Jurassic (Westermann, 1981; Taylor et al., 1984). Hallam (1977) characterized four provinces for the Early Jurassic based on bivalves. Surprisingly, no latitudinally distinct faunas were recognized in the Southern Hemisphere (see Stevens, 1978, p. 772). Hallam (1975, p. 210) adequately summarized the prevailing ideas on the subject: "If one is to apply an actualistic model to the Jurassic, then some degree of latitudinal bipolarity might have been expected, yet no Austral faunas have been convincingly demonstrated to match the Boreal." This has puzzled palaeogeographers and is indeed strange since other evidence, such as the

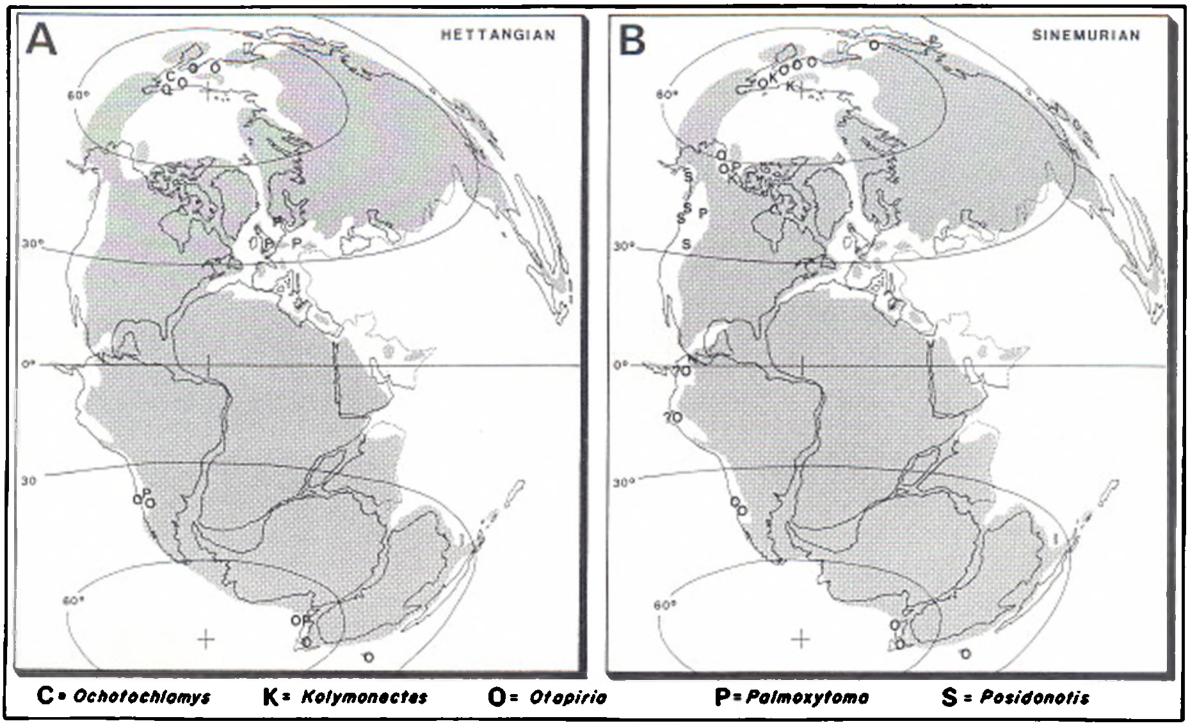


Fig. 1. Palaeogeographical distribution of selected bivalve taxa during (A) Hettangian and (B) Sinemurian. Palaeocontinental reconstruction from Smith and Briden (1977) for the Early Jurassic, hypothetic coastlines compiled from various sources. See comments for each taxon in text.

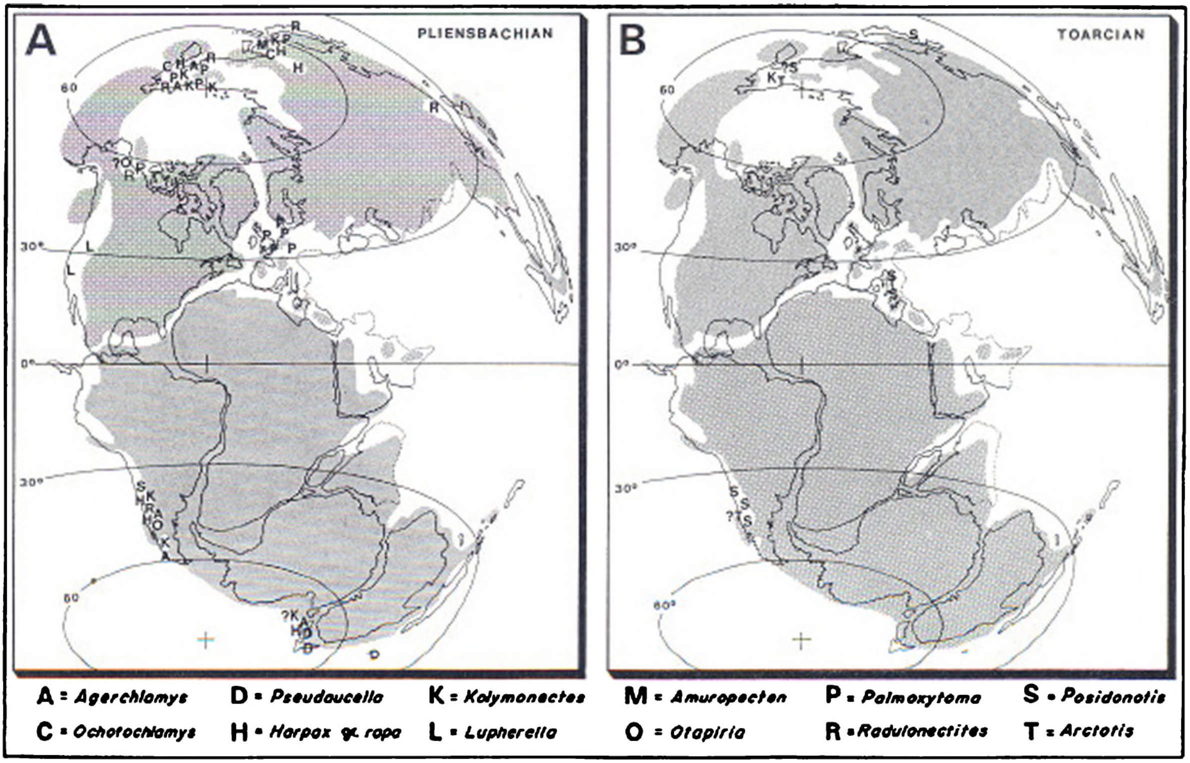


Fig. 2. Palaeogeographical distribution of selected bivalve taxa. (A) Pliensbachian. (B) Toarcian. Palaeocontinental reconstruction from Smith and Briden (1977) for the Early Jurassic, hypothetic coastlines compiled from various sources. See comments for each taxon in text.

distribution of thick carbonate sequences and other climatically controlled sediments do show a clear picture of latitudinal belts in both hemispheres (Drewry et al., 1974; Ager, 1975; Ushanov and Yasamanov, 1984; see also Brandt, 1986). A wide array of hypotheses was proposed to explain this situation. I agree with Crame (1986) that lack of data from the Southern Hemisphere has played a major role and that the western margins of the American continents are particularly important to understand bipolarity (Crame, 1991). His arguments, with reference to younger faunas, are relevant to the Early Jurassic as well. Data from Early Jurassic Antarctic faunas are still very fragmentary and will add key arguments to this discussion.

From the many factors which may have latitudinal control I will only analyze in detail here the distribution of genus group taxa. I have also detected in the southern Hemisphere latitudinal gradients in specific diversity, in relative abundance of species and in shell size within certain groups, which will be discussed elsewhere.

Pectinacean distribution

According to their palaeogeographic distribution and relative abundance, Early Jurassic pectinaceans can be grouped into the following categories:

Cosmopolitan: This includes a large number of genera widely distributed over the whole world, such as "*Chlamys*", *Entolium*, *Propeamussium*, *Camptonectes*, *Eopecten*, *Oxytoma (Oxytoma)*, *Placunopsis*, *Bositra*, *Atreta* and *Meleagrinella*. Several species of these genera have surprisingly wide geographical distributions.

Tethyan: Tethyan bivalve faunas are characterized by their high diversity, but in fact very few pectinacean genera or groups of species can be regarded as restricted to the Tethys. *Pseudopecten* is a cosmopolitan taxon which was far more common in this region and was mentioned by Hallam (1977) as characteristic of his European Province. Species of this genus also attain a larger size in low latitudes, while northern (e.g. Japanese) or southern (south Andean) species are of consistently smaller size. Rare endemic taxa of this region include *Anningella* and *Diotis*. These and other taxa such as *Ventalium*, *Varientolium* and *Subulatachlamys* may be even synonyms of cosmopolitan forms. There is virtually no equivalent during the Early Jurassic of typical Tethyan pectinids such as the Middle and Late Jurassic *Spondylopecten* and *Radulopecten*.

High latitude: Several pectinacean genera show a geographical distribution restricted to areas that, according to the palaeogeographic reconstruction of Smith and Briden (1977) and Scotese (1991), occupied a high latitude in the Early Jurassic times (see Figs. 1 and 2). Only few of them were pointed out in previous studies, as they were mostly thought to be East Asian or Southwest Pacific endemics (Hallam, 1977). The South American records, commented upon below, substantially alter this picture and "austral", "boreal" and, especially, "bipolar" or "antitropical" forms can now be recognized. As could be expected most of these high-latitude taxa are also restricted to the Pacific, the only ocean displaying the whole latitudinal range across the palaeoequator in the Jurassic.

Boreal: The genera *Ochotochlamys* and *Amuropecten* have only been found in northeastern Russia and nearby regions. They are still poorly known and their distribution could be wider.

Austral: Only *Pseudaucella* still remains as a "Maorian" endemic genus, restricted to New Zealand and New Caledonia.

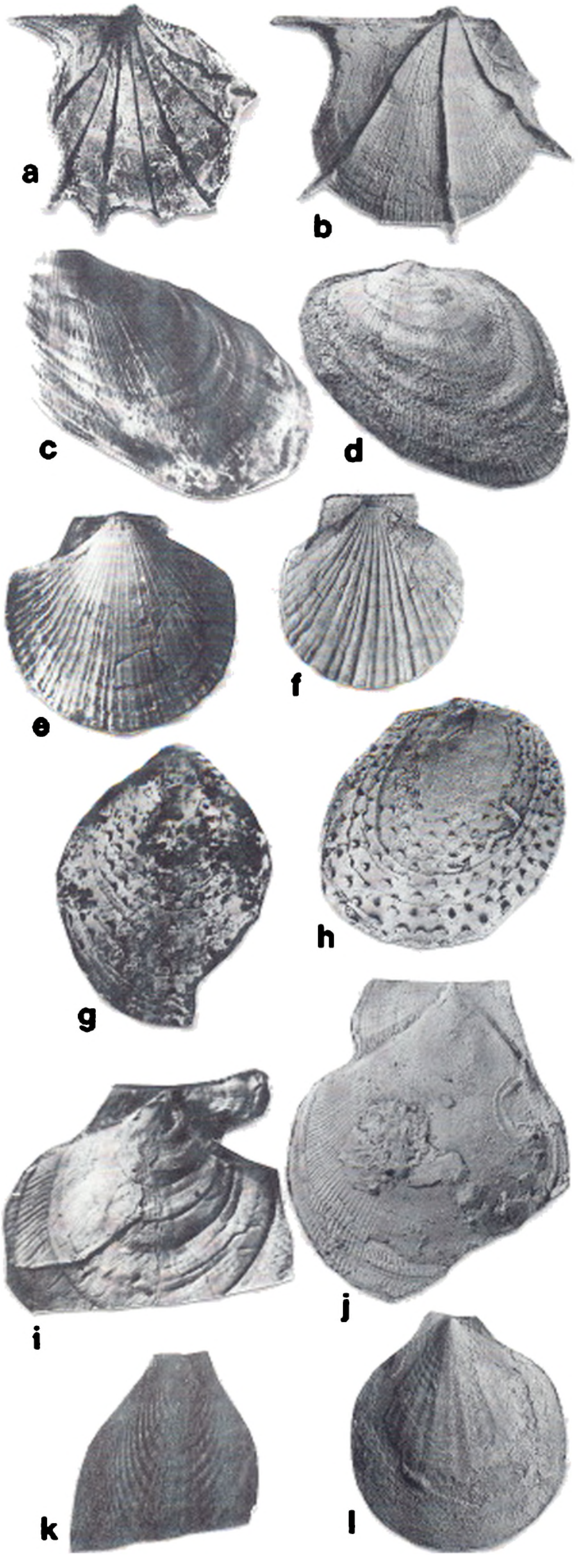
Bipolar: Various pectinacean taxa, previously thought to be restricted and characteristic of Boreal regions, have been found in southern South America and their distribution appears now to be antitropical (Fig. 3). These include *Palmoxytoma*, *Kolymonectes*, *Radulonectites*, *Agerchlamys* n. gen. (see Appendix) and *Plicatula (Harpax)* gr. *rapa* Bayle and Coquand. In latest Toarcian–Aalenian times *Arctotis* can be added (Damborenea, 1991).

Pacific: Apart from most of the high-latitude taxa just mentioned, there are several groups of Early Jurassic pectinaceans which do not occur outside the circum-Pacific regions or which appear only sporadically outside this area. *Otapiria* and *Posidonotis* belong to this category (Damborenea, 1987b, 1989) and they tend to be more abundant in high- and mid-latitude regions respectively. *Weyla* is a chiefly East Pacific genus widely distributed along the Andes in low and mid-latitude regions (Damborenea and Manceñido, 1979, 1988). Within this wide range, some species, like *Weyla alata* (v. Buch) are more abundant at lower palaeolatitudes (<40°) than others, like *W. bodenbenderi* (Behrendsen), which seem to be restricted to mid-palaeolatitudes higher than 40°.

Distribution of selected taxa

The Early Jurassic distribution of some of the geographically restricted genera has been plotted in four maps (Figs. 1 and 2) and the following comments can be added.

Fig. 3. Some examples of Early Jurassic bivalves with bipolar distributions. Boreal examples to the left, Austral examples to the right. *TM* = New Zealand Geological Survey, Lower Hutt, New Zealand; *MLP* = Invertebrate Palaeontology Division, La Plata Natural Sciences Museum, La Plata, Argentina; *OU* = Geology Department, Otago University, New Zealand. (a) *Palmoxytoma cygnipes* (Y. and B.), Pliensbachian of South Primorye, far east of Russia, ×0.5. (b) *Palmoxytoma* n. sp., Aratauran (Hettangian–Sinemurian) of the Hokonui Hills, New Zealand, OU 17810, ×1. (c) *Otapiria omolonica* Polubotko, Sinemurian of the Korkodon River basin, northeast Russia, ×2. (d) *Otapiria marshalli* Trechmann, Aratauran (Hettangian–Sinemurian) of the Hokonui Hills, New Zealand, MLP 24888, ×1. (e) *Kolymonectes staeschei* (Polubotko), late Sinemurian of the Korkodon River basin, northeast Russia, ×1. (f) *Kolymonectes coloradoensis* (Weaver), Pliensbachian of the Neuquen basin, Argentina, MLP 23686, ×1. (g) *Plicatula (Harpax)* sp., late Pliensbachian of the Bureya River basin, far east of Russia, ×1.5. (h) *Plicatula (Harpax) rapa* Bayle and Coquand, late Pliensbachian of the Neuquén Basin, Argentina, MLP 20687, ×1. (i) *Radulonectites hayamii* Polubotko, late Pliensbachian of the Omolon river basin, northeast Russia, right valve, ×1. (j) *Radulonectites sosneadoensis* (Weaver), late Pliensbachian of the Neuquén Basin, Argentina, MLP 6033, left valve, ×1.5. (k) *Posidonotis balteata* (Hyatt), reproduced from Crickmay, 1928, plate 4. (l) *Posidonotis cancellata* (Leanza), early Toarcian of the Neuquén basin, Argentina, MLP 16498, ×1. (a, c, e, g, i) reproduced (with permission) from G. Westermann (Editor), *Circum-Pacific Jurassic, Atlas*. Cambridge University Press.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Palmoxytoma Cox (1961)

When Cox named this taxon he believed it to be restricted to the Early Jurassic of Europe. Forms referable to this taxon had, nevertheless, also been recognized from New Zealand (Trechmann, 1923; see also Arkell, 1956, p. 453). *Palmoxytoma* is also known from Canada (Frebold, 1957, 1964, 1966; Poulton, 1991) and Japan (Hayami, 1959, 1975) and was later illustrated from northeast Siberia (Polubotko, 1968b) and the far east of Russia (Sey, 1984). The New Zealand record seems to have been overlooked by later authors who analyzed the palaeogeographical distribution of Jurassic bivalves (Hallam, 1977, 1983). This Australasian occurrence, together with the Argentine one (see Damborenea in Riccardi et al., 1988, 1991; Damborenea and Manceñido, 1992) shows that the palaeogeographical distribution of this genus included, at least during the Hettangian, the southern circum-Pacific margins in addition to the well-known Northern Hemisphere records (Figs. 1A and 3a,b). By Sinemurian and Pliensbachian times *Palmoxytoma* seems to have been restricted to boreal regions (Figs. 1B and 2A), where it is locally abundant and forms conspicuous shell beds (Frebold, 1957; Poulton, 1991).

Otapiria Marwick (1935)

For the synonymy and comments on systematic affinities and palaeogeographical distribution see Damborenea (1987b, pp. 154–156) and Ando (1988). This genus is represented in southern South America by two species with a different biostratigraphical distribution: *O. pacifica* Covacevich and Escobar (1979) extends from the latest Hettangian to the early Sinemurian and *O. neuquensis* Damborenea (1987b) from latest Sinemurian to early Pliensbachian times. The former species has very close affinities to the boreal and older *O. limaeformis* Zakharov, but also to some poorly known early Aratauran New Zealand specimens (material seen at Auckland University). The distribution of the genus is circum-Pacific for the Early Jurassic (Figs. 1A,B, 2A and 3c,d) and if the doubtful Colombian and Ecuadorian records (Geyer, 1973) are taken into account, no latitudinal control can be recognized. Nevertheless, *Otapiria* may still be regarded as adapted to cool/cold water environments. It is interesting to point out in this connection that *Otapiria* is far more common and attains normally a much larger size in high latitudes than in mid-latitudes, where it is also only a subordinate element of the faunas. This is the case of *Lupherella* Imlay (1967), a closely related taxon, known from the Pliensbachian of California and Oregon, USA.

Kolymonectes Milova and Polubotko (in Bychkov et al., 1976)

This genus has hitherto been cited as a typical element of boreal faunas, restricted to the Late Triassic–Middle Jurassic (mainly Sinemurian–Pliensbachian, see Figs. 1 and 2) of northeast and far east Russia (Polubotko, 1968b; Milova, 1976; Bychkov et al. 1976; Fig. 3e) and northwest Canada (Poulton, 1991). It has been used by some authors to define the outline of the arctic subprovince of the Boreal province. *Pecten coloradoensis* Weaver (1931) from western Argentina is assigned to this genus and thus its geographical range is extended to the southeastern Pacific, at least during the Pliensbachian (Figs. 2A and 3f). A doubtful specimen from New Zealand could perhaps also be added (material seen at Otago University, see Damborenea and Manceñido, 1992). This is then another pectinacean genus with a seemingly bipolar distribution during at least part of Early Jurassic times. *Kolymonectes coloradoensis* only occurs in very fine grained, mostly light-coloured sediments, forming beds with a great abundance of specimens. They are rare, though, in black shales and seem to have preferred open sea conditions. Populations from different localities differ greatly in mean shell size and I think this is related to depth and/or oxygen availability rather than temperature or other latitude-controlled factors. Larger sizes are attained at greater depth and/or less water turbulence, the only accompanying fauna being ammonites. Young individuals were probably byssally attached but the byssal notch became obsolete in adults and was then probably not functional. Adults are supposed to have lived resting on the substrate and have been very good swimmers. *Ochotochlamys* Milova and Polubotko (in Bychkov et al., 1976; Milova, 1976) is a closely related genus characterized by unequal auricles and the deep byssal notch retained in the adult shell.

Agerchlamys n. gen.

This group (see Appendix and Fig. 4) includes finely ornamented species known from the circum-Pacific Late Triassic–Early Jurassic. The palaeogeographical distribution of this genus shows a distinctively bipolar pattern during the Pliensbachian (Fig. 2A), with records from northeast Russia (Milova, 1976), New Zealand (Marwick, 1953) and west-central Argentina (Damborenea, 1991, in press b). During the Late Triassic the distribution was similar and it has been found in Boreal (Kiparisova et al., 1966) and Austral regions (material seen at Otago University, New Zealand). *Agerchlamys wunschae* (Marwick) is found in New Zealand and the Andes only in very fine grained sediments, from marls to tuffaceous siltstones, but never in laminated dark mudstones. Although locally abundant in certain beds, it is otherwise not widespread and seems to have been a stenotopic species limited to very low-energy but well-oxygenated environments. It is generally associated with a variety of limid species and commonly occurs with sponge spicules. It is never associated with corals or thick-shelled epifaunal bivalves. *Agerchlamys wunschae* was a byssally attached pectinid, as shown by the deep byssal notch and strong ctenolium (Fig. 4). Sponges could have provided a suitable substrate for this species.

Plicatula (Harpax) Parkinson

Both in Boreal and Austral regions a very conspicuous group of *Plicatula (Harpax)*, which can be named the "*P. (H.) rapa* Bayle and Coquand group", has been recognized in Pliensbachian sediments (Figs. 2A and 3g,h). The distinctive characters include a peculiar hinge which has prompted the separation of *Harpax* as a subgenus and also a set of external features such as a peculiar scaly ornamentation. The group includes *Plicatula (Harpax) rapa* Bayle and Coquand (1851) from the Pliensbachian of South America (and possibly also New Zealand, see Damborenea and Manceñido, 1992) and *P. (H.) kolymica* Polubotko (in Kiparisova et al., 1966; Polubotko, 1968a; Bychkov et al., 1976), from the Late Triassic (Norian–Rhaetian) of Siberia. The specimens from northeast Siberian and northwest Canadian Pliensbachian deposits, which Polubotko (1968b), Sey (1984) and Poulton (1991) referred to *Harpax* cf. *spinosus* (Sow.) lack radial costae and their ornamentation is very similar to that of *P.(H.) rapa* and *P.(H.) kolymica* instead.

Radulonectites Hayami (1957)

Radulonectites is a pectinid genus similar to *Pleuronectites* and *Camptonectes*, characterized by a slightly inequivalve shell with a deep byssal notch and an external surface with numerous wavy radial grooves. Hayami originally included in his new genus the specimens referred by Leanza (1942) to *Camptonectes lens* Sow. and also *Pecten (Pleuronectites) laterestriatus* Philippi (1899). The same author (Hayami, 1961, p. 320) stated that *Pecten sosneadoensis* Weaver (1931) is morphologically similar to the type species. His opinion is fully confirmed here. Since the original description of the genus, *Radulonectites* species were described from East Siberia and East China (Polubotko, 1968b; Chen, 1982; Polubotko and Milova, 1986), also from Pliensbachian sediments. Hayami (1985, pp. 44, 48) considered that *R. japonicus* is probably late Pliensbachian in age, although it is not accompanied by index fossils in Japan. This genus has thus become a typical element of Early Jurassic circum-Pacific faunas (see Figs. 2A and 3i,j). Hayami (1957) doubtfully included *Chlamys kakanuia* Marwick (1956, fig. 1) in the genus, a species from the Late Triassic of New Zealand that is only known by a badly preserved valve which does not allow a definite opinion about its affinities.

Posidonotis Losacco (1942)

This genus is present in several localities of the southern Andes and in other regions of the circum-Pacific belt, although there are also sporadic occurrences in Europe. The palaeobiogeographic distribution of this genus and related forms was discussed by Damborenea (1987b, 1989; see also

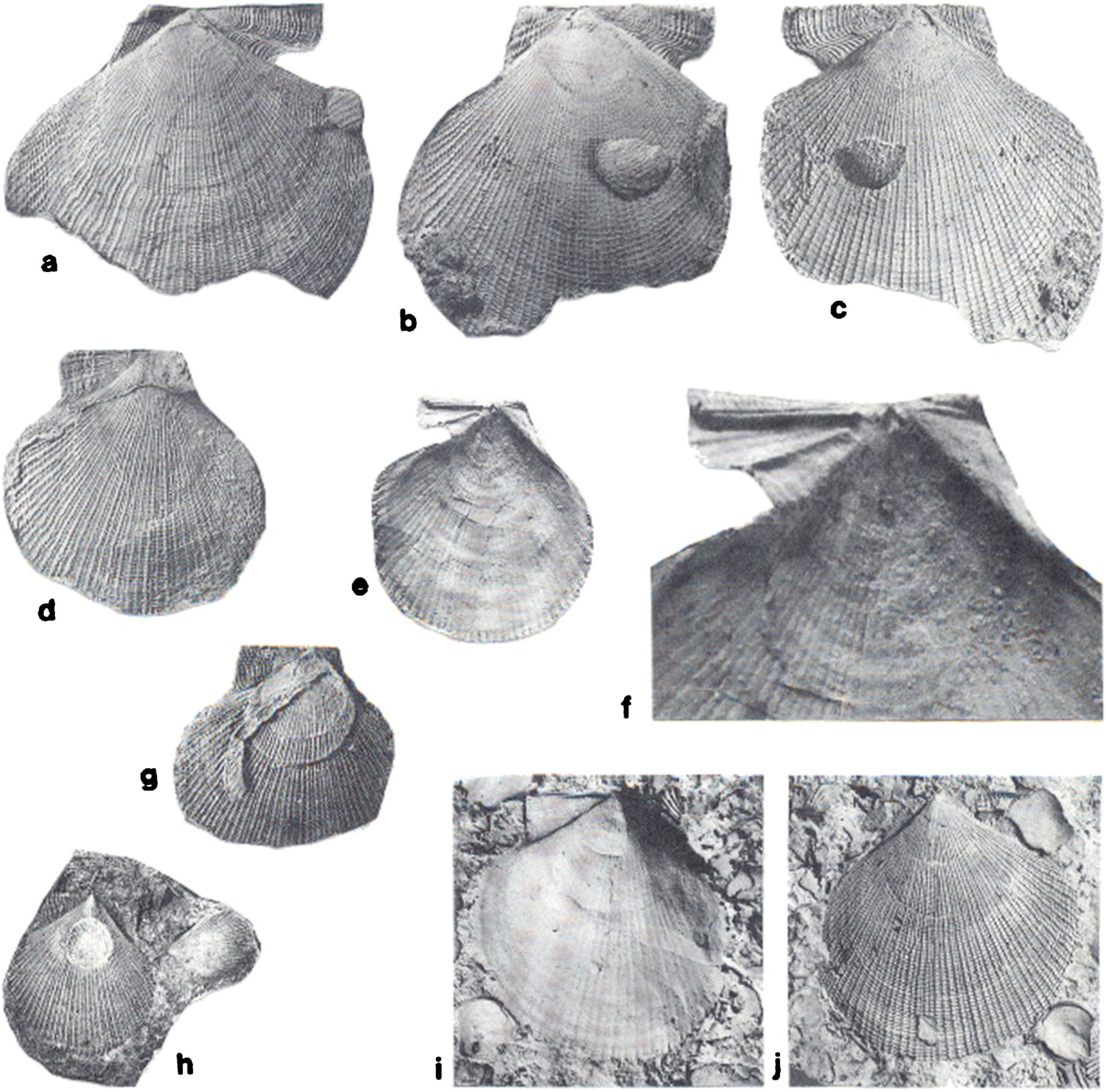

Fig. 4. (a–j) *Agerchlamys wunschae* (Marwick), all × 1, unless otherwise indicated. *TM* = New Zealand Geological Survey, Lower Hutt, New Zealand; *MLP* = Invertebrate Palaeontology Division, La Plata Natural Sciences Museum, La Plata, Argentina; *OU* = Geology Department, Otago University, New Zealand. (a) Holotype, TM 2406, right valve, Windham River Rapids, Hokonui Hills, New Zealand, Ururoan; photograph taken from rubber cast MLP 24572. (b) MLP 23658, right valve latex cast, Arroyo Ñireco, Neuquén, Argentina, Pliensbachian. (c) Same specimen, natural external mould. (d) Paratype, TM 2407, left valve, Otapiri Gorge, Hokonui Hills, New Zealand, Ururoan; photograph taken from rubber cast MLP 24573. (e) MLP 23655, interior of right valve, latex cast, Arroyo Lonqueo, Neuquén, Argentina, Pliensbachian. (f) Same specimen, × 3. (g) MLP 23656, left valve latex cast, South Cordillera del Viento, Neuquén, Argentina, Pliensbachian. (h) MLP 23660, left valve latex cast, Arroyo Ñireco, Neuquén, Argentina, Pliensbachian. (i) OU 14940, left valve internal mould, Heale Ridge, Hokonui Hills, New Zealand, lower Ururoan. (j) Same specimen, external mould.

Figs. 1B, 2A,B and 3k,l). The oldest occurrences seem to be those from North America, where they have long been known in late Sinemurian sediments (Damborenea, 1989; Pálfy et al., 1990). They belong to a group of nominal species which are probably synonyms (as already pointed out by Crickmay, 1933; see also Damborenea, 1987b, 1989; Pálfy et al., 1990). They are *P. semiplicata* (Hyatt, 1894; Crickmay, 1933), *P. symmetrica* (Hyatt, 1894; Crickmay, 1933) and *P. balteata* (Crickmay, 1928). In South America *Posidonotis* ranges from the latest Pliensbachian to the earliest Toarcian. This apparently agrees with the known occurrences in Greece and Japan (see Damborenea, 1987b, 1989; Hayami, 1988). The genus *Posidonotis* could also be represented in Siberia by the bivalves which characterize the "*Amonotis borealis* Polubotko beds" mentioned by Polubotko and Repin (1976, pp. 134, 135) from the early Pliensbachian of the river Viliga region. A closely related boreal genus is *Amuropecten* (Sey, 1984) from the Pliensbachian of far east Russia.

Arctotis Bodylevsky (1960)

This genus was first thought to be typically boreal, known from Arctic regions from latest Early Jurassic to Late Jurassic times (Lahusen, 1886; Borissjak, 1915; Bodylevsky, 1960; Koshelkina, 1963; Kelly, 1984). The discovery of species of *Arctotis* in Late Jurassic beds from austral regions (Kauffman, 1976; Jeletzky, 1983; Crame, 1985) has changed this view and a bipolar distribution for this genus during that time has been proposed (Kelly, 1984) and is now fully accepted with knowledge of good material from Antarctica (Crame, 1985, 1987). The species *Arctotis ? frenguellii* (Damborenea, 1987b), from Toarcian–Aalenian deposits in western Argentina, shows that the bipolar distribution may have extended over the whole time range of this genus (Fig. 2B).

Evidence from other bivalves

Other bivalve groups which show a bipolar Pacific distribution during the Late Triassic–Early Jurassic are the Kalenteriidae *Kalentera* and *Triaphorus* (Marwick, 1953; Damborenea and Manceñido, 1992) and some Trigoniidae (see Fleming, 1964, 1987). The Fimbriidae *Sphaeriola* appeared almost simultaneously in Sinemurian beds of Boreal (Siberia and Japan, Hayami, 1959, 1961) and Austral (New Zealand, Marwick, 1953) regions. This genus spread only later into Tethyan regions. Though still preliminary, there is growing evidence that some inoceramid groups (e.g. *Parainoceramus*) may show a similar distribution pattern.

The case for an Early Jurassic Austral Realm

This analysis indicates that, according to evidence derived from pectinaceans, east–west faunal differentiation was weaker than the latitudinal one in the Pacific during the Early Jurassic. Hallam's study (1977) on Jurassic bivalves emphasized east–west differences in the Pacific, with a distinct West American Province as opposed to an East Asian Province and a Southwest Pacific Province (see also Hallam, 1986). The data used by Hallam have been considerably altered by recent research, especially in eastern Russia, Antarctica and South America. Within the scope of this paper, only *Lupherella* and *Weyla* could be claimed to be East Pacific forms. *Lupherella boechiformis* (Hyatt) is clearly related to *Otapiria* (could be distinguished as a local subgenus at most; see Damborenea, 1987b). The distribution of *Weyla* has been already revised (Damborenea and Manceñido, 1979, 1988) and although this is a typical East Pacific bivalve, the record claimed from the Alazei Plateau, northeast Siberia (Polubotko and Repin, 1984) cannot be overlooked. The facies in which *Weyla* and other littoral bivalves of the Andean faunas thrive are missing in New Zealand. It is therefore extremely difficult to evaluate the absence of such faunal elements in the Southwest Pacific (see Damborenea and Manceñido, 1992).

Well-developed Austral faunas are recognized in the Permian and the Triassic (cf. Fleming, 1962, 1967; Stevens, 1980, 1989) and again in the Late Jurassic–Cretaceous (cf. Fleming, 1967; Kauffman, 1973; Stevens, 1973; Enay, 1980; Crame, 1985, 1986, 1987, 1991). For the Early Jurassic, "Maorian" faunas of New Zealand and New Caledonia were repeatedly discussed by New Zealand authors as being related to cool or cold water temperature (Fleming, 1967; Stevens, 1977, 1980, 1989, 1990), but because of their apparent areal restriction these were understated in global discussions. This is no longer the case and *Pseudaucella* remains the only Early Jurassic strictly Maorian endemic bivalve genus, since others such as *Kalentera* are now known to occur in South America as well (Riccardi et al., 1991; Covacevich et al., 1991; Damborenea and Manceñido, 1992). Fleming (1975) and Stevens (1980) have already mentioned the occurrence of Maorian elements in other places in southern Gondwana and they pointed out that the Maorian Province could be seen as a remnant of the Triassic and Early Jurassic Palaeoaustral Realm. They nevertheless preferred to retain the term Maorian which helped to emphasize the idea of the isolation of New Zealand at that time.

Fleming's and Stevens' ideas, together with the data discussed here, fit quite naturally with the concept of a latitudinally distinct Early Jurassic bivalve fauna, most probably climatically controlled. I believe there are enough arguments to characterize an Early Jurassic Austral Realm, with a Maorian Province (if worth distinguishing) as a subordinate unit. Although recognized through the whole of the Early Jurassic, this Austral Realm is more distinctly characterized in Pliensbachian times than for other stages (Figs. 1 and 2). This may just reflect the higher diversity of bivalve faunas worldwide at that time (and then better known), but other climatic and palaeogeographic factors may have also contributed to this picture. Further research is needed to assess adequately these differences.

As Crame (1985, 1986, 1987) pointed out for the late Mesozoic, there are distinct groups of bivalve taxa with clear high-latitude affiliations, which can be also recognized in the Early Jurassic (herein) and even earlier. High-latitude groups within the families Monotidae, Trigoniidae and Kalenteridae are evident since the Late Triassic (Fleming, 1962, 1964, 1987; Kobayashi and Tamura, 1983). To these some Pectinidae, Plicatulidae and Oxytomidae are added in the Early Jurassic (this paper). This high-latitude bipolar core is still noticeable (though weaker) during the Middle Jurassic with the addition of some Inoceramidae (Damborenea, 1990) and is well defined for the Late Jurassic as already discussed by Crame (1985, 1986, 1987).

These high-latitude stocks have similar evolutionary histories: their origin can always be traced to Boreal or Austral Triassic groups, they persisted and diversified during the Late Triassic and through the Jurassic of high-latitude regions, occasionally spreading to low latitudes, they declined in the Cretaceous and disappeared by the end of the Mesozoic. This can be best exemplified by the Monotacea. The origin and history of the four Mesozoic families recognized by Begg and Campbell (1985) are definitively linked with high palaeolatitudes. Faunas from Mesozoic polar regions (either Boreal or Austral) have a distinct "flavour" given by the abundance and diversity of monotacean genera: *Hokonuia*, *Sichuania*, *Etalia*, *Asoella*, *Monotis* and *Otapiria* in the Triassic; *Otapiria*, *Palmoxytoma* and *Pseudaucella* in the Early Jurassic; *Arctotis* and *Praebuchia* in the Middle Jurassic; *Arctotis*, *Canadotis*, *Buchia* and *Malayomaorica* in the Late Jurassic; and *Maccoyella* and *Aucellina* in the Cretaceous. Even cosmopolitan genera within this group, such as *Oxytoma* and *Meleagrinella*, are more diversified in these regions than in lower latitudes. An open-minded comparison between northern and southern monotacean taxa will certainly improve knowledge on the evolutionary history of this very interesting bivalve group. As Crame (1987) pointed out for later times, it is also relevant to the understanding of the role of polar regions as evolutionary and dispersal centers. These new data also add to the discussion of the origin of antitropical distributions (see Crame, 1986; Lindberg, 1991), especially related to marine Pacific Ocean biotas.

We should now briefly consider the boundaries of the Austral Realm in the Early Jurassic. It is evident from the palaeopositions of different parts of Gondwana at that time that only along the Andes such boundaries could be recognized. In the west Pacific this boundary should be somewhere between New Caledonia (with mainly Austral faunas) and Misol, Timor and Rotti (with Tethyan faunas), but there are no data from the intermediate areas.

Although no sharp limits can be traced in the Andes, a rather wide area with mixed bivalve faunas is present in central and southern Argentina and Chile. The occurrence of typically Tethyan (e.g. *Gervilleioperna*, hermatypic corals, thecideacean brachiopods, etc.) in the same areas and even the same sections as high-latitude bivalve genera (e.g. *Kolymonectes*, *Radulonectites*) is therefore not conflicting. It is just a consequence of the mid-latitude geographical position of this region during the Early Jurassic, the absence of barriers along the East Pacific margin, the probable pantropic nature of Tethyan faunas (Newton, 1988) and a shallow sea connection with western Tethys from middle Early Jurassic times onwards (Hispanic Corridor, see Damborenea and Manceñido, 1979, 1988; Hallam, 1983). Further north (northern Chile and Peru) bivalve faunas show very few (if any) Austral elements and the Tethyan influence is more evident (e.g. *Lithiotis*/*Plicatostylus*, cf. Broglio Loriga and Neri, 1976; Nauss and Smith, 1988). As more data on the distribution of Andean faunas become available, the latitudinal position of this boundary at different moments of the Jurassic could be worked out.

Similar palaeogeographical situations with mixed faunas in the Pacific margins of the Northern Hemisphere have been postulated for Japan (Hayami, 1984) and the far east of Russia (Sey and Kalacheva, 1984). These regions have mixed Boreal and Tethyan faunas and according to the evidence now at hand, were placed at a slightly higher latitude than central Argentina in the Early Jurassic. A detailed and updated knowledge of the affinities and distribution of Jurassic benthonic faunas in western North America is lacking.

Conclusions

(1) The distribution of Early Jurassic "pectinaceans" shows latitudinal, probably climatically controlled, compositional changes in both Northern and Southern hemispheres.

(2) In the Jurassic Pacific, the east–west faunal differentiation was, based on pectinaceans, very tenuous and much weaker than the latitudinal one.

(3) Some groups of Early Jurassic bivalves clearly show bipolar distributions. They include Monotidae, Oxytomidae, some Pectinidae and some Plicatulidae.

(4) Three realms can be recognized for the Early Jurassic: Boreal, Tethyan and Austral. Due to equable climatic conditions during the Jurassic, these were ill-defined with wide transitional zones.

(5) The Austral Realm can be traced from the Triassic through the Early and Middle Jurassic up to the Late Jurassic and beyond.

(6) The Austral Realm is best characterized for Pliensbachian times but it is also recognizable for the Hettangian, Sinemurian and Toarcian.

(7) A mixed influence from both low-latitude (Tethyan) and high-latitude (Austral) benthonic faunas in the southern Andean region (west-central Argentina and central Chile) is evident from the analysis of Early Jurassic bivalves.

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Appendix: Description of *Agerchlamys* new genus

Superfamily: PECTINACEA Rafinesque 1815

Family: PECTINIDAE Rafinesque 1815

Subfamily: CAMPTONECTINAE Habe 1977

Genus: Agerchlamys n. gen.

Type species: *Chlamys (Camptochlamys) wunschae* Marwick, 1953, from the Early Jurassic (Aratauran) of New Zealand and Pliensbachian of the Andes (type specimen figured in Marwick, 1953, plate 10, figs. 23, 24; Speden and Keyes, 1981, plate 13, figs. 2, 7; Fig. 4). A detailed description of the species will be provided elsewhere (see Damborenea, 1991).

Etymology: This genus is dedicated to Professor Derek Ager. It is especially appropriate taking into account Derek's interest in palaeobiogeography of benthonic invertebrates during the Mesozoic (Ager, 1986).

Diagnosis

Medium to large-sized pectinids, with sub-equivalve and sub-equilateral thin, discoidal, compressed shells. Umbonal angle wider than 90°. Anterior auricle at least twice as long as the posterior. Right anterior auricle with deep ctenoliate byssal notch. Fine cancellate ornamentation comprises very numerous (more than 40) narrow, nearly straight radial costae, dense continuous comarginal lamellae and fine antimarginal striae over the whole shell surface. Disc and auricles equally ornamented. Inner shell surface almost smooth. Central triangular resilifer, one cardinal crus (or dorsal tooth) parallel to the hinge axis and one tooth-like crus (or resilial tooth) to each side of resilifer. No auricular crura.

Included species

Chlamys (Camptochlamys) inspecta Kiparisova, 1966 (in Kiparisova et al., 1966, pp. 124-126, plate 17, figs. 7-10, plate 18, fig. 1, 2) from the Carnian–Norian of Siberia.

Chlamys (Camptochlamys) wunschae Marwick, 1953 (pp. 98, 99, plate 10, figs. 23, 24; Fig. 4) from the Pliensbachian of New Zealand and Argentina.

Chlamys (Camptochlamys) proprius Milova, 1976 (pp. 60, 61, plate 7, figs. 10, 11) from the Pliensbachian of Siberia.

To the above-mentioned species, perhaps *Chlamys* ex. gr. *textoria* (Schlot.) in Polubotko, 1968b (pp. 78, 79, plate 23, figs. 5, 6) from the Pliensbachian of Siberia could be added. Some northern European specimens, generally referred to *Chlamys torulosi* (Quenstedt) are superficially similar (see for instance Staesche, 1926, p. 33, plate 1, fig. 1), though nobody reported antimarginal ornamentation on these forms. In his revision of Jurassic European pectinids, Johnson (1984, p. 170) includes them all within *Chlamys textoria*, accepting a very wide range in the number of radial costae. It is interesting to point out that *C. wunschae* was also doubtfully included in Johnson's (1984) synonymy of *Chlamys textoria*, but he later states (p. 173) that the antimarginal ornamentation "probably serves to distinguish the species."

Also some Middle Jurassic material from European regions may also be related to this taxon, but a full analysis must wait until more information about them becomes available.

Discussion

Species of this taxon have been referred either to *Chlamys* or to *Camptochlamys* in the past, though it has been regarded as a distinct group.

According to the general shell shape, hinge details, presence of antimarginal ornamentation and type of ornamentation pattern the group of *A. wunschae* can be referred to the Camptonectinae in the sense of Waller and Marincovich (1992) and has affinities to *Camptochlamys*. The group has, nevertheless, a more delicate and wavy nature of the concentric lamellae that, together with the higher density of both radial and comarginal elements of the ornamentation, gives the shell a finer appearance if compared with the type species of *Camptochlamys*. The numerous, regularly spaced, fine comarginal lamellae, are normally stronger and convex outwards on the interspaces than on the costae in *Agerchlamys*. The shell is also thinner in the group of species under consideration, which also have radial ornamentation on the auricles and a gently scalloped inner shell margin.

This group of species could also be compared to some finely-ornamented pectinids referred to *Chlamys* or *Lyriochlamys* by most authors, but in this case, the *Camptonectes*-like shape of the shell, the wide umbonal angle, the presence of costae instead of plicae, of antimarginal striae over the whole shell and of continuous comarginal lamellae are the characters which prevent assignment to this genus. Relations with a Boreal stock of finely ribbed pectinids, which flourished from Late Triassic to mid-Jurassic times, is still unclear. These are traditionally referred to *Chlamys*. The most conspicuous member of this group is *C. mojsisovicsi* Kobayashi and Ichikawa (1949; see also Hayami, 1975) from the Late Triassic of Japan, Siberia and western North America. Though the ornamentation pattern is comparable, species of this group seem to lack antimarginal ornamentation.

Distribution

Agerchlamys ranges in age from the Late Triassic to the Toarcian of the Boreal and Austral Pacific regions (Fig. 2A).

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