# A comparison of Jurassic marine benthonic faunas from South America and New Zealand

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A direct comparison of Jurassic marine bivalves and brachiopods from the Murihiku terrane of New Zealand and the Argentinian-Chilean basins indicates that faunal links between equivalent facies settings of the two regions were even stronger than previously acknowledged. Some faunal elements usually regarded as Maorian endemics are also present in South America, particularly during the Early Jurassic (Aratauran and Ururoan). Middle Jurassic (Temaikan) inoceramid sequences share key elements, probably forming a latitudinally distinct stock. Two successive Retroceramus lineages that repeat general morphological trends are now recognized in South American and New Zealand Middle and Late Jurassic deposits, providing new data on correlation at the Temaikan – Heterian boundary. Since the New Zealand local stage system was based mostly on bivalves, as ammonite faunas are sparse, information from accurately dated Argentinian faunas will help improve correlation with the International Standard. From a paleogeographical point of view, the remarkable degree of faunal exchange suggests the existence of suitable neritic habitats along the margins of Gondwana and is also relevant to the issue of the provenance of New Zealand terranes.

Keywords: Palaeozoology, bivalves, brachiopods, Murihiku terrane, Andes, Early Jurassic (Aratauran, Ururoan), Middle Jurassic (Temaikan), Retroceramus, New Zealand, Argentina, Chile, palaeogeography, Gondwanaland

#### INTRODUCTION

There has been considerable debate about the configuration of crustal blocks along the southern rim of the Mesozoic Pacific and the provenance of the pre-Cretaceous terranes that make up modern New Zealand (Howell, 1980; Bishop *et al.*, 1985; Hallam, 1986; Bradshaw, 1989). An important line of evidence for paleogeographic relationships is the composition of shallow water marine invertebrate faunas. Although South American and New Zealand Jurassic benthonic faunas have often been considered in global paleogeographic syntheses (Hallam, 1977, 1986; Hölder, 1979; Stevens, 1980, 1990; Ager, 1986; Crame, 1986, 1987; Ager and Sun, 1988), the faunas have never been compared in detail by someone with direct knowledge of both regions, so important similarities have been missed. This paper reports the first direct comparison of Jurassic marine invertebrate faunas from the Murihiku terrane of New Zealand and the Argentinian – Chilean basins of South America.

This review is based on examination of collections housed at Otago University (OU) and Auckland University (AU) and additional materials held at Lower Hutt (New Zealand Geological Survey, NZGS) and Christchurch (Canterbury Museum), supplemented by field work in the North and South Islands. South American material referred to is mostly held at La Plata Natural Sciences Museum (MLP), but representative casts and molds, including some of the figured specimens, have been deposited in AU (bivalves) and OU (brachiopods).

Jurassic bivalves from New Zealand are relatively well-known, brachiopods less so (Trechmann, 1923; Marwick, 1953b; Speden, 1970; Fleming, 1987), although there are no recent systematic revisions and some information is available only in unpublished theses

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(Hudson, 1983; Braithwaite, 1984; MacFarlan, 1985). South American bivalve and brachiopod faunas are now being systematically revised by us and some results have already been published (Damborenea, 1987a, 1987b, 1989, 1990; Manceñido, 1981, 1983). However, much remains unpublished by the authors (Damborenea 1982, 1991; Manceñido, 1978) or has appeared only in preliminary reports (in Riccardi *et al.*, 1988, 1990a, 1990b, 1991; Damborenea, in press a, b; Manceñido and Damborenea, 1990; Manceñido, 1990; Manceñido and Dagys, in press).

# FAUNAL COMPARISON THROUGH TIME

A direct correlation between the New Zealand and the South American Jurassic has never been attempted. Instead, the stratigraphy in each region has been related independently to the European Standard Zonation, with differing degrees of accuracy, and so presently available correlations suffer from the accumulated distortions introduced at each step. In this contribution we have adopted the Global Stratigraphic Chart published by Cowie and Bassett (1989). Knowledge of the ammonite faunas in Argentina allows a direct correlation with the Standard Zones (Riccardi, 1984; Riccardi et al., 1988, 1990c). Unfortunately, this is not the case in New Zealand. Nevertheless, the New Zealand ammonite fauna is rich and diverse, and its systematic study will certainly allow a more accurate stage by stage comparison of the two regions in the future. Correlation of the New Zealand Jurassic with the international zonation is possible only at some isolated horizons and therefore a local system of stages has been developed (Marwick, 1953b; Carter, 1974; Stevens and Speden, 1978). We believe that the correlation of the local stages could be improved by reference to the distribution in South America of some of the bivalve groups discussed below (see Table 1).

The following stage by stage comparison must be regarded as preliminary, particularly concerning the ranges in New Zealand of the species considered. Several examples of apparently displaced vertical ranges between the two regions have been detected. Further work is necessary to interpret their significance because the stratigraphic framework is not sufficiently well-known.

# HETTANGIAN - SINEMURIAN (EARLY ARATAURAN)

Several elements of Lower Aratauran bivalve faunas from New Zealand are present in the Andes, or are represented in both regions by very closely related forms. They include the following:

# Palmoxytoma (Pl. 1, Fig. 1)

When first described (Cox, 1961), Palmoxytoma was thought to be restricted to Europe, but it was already known (as Oxytoma) or was later reported from many other Boreal-Pacific areas, such as Canada (Frebold, 1957, 1966), Japan (Hayami, 1959, 1975) and Siberia (Polubotko, 1968b). An early record of material from New Zealand, originally referred to as Oxytoma sp. by Trechmann (1923) and later to the type species of Palmoxytoma by Arkell (1956), seems to have been overlooked by later authors analyzing the paleogeographic distribution of Jurassic bivalves (Hallam, 1977, 1983; Hölder, 1979), and so Palmoxytoma has been cited as typically Boreal. Although this seems to be the case for later Sinemurian and Pliensbachian times, both the New Zealand and the Argentinian records show that during the Hettangian-earliest Sinemurian its distribution included the southern circum-Pacific. Although scarce, Argentinian specimens of Palmoxytoma sp. have been figured (Riccardi et al., 1988, 1991; Damborenea, in press a; Pl. 1, Fig. 1a here). They appear more similar to coeval New Zealand specimens from the South Island Aratauran (Pl. 1, Fig. 1b) than to Boreal forms. The New Zealand species has yet to be formally described, despite the fact that it seems to be relatively abundant at certain levels, such as the Psiloceras beds of the Hokonui Hills (several specimens seen at OU, also personally collected at Otapiri Stream). Most of the New Zealand material has been labelled and listed as Oxytoma sp. in the past and so remained unrecognized.

In Argentina Palmoxytoma is found in the upper Hettangian of southern Mendoza Province,

associated with ammonites of the Waehneroceras - Schlotheimia and Badouxia canadensis Ammonite Zones (Riccardi et al., 1988, 1991).

# Otapiria (Pl. 1, Fig. 2)

Early Jurassic Otapiria is common and well known both in New Zealand and in Argentina (Stevens and Speden, 1978; Damborenea, 1980). In the Andes the genus is represented by two species with different biostratigraphic ranges: the older is O. pacifica Covacevich and Escobar (1979) from the latest Hettangian to the early Sinemurian (Pl. 1, Fig. 2a; see also Riccardi et al., 1988, 1991). This species gives its name to a bivalve Assemblage Zone (Damborenea in Riccardi et al., 1990a).

As it has a finely ribbed right valve and an almost smooth left valve, *Otapiria pacifica* is very similar to, or may be even conspecific with, *O. limaeformis* (Zakharov) from northeastern USSR (Zakharov, 1962; Polubotko, 1968b). It is therefore quite different from coeval *O. marshalli* from New Zealand, yet somewhat reminiscent of latest Triassic (Otapirian) *O. dissimilis* Marwick and of early Aratauran forms from the North Island traditionally identified as *O. marshalli* (Pl. 1, Fig. 2b).

## Finely ribbed Chlamys

Both in New Zealand and the Andes a species of finely ribbed *Chlamys* is found in the Hettangian – Early Sinemurian. This non lamellose species is allied to the group of *Chlamys valoniensis* (Defrance) (Damborenea, 1991).

# LATE SINEMURIAN - EARLY PLIENSBACHIAN (LATE ARATAURAN)

In addition to having a number of bivalves in common, similarities between New Zealand and Andean brachiopods are apparent during this interval (see below).

# Otapiria (Pl. 1, Fig. 3)

The species *O. neuquensis* Damborenea (1987b), Pl. 1, Fig. 3a, is very close to the typical Aratauran *O. marshalli* Trechmann (1923), Pl. 1, Fig. 3b, but Andean specimens are consistently smaller in size and, although they appear in similar facies settings, they are never so abundant as in New Zealand – New Caledonia. This species was initially known only from southern Neuquén, but it was later also found in southern Mendoza Province. Its stratigraphic range is from the latest Sinemurian to the earliest Pliensbachian in Argentina (uppermost Miltoceras to Dubariceras Ammonite Zones, Riccardi *et al.*, 1988, 1991) and it gives its name to a bivalve Assemblage Zone (Damborenea in Riccardi *et al.*, 1990a). In New Zealand *Otapiria marshalli* is used as an index fossil for the Aratauran Stage in the North Island, where ammonites are uncommon. At the type locality in the Hokonui Hills *O. marshalli* does not appear with the earliest Jurassic ammonites but a few metres above them.

# Kalentera (Pl. 1, Fig. 4)

Since its initial description (Marwick, 1953b) this peculiar bivalve genus has been regarded as an endemic Maorian taxon (Grant-Mackie, 1960; Hallam, 1977; Stevens and Speden, 1978; etc.), known only from the Late Triassic and Early Jurassic rocks of New Zealand – New Caledonia.

The discovery of material clearly belonging to *Kalentera* in Lower Jurassic sediments of western Argentina (Damborenea, in press a, c; in Riccardi et al., 1991), Pl. 1, Fig. 4a, is therefore of great paleobiogeographic interest. By Early Jurassic times this group of bivalves seems to have been restricted to the South Pacific. The Argentine specimens are very close to *K. mackayi* Marwick (Pl. 1, Fig. 4b), with only minor differences in shell proportions. The faunal association and inferred paleoenvironment of Argentinian localities correspond exactly with those recorded in New Zealand. Shell morphology suggests a superficial infaunal mode of life for *Kalentera* species. Type and stability of substrate seem to have been significant factors controlling their distribution. As in New Zealand, the associated fauna is dominated

by shallow burrowers and epifaunal bivalves, such as *Grammatodon costulatus* (Leanza), *Otapiria neuquensis* Damborenea, *Palaeonucula* n. sp., pectinids, limids and ammonoids. Grant-Mackie (1960) envisaged a "relatively flat area of the sublittoral zone of the continental shelf with fairly uniform bottom conditions", as a likely environment.

# Minetrigoniidae (Pl. 1, Fig. 5)

This trigoniacean family was very diverse in the Triassic of the Pacific-Arctic region, but apparently disappeared from New Zealand at the end of the Triassic (Fleming, 1987). Some forms, probably representing descendants of Pacific Triassic stocks such as *Maoritrigonia* (Pl. 1, Fig. 5b) and referred to the genus *Myophorigonia*, are known from the Early Jurassic of the Argentinian and Chilean Andes (Groeber, 1924; Levy, 1967; Pérez and Reyes, 1977; Damborenea, in press a), Pl. 1, Fig. 5a. The fact that most of the abundant and varied Early Jurassic trigoniacean fauna of the Andes is restricted to littoral and sublittoral environments, with medium to coarse-grained sediments, may explain the absence (or extreme scarcity) of trigoniaceans in the New Zealand Early Jurassic. The appropriate facies is not preserved in New Zealand rocks dating from that time. This interpretation is an alternative to the mass extinction explanation proposed by Fleming (1964:200; 1987:16).

Minetrigoniidae from the Andes extend at least from late Sinemurian to late Pliensbachian times, represented by "Myophorigonia" neuquensis (Groeber) and its allies. The group is

now under revision (Pérez and Damborenea, in preparation).

Plate 1-Some of the Late Triassic – Early Jurassic bivalves from New Zealand and Argentina which show close relationships. a: Argentinian specimens; b: New Zealand specimens. More details given in text. All specimens  $\times$  1 and collected by the authors, except where otherwise indicated. Locality number data between parentheses.

 Palmoxytoma sp.; 1a: MLP 22253, Arroyo Malo, Rio Atuel area, Mendoza Province (M1394), Hettangian; 1b: OU 17810 (2), junction of Otapiri Stream and Taylors Creek, Hokonui Hills, (S169/

f455, coll. Grebneff), Aratauran.

2.– 2a: Otapiria pacifica Covacevich y Escobar, MLP 22261, Arroyo Malo, Rio Atuel area, Mendoza Province (M1722), Sinemurian; 2b: Otapiria cf. marshalli (Trechmann), MLP 24871, N of Arataura Point, south Kawhia coast (R15/f8587), Aratauran.

3a: Otapiria neuquensis Damborenea, MLP 19997, Puesto Araya, Rio Atuel, Mendoza Province

(M352), lower Pliensbachian;

3b: Otapiria marshalli (Trechmann), MLP 24872, N face of Ben Bolt, Hokonui Hills (S169/f676), upper Aratauran.

4.- 4a: Kalentera n. sp. Damborenea, MLP 24294 (¹), composite mold, Arroyo Las Chilcas, Rio Atuel area, Mendoza Province (M1423), lower Pliensbachian; 4b: Kalentera mackayi Marwick, MLP

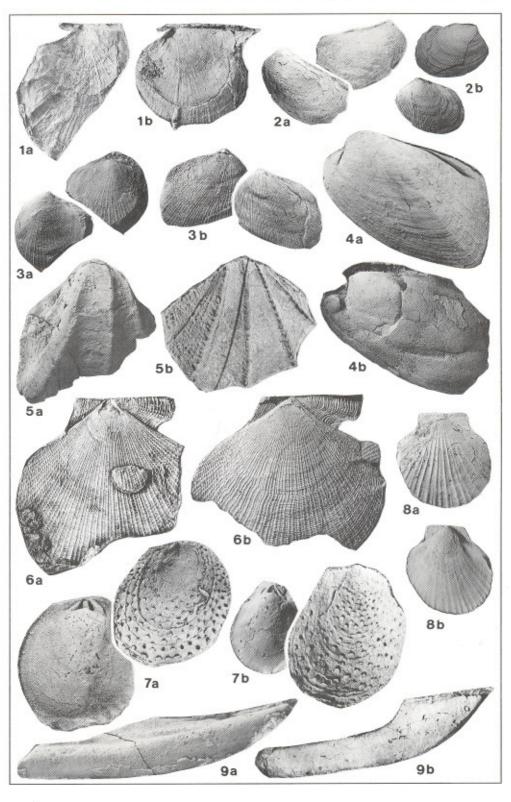
24873, internal mold, N face of Ben Bolt, Hokonui Hills (S169/f676), upper Aratauran.

5.- 5a: "Myophorigonia" neuquensis (Groeber), MLP 24324 (¹) (holotype), Puruvé Pehuén, upper Catan Lil river, Neuquén Province (coll. P. Groeber), Pliensbachian; 5b: Maoritrigonia sp., AU 576 = L 3829, external mold, S of Arataura Point, south Kawhia coast (R15/f8833, coll. Claridge), Otapirian.

- 6.— "Camptochlamys" wunschae (Marwick); latex casts.; 6a: MLP 23658 (¹), Arroyo Ñireco, Neuquén Province (M1362), Pliensbachian; 6b: NZGS TM 2406 (²) (holotype), Wyndham Rapids, Southland (S178/f490, coll. P. Wunsch), Ururoan.
- 7a: Plicatula (Harpax) rapa Bayle & Coquand, MLP 19643, X2, Arroyo Serrucho, Mendoza Province (M1316); MLP 20687-a, Arroyo Ñireco, Neuquén Province (M1362), Pliensbachian;

7b: Plicatula (Harpax) cf. rapa Bayle & Coquand, OU 14943 and 14947, X2; internal and external molds, Heale Ridge, right slope of Otapiri Valley (E49, coll. D. MacFarlan), Ururoan.

- 8.- 8a: Kolymonectes coloradoensis (Weaver), MLP 23686 (¹), Cerro Roth, Piedra Pintada, Neuquén Province (M112), Pliensbachian; 8b: Kolymonectes ? sp., OU 14289, Conical Hill, left slope of Otapiri Valley (S169/f860, coll. D. MacFarlan), Ururoan; internal molds.
- 9.— Gervillia (Cultriopsis) sp., 9a: MLP 16386, ×2, Cerro Roth, Piedra Pintada, Neuquén Province (M104), Pliensbachian; 9b: OU 14942, Heale Ridge, right slope of Otapiri Valley (E49, coll. D. MacFarlan), Ururoan; internal molds.
- (1) Casts at AU also.
- (2) Casts at MLP also.



"Spiriferina" ongleyi Marwick (Pl. 2, Fig. 1-3)

Andean material from late Sinemurian beds of western Argentina (Manceñido, 1990; Riccardi et al., 1991) most closely resembles this characteristic species of the Aratauran of the South Island (Marwick, 1953b). A redescription of the New Zealand form is being jointly undertaken with Prof. J.D. Campbell. It has been suggested by Wright and Campbell (1990) that Marwick's species may have evolved from the Otapirian (Rhaetian) Mentzelia kawhiana (Trechmann, 1923), the two representing a single lineage.

# Furcirhynchia (Pl. 2, Fig. 4-5)

This genus is widespread although sporadic in early Jurassic deposits throughout Europe, western North America, Japan, Indonesia, New Zealand (Trechmann, 1923; MacFarlan, 1985, 1990; Ager and Sun, 1988) and Argentina (Manceñido, 1978, 1990, in Manceñido and Dagys, in press). Earliest occurrences in the lower Aratauran (probably as old as Hettangian) of the Otapiri valley are followed in New Zealand by records up into the upper Ururoan (Toarcian) of the Kawhia syncline and include two successive different species. The Argentinian early Pliensbachian material identified as *Furcirhynchia* sp. (Pl. 2, Fig. 4a) is broad and depressed and more akin to the Aratauran species (Pl. 2, Fig. 4b) than to the more everted Ururoan one (Pl. 2, Fig. 5b).

## PLIENSBACHIAN (EARLY URUROAN)

This time interval is marked by an apparent increase in the similarity between South American and New Zealand faunas, and the pre-Dactylioceras Ururoan bivalve and brachiopod faunas of the two regions have several elements in common. However, the diagnostic Ururoan bivalve Pseudaucella marshalli (Trechmann) appears to be absent from the Andes. Conversely, one of the commonest Pliensbachian Andean pectinaceans, presently referred to Kolymonectes (Pl. 1, Fig. 8a), may be poorly represented in New Zealand, as limited material is available (Pl. 1, Fig. 8b).

Some faunal associations found in both regions are almost identical to the species level. They include certain pteriaceans, such as *Gervillia* (*Cultriopsis*) sp. (Pl. 1, Fig. 9), in addition to the taxa discussed below.

Plate 2 – Some of the Lower Jurassic brachiopods from New Zealand and Argentina which show close relationships. a: Argentinian specimens; b: New Zealand specimens. More details given in text. All specimens  $\times$  1.5 and collected by the authors, except where otherwise indicated. Locality number data between parentheses.

1-3.- 1a, 2a, 3a: "Spiriferina" cf. ongleyi Marwick, MLP 24483 (1), 24482 (1), 24481; Arroyo Las Chilcas, River Atuel area, Mendoza Province (M1419), uppermost Sinemurian;

1b, 2b, 3b: "Spiriferina" ongleyi Marwick, MLP 24875, W face of Ben Bolt, opposite Harrington Bridge, Hokonui Hills (JDC4069), Aratauran; MLP 24876, N face of Ben Bolt, Hokonui Hills (S169/f676), upper Aratauran.

4–5.– 4a: Furcirhynchia sp., MLP 24415, Roadside to Sañicó, Piedra Pintada area, Neuquén Province (coll. A. Leanza), Pliensbachian;

4b: Furcirhynchia sp., MLP 24877, × 2, junction of Otapiri Creek and Taylors Stream, Hokonui Hills (S169/f455), lower Aratauran;

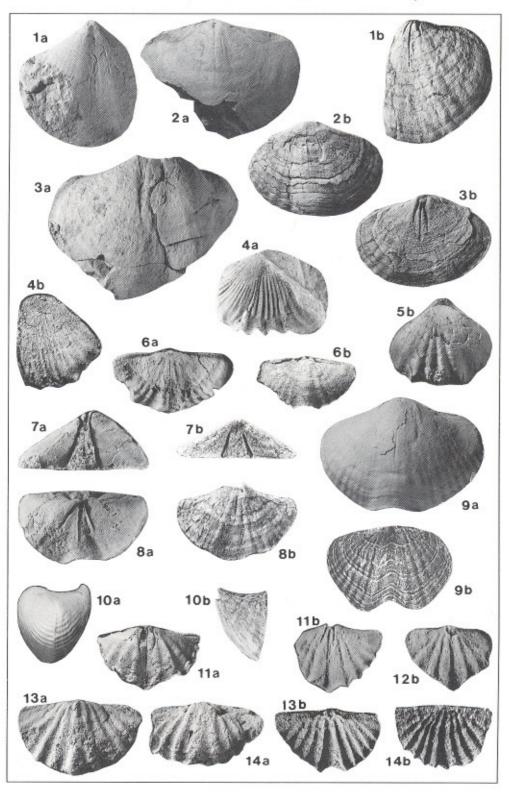
5b: Furcirhynchia sp., MLP 24878, × 2, N of Ururoa Point, south Kawhia coast (N73/f5), upper Ururoan.

6–10.– 6a, 7a, 8a, 9a, 10a: "Spiriferina" tumida ericencis de Greg., MLP 10015-b, 10015-c, Carrin Cura Creek, SW of Bayo Hill, Neuquén Province (coll. G. Parker), Pliensbachian; MLP 15285, Arroyo La Laguna, River Los Patos area (M431), upper Pliensbachian; (10a × 1);

6b, 7b, 8b, 9b, 10b: "Spiriferina" radiata Hector, MLP 24879-a, 24880-a, OU C4050', Conical Hill, left slope of Otapiri Valley (S169/f860, coll. J.D. Campbell et al.), lower Ururoan.

11–14.– 11a, 13a, 14a: "Spiriferina" cf. muensteri (Davidson), MLP 24884, 24882, 24883, 8 km S of Estancia Santa Isabel, Neuquén Province (M1055), upper Pliensbachian; × 2;

11b, 12b, 13b, 14b: "Spiriferina" cf. muensteri (David.), OU C4040, C4042, C4041, C4051, Conical Hill, left slope of Otapiri Valley (S169/f860, coll. J.D. Campbell), lower Ururoan; × 3.
(¹) Casts at OU also.



"Camptochlamys" wunschae (Marwick) (Pl. 1, Fig. 6)

"Camptochlamys" wunschae (Marwick, 1953b) belongs to a group of species known from the Upper Triassic to Toarcian of both Boreal and Austral Pacific margins. Upper Triassic forms include "C". inspecta Kiparisova (in Kiparisova et al., 1966) from Siberia and material from Otapirian and even Otamitan of New Zealand (OU collections). During the Pliensbachian this group includes "C". wunschae (Marwick, 1953b) in New Zealand (Pl. 1, Fig. 6b) and Argentina (Damborenea, in press a, b; see Pl. 1, Fig. 6a here) and "C". proprius Milova (1976) in Siberia.

It is a fairly homogeneous group, but its systematic relationships are still unclear. Although it is currently referred to *Camptochlamys*, it is distinct enough to justify the erection of a new genus (Damborenea, in press b). Reference to *Camptochlamys* obscures its real relationships, giving rise to the view proposed by Marwick (1953a) that this is a typical Tethyan element of

the New Zealand fauna.

Specimens from the Andes had been referred to *Pecten* or *Chlamys* in the past and so their true relationships were not realised. "*Camptochlamys*" wunschae is known in Argentina from southern Mendoza to southern Neuquén (and probably Rio Negro) Provinces and ranges in age from mid to late Pliensbachian. It is found only in very fine-grained sediments, from marls to tuffaceous siltstones, but never in laminated dark shales. This species is locally abundant rather than widespread and seems to have been limited to very low energy but well-oxygenated environments. It is generally associated with a variety of limid species, commonly with sponge spicules but never with corals or thick-shelled epifaunal bivalves. "*Camptochlamys*" wunschae was a byssally attached pectinid and sponges could have provided a suitable substrate. The left valve often bears epizoans (such as plicatulids, small oysters and serpulids) on its external surface.

# Plicatula (Harpax) rapa Bayle and Coquand (Pl. 1, Fig. 7)

Within the cosmopolitan genus *Plicatula* several groups of species can be recognized. Here we refer this group to the subgenus *Harpax* which shows many shell features that distinguish it from *Plicatula* s.s. (Damborenea, 1982, 1991). The two taxa (*Plicatula* and *Harpax*) coexisted during the early Jurassic, but whilst *Harpax*, known from the Triassic and early Jurassic, seems

to have dissappeared shortly afterwards, Plicatula s.s. has persisted to the present.

Within *Harpax* there is a group of late Triassic – early Jurassic species distributed in both Boreal and Austral regions of the Pacific (Damborenea, in press b). The group includes *P.(H.) kolymica* Polubotko (in Kiparisova *et al.*, 1966; Polubotko, 1968a; Bychkov *et al.*, 1976) from the Triassic of Siberia. Pliensbachian forms comprise *P. (H.) rapa* Bayle and Coquand (1851) from Argentina (Pl. 1, Fig. 7a) and Chile, *P. (H.)* cf. *rapa* from New Zealand (Pl. 1, Fig. 7b) and "*H. spinosus* (Sow.)" in papers by Polubotko (1968b) and Sey (1984). *P. (H.) rapa* is widespread in Argentina, ranging in age through most of the Pliensbachian, reaching probably the earliest Toarcian.

Juvenile specimens of *P. rapa* have been observed cemented to the outer surface of other shells, mostly "Camptochlamys" wunschae and some left valves of *P. rapa* show xenomorphic sculpture (Pl. 1, Fig. 6a). The abundance of isolated and unattached right valves suggests that this bivalve changed to a reclining mode of life during ontogeny, probably due to loss or destruction of the substrate shell. The range of sediment types in which this is known to occur in Argentina is quite similar to that of "C." wunschae, but *P. rapa* seems to be more widespread.

The identity of the material from New Zealand is still in doubt pending revision, but it appears that specimens formerly identified merely as *Plicatula* sp. belong to the same group of species and may be conspecific. Not only is the morphological similarity great, but also its frequent association with "C". wunschae is strikingly alike.

#### Limidae

Both in the Hokonui Hills and in several Andean localities, an assemblage dominated by limids developed during the Pliensbachian. In both areas very similar species of Antiquilima,

Pseudolimea and Plagiostoma may be found in association with "Camptochlamys" wunschae and Plicatula (Harpax) rapa. A recent revision of this group is available (although not published) for New Zealand (Braithwaite, 1984). In contrast, large thick-shelled species of Ctenostreon are conspicuous elements of shallow water faunas in the Andes. The absence of Ctenostreon in New Zealand may be accounted for by the lack of appropriate facies.

"Spiriferina" tumida - radiata plexus (Pl. 2, Fig. 6-10)

"Spiriferina" radiata Hector has not been studied in sufficient detail and only the morphology of its pedicle valve has been illustrated. It is a conspicuous element of New Zealand Ururoan assemblages, as indicated by collections held at OU, NZGS, AU and additional re-sampling (cf. also Trechmann, 1923; Marwick, 1953b; and Pl. 2, Fig. 6b–10b).

Similar material is known from Late Pliensbachian deposits of western Argentina, where it has been considered to differ subspecifically from *S. tumida* (von Buch) (*cf.* Manceñido 1978, 1981, 1990; Manceñido and Dagys, in press; and Pl. 2, Fig. 6a–10a), but accurate determination awaits the completion of current revision.

"Spiriferina" cf. muensteri (Davidson) (Pl. 2, Fig. 11-14)

In New Zealand, "Spiriferina" radiata is sometimes accompanied by a small but unmistakeable, strongly plicate spiriferinacean which is very rare and still undescribed. During this project, re-collection made with Prof. J.D. Campbell has substantially increased the amount of material from earliest Ururoan of the Hokonui Hills and we are now able to make comparisons with our abundant material of a larger size range from the Late Pliensbachian of western Argentina. "Spiriferina" muensteri from the Lower Jurassic of central Chile was mentioned but not figured at the end of the last century by Moericke (1894) and recently also by Ager (1986).

## TOARCIAN (LATE URUROAN)

In late Ururoan times, a number of New Zealand brachiopods (including some rhynchonellides and the last spiriferinaceans from the *Dactylioceras* beds) point to much stronger relationships with core Tethyan elements than with Andean ones and the probable connection was via Indonesia (cf. Manceñido, in press; Manceñido and Dagys, in press). Although typical elements of the Andean bivalve faunas, such as *Posidonotis cancellata* (Leanza) appear to be absent, some bivalves are still common to both, mostly belonging to cosmopolitan genera such as *Entolium*, *Oxytoma*, *Chlamys*, *Pseudolimea*, *Pleuromya*.

## AALENIAN (LATEST URUROAN ?, EARLIEST TEMAIKAN ?)

Meleagrinella (Pl. 3, Fig. 1)

Meleagrinella beds are a common feature both in the Andes and in New Zealand, as in other parts of the world. In both areas the European species Meleagrinella echinata (W. Smith) has been cited, but they are less similar to that than to each other.

For many decades, the incoming of *Meleagrinella* (Pl. 3, Fig. 1a) was thought to mark the base of the Aalenian deposits in the Andes (Weaver, 1931). However, recent studies show that the first appearance of this genus marks the base of one of the sedimentary cycles recognized in the area, varying in age from Toarcian to Aalenian or even Bajocian in different localities and usually associated with coarse calcareous sandstone beds (Damborenea, 1991).

In New Zealand, the incoming of *Meleagrinella* (Pl. 3, Fig. 1b) has been used to mark the base of the Temaikan local stage (Marwick, 1953b). However, Hudson (1983) regards that usage as unsuitable because its incoming is controlled by facies change.

#### BAJOCIAN (EARLY TEMAIKAN)

Several elements of the rich Bajocian bivalve fauna from the Andes closely resemble

Temaikan bivalves. Most of them belong to cosmopolitan groups (Camptonectes s.s., Vaugonia, Pleuromya, Myophorella, etc.) but a few are distinctive enough to be commented upon here.

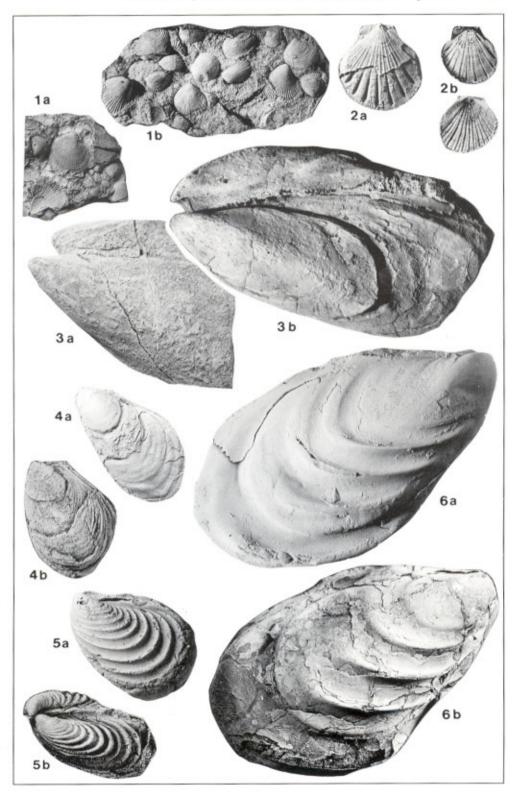
# Propeamussium (Pl. 3, Fig. 2)

A group of species of *Propeamussium*, characterized by small size and strong external ribbing of the left valve, is known from several places, including the Andes and New Zealand. In both regions they have been thought to differ sufficiently from other *Propeamussium* to be described as distinct species, and have been called *Variamussium clamosseum* Marwick (1953b) in New Zealand (Pl. 3, Fig. 2b) and *Pecten andium* Tornquist (1898) in Argentina (Pl. 3, Fig. 2a). Also similar is *P. geelvinki* Skwarko (1974) from the Lower Bajocian of western Australia. A *Propeamussium andium* bivalve Assemblage Zone has been proposed (Damborenea, in press c) for the Andean Bajocian, whereas *P. clamosseum* seems to have a longer vertical range, reaching the upper Temaikan in New Zealand (cf. Westermann and Hudson, 1991).

# Retroceramus (Pl. 3, Fig. 3, 4)

The succession and distribution of Middle Jurassic inoceramid species in New Zealand are complex, and understanding them has been inhibited by several problems, such as the poor preservation of most of the material, inadequate knowledge of their intraspecific variation and the occurrence of intermediate forms. Associated ammonites are scarce and yet to be adequately described. By far the most accurately dated succession of Middle Jurassic inoceramid species in the southern Hemisphere is that from Argentina, where the succession has a well studied ammonite zonation (see Riccardi et al., 1990c). Argentina can therefore assist in understanding other regions (Damborenea, 1990) such as New Zealand, since the Andean and New Zealand successions have some Retroceramus species in common.

- Plate 3 Some of the Middle Jurassic bivalves from New Zealand and Argentina which show close relationships. a: Argentinian specimens; b: New Zealand specimens. More details given in text. All specimens × 1 and collected by the authors, except where otherwise indicated. Locality number data between parentheses.
- Meleagrinella cf. echinata (Smith); 1a: MLP 24874, Bardas Blancas, Mendoza Province (M289), Aalenian;
- AU 9228 = L 3830, Pomarangei Road, Herangi Range, (R16/f115, coll. N. Hudson), Temaikan.
   2.- 2a: Propeamussium andium (Tornquist), MLP 24323, x 2, Carro Quebrado, Neuquén Province
- (M 154), Bajocian; 2b: Propeamussium clamosseum (Marwick), AU 11429 =L 3831, × 2, Te Whakapatiki Stream, above
- junction with Awakino river, Mahoenui (R17/f566, coll. N. Hudson), upper Temaikan.
   3.- 3a: Retroceramus aff. inconditus (Marwick), MLP 23375, Aguada de la Mula, Sierra de Reyes, Mendoza Province (M218), Bajocian;
- 3b: Retroceramus inconditus (Marwick), OU 16404, Lindern Hills Quarry, Marokopa Valley (coll. D. MacFarlan), Temaikan.
- 4.- 4a: Retroceramus cf. marwicki (Speden), MLP 23372, Chacay Melehue, Neuquén Province (M1496), upper Bajocian;
- 4b: Retroceramus marwicki (Speden), AU 12155, Opouatia Cliff, Port Waikato area (R13/f213, coll. J. Grant-Mackie & G. Westermann), Temaikan.
- 5a: Retroceramus patagonicus (Philippi), MLP 23384 (1), Chacay Melehue, Neuquén Province (M1507), upper Bathonian;
- 5b: Retroceramus cf. patagonicus (Philippi), AU 11583 = L 3828, SE end of Oraka Bay, Totara Peninsula, Kawhia Harbour, (R17/f219, coll. N. Hudson et al.), Oraka Sandstone.
- Retroceramus stehni Damborenea, 6a: CPBA 7392 (original at Buenos Aires University, <sup>1</sup>, <sup>2</sup>),
   Chacay Melehue, Neuquén Province (coll. J. Keidel), lower Callovian;
- 6b: AU 11442 = L 3832, Awakino river, above junction with Te Whakapatiki Stream, Mahoenui (R17/f376, coll. N. Hudson), Kirikiri Group.
- (1) Casts at AU also.
- (2) Casts at MLP also.



Retroceramus inconditus (Marwick, 1953b) is present in the lower Temaikan of New Zealand (Pl. 3, Fig. 3b), and the poorly known early Bajocian R. ? sp. (Damborenea, 1990) from Argentina (Pl. 3, Fig. 3a) is closely related. They are followed by Retroceramus marwicki (Speden, 1970) in both regions. This easily recognizable species is found abundantly in upper Temaikan beds of the South and North Islands (Pl. 3, Fig. 4b). Although the Argentinian specimens were referred to as R. cf. marwicki (Damborenea, 1990; see also Pl. 3, Fig. 4a here), we consider, after our examination of material from both regions, synonymy of the two forms to be almost certain. In the Andes this species was found in upper Bajocian beds of the Rotundum Ammonite Zone, below the incoming of Retroceramus patagonicus (Philippi) and characterizes a bivalve Assemblage Zone (Damborenea, in press c).

Retroceramus marwicki belongs to the group of R. lucifer (Eichwald) which lived during the early Bajocian in Arctic regions (Imlay, 1955; Polubotko, 1968b). This, and the age (also Bajocian) of the material from the Andes, suggest the need to adjust the age of the marwickibearing Temaikan in New Zealand, which has been referred to the Callovian, or Bathonian Callovian, on the basis of preliminary ammonite identifications (Stevens and Speden, 1978).

# BATHONIAN - CALLOVIAN (LATE TEMAIKAN - EARLY HETERIAN ?)

Retroceramus (Pl. 3, Fig. 5, 6)

The recent description (Damborenea, 1990) of a Bathonian – Callovian lineage of *Retroceramus* species from Argentina, which had previously been referred to *R. galoi* (in Stehn, 1923; see also Cox *et al.*, 1969), may help us to understand similar forms from New Zealand which had either been likewise referred to *R. galoi* or had remained undescribed. The presence of strongly folded *Retroceramus* below typical *R. galoi* was recognized by Hudson (1983: 83–86; see also Westermann and Hudson, 1991: 690). The identity of these forms is particularly important in New Zealand, since the incoming of *R. galoi* marks the base of the Heterian local stage.

The description of *Inoceramus patagonicus* by Philippi (1899) has been overlooked by later authors. The analysis of topotypic material shows that this is a distinct taxon (Damborenea, 1990), characterized by only slightly prosogyrous umbones, long ligamental area and ornamented by regularly spaced, narrow concentric folds separated by intervals up to twice as wide (Pl. 3, Fig. 5a). The Argentinian specimens are associated with a rich ammonite fauna of the Steinmanni Zone and the Retroceramus patagonicus bivalve Assemblage Zone (Damborenea, in press c) is thus late Bathonian in age. Some New Zealand specimens collected by N. Hudson (Pl. 3, Fig. 5b) from localities of the Waikato, Kawhia and Awakino areas (cf. Westermann and Hudson, 1991) do seem to belong to this group rather than to the younger R. galoi. The true identity of this and similar material from New Zealand, such as Inoceramus n. sp. from Loc. 613 in Purser (1961: 28), is vital to the understanding of the basic stratigraphy of the region, because if they are referred to R. galoi as has been common up to now, the beds should be referred to the Heterian (by definition). On the other hand, if they are referable to R. patagonicus as proposed here, the beds would still be included in the Temaikan, since true R. galoi only appears much later in the sequence. At the type locality of both stages (Kawhia Harbour), late Temaikan as presently understood is predominantly represented by apparently non-marine deposits, and a very careful reassessment of the stratigraphy of other areas with a more complete marine succession of this age is necessary. For instance, the Awakino area has yielded "Retroceramus (R.) n. sp. A aff. R. galoi" and recently described ammonites. The latter confirm close "ties to species from the latest Bathonian Steinmanni Standard Zone of the Andean Province" (Westermann and Hudson, 1991).

In the Andes R. patagonicus is followed by Retroceramus stehni Damborenea (1990), characterized by large shells ornamented by sharp concentric folds which become lower or fade out dorsally (Pl. 3, Fig. 6a). This species (Pl. 3, Fig. 6b) has also been found in New Zealand below the appearance of typical and abundant R. galoi by Hudson (1983) and, as

Retroceramus (R.) n. sp. B, has just been mentioned by Westermann and Hudson (1991). In Argentina and Chile the R. stehni bivalve Assemblage Zone (Damborenea, in press c) extends from the latest Bathonian (uppermost Gerthi Ammonite Horizon) to the early Callovian (lower Bodenbenderi Ammonite Zone). It is worth pointing out that the accurate dating of "R. n. sp. B" from New Zealand (Westermann and Hudson, 1991) seems to be dependent on preliminary determinations of ammonites from the middle Oraka Formation, which deserve further study on more and better preserved material in view of the Callovian age suggested by inoceramids (here) and dinoflagellates (Helby et al., 1988).

There is strong morphological evidence, supported by the stratigraphic distribution of each species, that *R. patagonicus* and *R. stehni* from the Andes belong to a single evolutionary lineage (Damborenea, 1990), equivalent to the clade observed in the group of *R. bulunensis* – *R. vagti* (Koshelkina) during the late Bajocian – Bathonian of Arctic regions (Polubotko and Repin, 1988).

# OXFORDIAN - TITHONIAN (HETERIAN - PUAROAN)

Retroceramus (Pl. 4, Fig. 1)

The Oxfordian and Kimmeridgian deposits from the Neuquén Basin in Argentina are generally poorly fossiliferous and in part non-marine. Nevertheless, a species of Retroceramus very close to the type specimen of R. galoi (Boehm, 1907) has recently been figured (Damborenea, 1990) from probably upper Callovian beds in Neuquén (Pl. 4, Fig. 1a). In the Sula Islands R. galoi appears in beds of probable Oxfordian age (Boehm, 1907; Westermann et al., 1978) which overlie a Bathonian - early Callovian ammonite fauna (Westermann and Callomon, 1988). In New Zealand the first appearance of R. galoi defines the base of the Heterian Stage, which is traditionally referred to the early Kimmeridgian (see Steven and Speden, 1978). On a regional scale, an inoceramid biozone based on R. galoi (Crame, 1982) was referred to the ?Early Kimmeridgian - Tithonian. Some recent authors consider that R. galoi could range down into the late Callovian (Grant-Mackie et al., 1986; Hudson et al., 1987; Helby et al., 1988). The issue is further complicated by the confusion between R. patagonicus and R. galoi (see above) and so needs very careful consideration. Nevertheless, even if the name R. galoi is restricted to the forms which appear above R. stehni, the base of the Heterian is probably older than Kimmeridgian and could be sited somewhere in Callovian - Oxfordian times. The ammonite fauna which accompanies these inoceramids in New Zealand has not yet been revised, but dinoflagellates of Captain King's Shellbed and Ohineruru Formation indicate at least an Oxfordian age (Helby et al., 1988).

Upper Jurassic deposits are well developed in the Magallanes basin of southern Argentina and Chile and the presence of *R. cf. haasti* (Hochstetter) was mentioned by Fuenzalida and Covacevich (1988). This material, seen recently by us in Santiago de Chile, is certainly very similar to large specimens of the New Zealand species and is associated with ammonites of probable Kimmeridgian age. In New Zealand the appearance of *R. haasti* defines the base of the Ohauan local stage, referred to the Tithonian (Stevens and Speden, 1978). Crame (1982) recognized a Kimmeridgian – Early Tithonian *R. haasti* inoceramid biozone of regional significance. A diverse microplankton suite from the Kowhai Point Siltstone suggests a Kimmeridgian age (Helby *et al.*, 1988).

Retroceramus galoi and R. haasti are regarded as belonging to the same evolutionary lineage (Fleming and Kear, 1960; Speden, 1970; Spörli and Grant-Mackie, 1976) and the recognition of the base of the Ohauan is sometimes obscured by the presence of intermediate forms which are referred to R. cf. subhaasti (Wandel).

The material from the Tithonian of the Magallanes Basin figured by Feruglio (1937) as *Inoceramus* cf. *steinmanni* Wilckens was later referred by Crame (1982) to *Retroceramus* everesti (Oppel). Specimens compared with *R. everesti* are known from the Puaroan stage in New Zealand (Marwick, 1953b).

Otapiria (Pl. 4, Fig. 2)

The species *Otapiria masoni* Marwick (1953b) is found in Puaroan beds from the North Island (Pl. 4, Fig. 2b). Feruglio (1937) described a very similar taxon from probably Tithonian deposits in the Magallanes Basin as *Pecten degasperii* (Pl. 4, Fig. 2a). This species may belong to *Otapiria* and is very closely related to the New Zealand *O. masoni*. Also allied to the latter, is a small species of *Otapiria* reported from Tithonian rocks of Alexander Island and South Shetland Islands, in Antarctica (Crame, 1984, 1987).

#### Buchia

Though less abundant than in Arctic regions, *Buchia* species are a common element of New Zealand upper Jurassic faunas. The correlation of these faunas is not yet resolved, but it is generally agreed that in New Zealand *Buchia* appeared later than in other regions (Li and Grant-Mackie, 1988). The *Buchia* sequence in the Andes has not yet been established.

#### DISCUSSION

Our results indicate that faunal relationships between the Andean and New Zealand regions throughout the Jurassic were much closer than is usually acknowledged in previous reports, particularly when equivalent paleoenvironmental settings are compared.

A number of distinctive faunal elements that have hitherto been regarded as endemic to New Zealand appear instead to have attained wide distributions. By late Triassic times, conspicuous Maorian brachiopods (such as *Clavigera*) had spread to the Chilean Andes. Other examples are increasingly noticeable in early Jurassic times. This knowledge considerably alters the usual picture of high endemism during that time (Fleming, 1967; Stevens, 1977; Grant-Mackie, 1985) which led to the recognition of a Maorian Province developed in isolation. Instead, our results strengthen the view that the Maorian elements formed part of a persistent Paleoaustral Realm (Fleming, 1979; Stevens, 1980; Damborenea, 1991, in press b). In the Middle and Upper Jurassic, the inoceramid sequences which are presently well-known in Argentina show striking similarities with the New Zealand succession. That there was some similarity was already well known, but this study has provided the details. Our results have wide ramifications, but only those strictly related to paleogeography and biostratigraphy will be summarized below.

# Paleogeography

During the Early Jurassic (Aratauran and Ururoan) most of the characteristic taxa of New Zealand faunas have their counterparts in certain open water "outer shelf" facies in the southern Andes (Pl. 1, 2). The other more littoral elements of Andean faunas (such as Weyla,

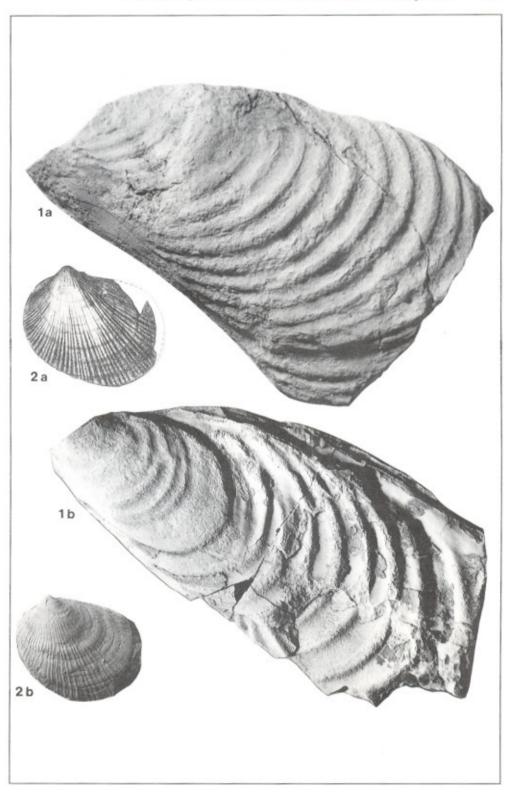
Plate 4 – Some of the Late Jurassic bivalves from New Zealand and Argentina which show close relationships. a: Argentinian specimens; b: New Zealand specimens. More details given in text. All specimens × 1 except where otherwise indicated. Locality number data between parentheses.

1.— 1a: Retroceramus aff. galoi (Boehm), MLP 19577, x 0.75, Agua de Reyes, Sierra de Reyes, Mendoza Province (G1213, coll. C. Gulisano), Callovian.

1b: Retroceramus galoi (Boehm), OU 14285, E side of Totara Peninsula, Kawhia Harbour (coll. D.S. Coombs), Heterian.

2a: Otapiria? degasperii (Feruglio), reproduction from Feruglio, 1937, tav. 3, fig. 1 (holotype, at Bologna University, IGPUB 1021), Todos los Santos Hill, Lago Argentino, Santa Cruz Province (coll. E. Feruglio), Tithonian;

2b: Otapiria masoni Marwick, NZGS TM 2389 (1), photograph of plaster cast (holotype), Maretai Stream, Kaawa Road, Waikato Heads, Puaroan (N51/f unregistered, coll. A. Mason).
(1) Casts at MLP also.



Lopha, Cardinia, Ctenostreon, trigoniids, etc.) are not present in New Zealand and New Caledonia, most probably because these facies are not preserved in the area. The only conspicuous element of New Zealand faunas which has not yet been found in the Andes is Pseudaucella, which again is a bivalve whose distribution is controlled by facies. The lack of appropriate environmental settings in New Zealand may also account for some phenomena that have previously been explained in different ways; for example, the apparent absence of trigoniaceans in the Early Jurassic of New Zealand, formerly attributed to extinction, and their sudden reappearance in Middle Jurassic times; or the absence of cardiniids, despite the presence of closely related forms, such as Torastarte, in the Triassic of New Zealand.

The observed similarities during the Middle Jurassic include numerous cosmopolitan groups and only the inoceramid sequence has been analyzed in detail here. This shows several elements in common, most of them at the species level. The distribution of this fauna seems to indicate a latitudinally distinct stock (Damborenea, 1990), similar to the upper Jurassic Austral faunas.

The comparison is more difficult for Late Jurassic times because the lithofacies represented in each region are not equivalent. This presumably accounts for: a) the scarcity of Oxfordian and Kimmeridgian inoceramids in the Neuquén Basin; b) the scarcity of buchiids in southern South America.

The similarities between the Jurassic faunas of the Murihiku terrane of New Zealand and those of the Andes may contribute to the discussion on the provenance of that terrane. The striking similarities detected (down to generic and even specific level) involve mainly benthonic organisms (such as bivalves and brachiopods), implying that there were suitable neritic habitats along the margins of Gondwana to allow this remarkable degree of faunal exchange.

It could be argued by those resorting to some extreme geotectonic reconstructions, such as closure of the Pacific Ocean under an expanding Earth assumption (cf. Shields, 1979, fig.1; Ager, 1986; Stevens, 1990, fig.1) or the much more speculative post-Jurassic atomization of a hypothetical Pacifica ancient continent (Nur and Ben-Avraham, 1977, fig. 1), that the paleodistances separating New Zealand from South America might have been very small indeed. Nevertheless, we feel that even within more conventional Gondwanaland reassemblies (cf. Quilty, 1982, fig. 82.6; Bradshaw, 1989, fig. 4; Stevens, 1989, figs. 1–3), the paleolatitudes and distances involved seem reasonable enough to account for the faunal links observed. Antarctica, where we might expect to find possible intermediate forms, is an important area for further research, especially since its bivalve faunas have only been analyzed biogeographically for the late Jurassic-Cretaceous interval (Crame, 1986, 1987).

Although no faunas from the Torlesse terrane have been included in this report, it may be worth recalling that within a group of specialized, cemented brachiopods such as the thecideaceans, the first Mesozoic representatives outside Europe-Africa, have only recently been independently discovered in undefined Mid (or Early?) Jurassic allochtonous rocks from the North Canterbury area (Maxwell, 1987) and in Early Jurassic deposits from west-central Argentina (Manceñido and Damborenea, 1990). Although specimens from the two areas do not appear strictly comparable in detail, it is interesting that they belong to a group usually regarded as indicating warm-temperate waters, dimly lit habitats, specially of reef environments. This stresses the presence of Tethyan affinities as pointed out by Grant-Mackie (1985) and Stevens (1989, 1990).

# Biostratigraphy

A correlation chart for the Jurassic of both regions based on their bivalve faunas is offered here (Table 1) in the hope of promoting further discussion on this subject. A more general

Table 1 - Correlation chart between South American and New Zealand Jurassic faunal successions according to marine bivalves.

		BIVAL	VES	
STAGES		SOUTH AMERICA	NEW ZEALAND	LOCAL STAGES
TITHONIAN	N C	R. aff. everesti O.? degasperii	R. aff. everesti B. plicata B. hochstetteri M. ? aff. misolica B. cf. plicata	PUAROAN
KIMMERIDGIAN		R. aff. haasti	R. haasti R. subhaasti Malayomaorica	OHAUAN
OXFORDIAN	UML		R. galoi	HETERIAN 
CALLOVIAN	M L	R. aff. galoi	R. stehni	*
BATHONIAN	M L	R, patagonicus	R. cf. patagonicus	TEMAIKAN
BAJOCIAN	U	R. marwicki P. ? westermanni R. cf. inconditus Propeamussium andium	R. marwicki Tancredia allani "I." brownei R. inconditus P. clamosseum	
AALENIAN		Tancredia sp. Meleagrinella sp.	Meleagrinella sp.	?
TOARCIAN	U  L	Meleagrinella sp. Propeamussium pumilum	I, ururoaensis	URUROAN
PLIENSBACHIA	UNL	Posidonotis cancellata  Radulonectites sosneadoensis "C" wunschae P. rapa  O. neuquensis  P. apollo	P. martini Pseudaucella marshalli "C," wunschae P. c1, rapa Kalentera mackayi	
SINEMURIAN	U	Kalentera sp.  Cardinia cf. listeri  O. pacifica	Sphaeriola leedae  O. marshalli	ARATAURAN
HETTANGIAN		Palmoxytoma sp.	Palmoxytoma sp.	

approach to a circum-Pacific correlation has been compiled by Damborenea (in press c and in Damborenea et al, in press). From a biostratigraphical point of view, the faunal elements in common between the New Zealand and Andean Jurassic add to the debate on the problem of the worldwide correlation of New Zealand Jurassic local stages, which are mostly based on bivalves.

This is best exemplified for the Lower and Middle Jurassic. In the Lower Jurassic there are many species in common. The vertical range of these species is well-known in the Andes (Damborenea in Riccardi *et al.*, 1990a). Although we could expect slight differences from one region to the other according to the different taxa involved, we believe these are not significant, whereas the similarities allow a relatively sound basis for correlation with the international Stages (see Table 1).

In the Middle/Upper Jurassic the existence of successive lineages (R. patagonicus – R. stehni below and R. galoi – R. haasti above) that repeat general morphological trends are now known to occur at least in South America and in New Zealand. Extreme caution must be taken when referring fragmentary material to any of the species involved from these and other intermediate regions. Biogeographic, evolutionary and taxonomic generalizations must be limited to reasonably well preserved material. From the New Zealand point of view, awareness of this fact will greatly assist in understanding the stratigraphy of Middle and Upper Jurassic deposits. It is especially relevant to the question of definition and correlation of the Temaikan – Heterian boundary.

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