

Early Jurassic *Kalentera* (Bivalvia) from Argentina and its palaeobiogeographical significance

Susana E. DAMBORENEA¹

Abstract. The Triassic-Early Jurassic genus *Kalentera* belongs to a bivalve group which was diverse and widely distributed during Late Palaeozoic times (family Kalenteridae). The family survived the Permo-Triassic crisis but only represented by a few genera, and *Kalentera* lingered into the Jurassic to become extinct at the end of the Early Jurassic (Toarcian). A new species of *Kalentera* from latest Sinemurian - early Pliensbachian deposits of Mendoza and Neuquén provinces is described herein. The species is restricted to siltstones and fine-grained sandstones. These substrate conditions seem to have been the main limiting factor to their distribution. These conditions agree with the occurrences of species of this genus in New Zealand, Nevada and Chile. Shell morphology suggests that *Kalentera* species were semi-infaunal or superficial infaunal. At Las Chilcas, Mendoza, the locality which yielded most of the specimens, the species is associated to other superficial infaunal bivalves (such as *Grammatodon* and *Palaeonucula*), to epifaunal bivalves (*Otapiria*, limoids and pectinoids) and to ammonoids. *Kalentera* was regarded as endemic to the Maorian Province, and indeed the genus was restricted to that biochore during the Late Triassic. From the Triassic/Jurassic boundary onwards, the distribution of the genus is clearly bipolar, being apparently absent from Tethys. *Kalentera* is characteristic to the austral biochore as recognized on the bases of bivalve distribution during the Early Jurassic. The new species from the Neuquén Basin has a stratigraphical range restricted to the *Otapiria neuquensis* bivalve Assemblage Zone, and to the *Miltoceras* and *Dubariceras* Zones of the local biostratigraphic scale.

Resumen. EL GÉNERO *KALENTERA* (BIVALVIA) EN EL JURÁSICO TEMPRANO DE ARGENTINA Y SU SIGNIFICACIÓN PALEOBIOGEOGRÁFICA. El género Triásico-Jurásico *Kalentera* pertenece a un grupo de bivalvos bien diversificado y ampliamente distribuido en todo el mundo durante el Paleozoico Tardío (familia Kalenteridae). La familia logró apenas sobrevivir a la extinción permo-triásica, estando representada en el Triásico por unos pocos géneros. *Kalentera* sobrevivió a la siguiente crisis cerca del límite Triásico-Jurásico, para extinguirse a fines del Jurásico temprano (Toarciano). Se describe material de una nueva especie de *Kalentera* procedente de estratos del Sinemuriano más tardío al Pliensbachiano temprano de las provincias de Mendoza y Neuquén. Esta especie está restringida a limolitas y areniscas de grano muy fino, y las condiciones del sustrato parecen ser el factor limitante más estricto. Estas condiciones coinciden con las de los registros de *Kalentera* en Nueva Zelanda, Nevada y Chile. La morfología de la conchilla sugiere que las especies de *Kalentera* eran semi-infaunales o infaunales superficiales. En Las Chilcas, Mendoza, de donde procede la mayor parte del material, la especie se halla asociada a otros bivalvos enterrantes superficiales (como *Grammatodon*, *Palaeonucula*) y epifaunales (*Otapiria*, limoideos, pectinoideos) y a amonoides. Desde el punto de vista paleobiogeográfico, *Kalentera* había sido considerado un género endémico de la Provincia Maoriana, y tal parece ser su distribución durante el Triásico Tardío. Ahora se conoce que esta distribución se amplió al hemisferio norte a partir del límite Triásico/Jurásico, para llegar a ser bipolar, hallándose aparentemente ausente del Tethys. Es por lo tanto un integrante característico del biocore ma austral reconocido sobre la base de la distribución de los bivalvos. La nueva especie de la cuenca neuquina tiene un rango estratigráfico restringido a la Zona de *Otapiria neuquensis*, y a las Zonas de *Miltoceras* y *Dubariceras* de la escala bioestratigráfica local.

Key words. Early Jurassic. Bivalvia. Modiomorphoidea. Kalenteridae. Neuquén Basin. Argentina. Bipolarity.

Palabras clave. Jurásico Temprano. Bivalvia. Modiomorphoidea. Kalenteridae. Cuenca de Neuquén. Argentina. Bipolaridad.

Introduction

Kalenteridae were diverse and abundant all over the world during the Late Palaeozoic, represented, among others, by the genera *Permophorus*, *Celtoides*, *Pseudopermophorus*, *Rimmyjimina* and *Bowlandia* (Newell, 1957; Fang and Morris, 1997). After the Permo-Triassic crisis the family was represented by

only a few genera (*Curionia*, *Triaphorus*, *Somareoides*, *Kalentera*), with a more restricted geographical distribution. They were severely checked again by the end-Triassic extinction event, but the genus *Kalentera* lingered into the Early Jurassic, when it had a mainly bipolar distribution. This interesting bivalve group became extinct during the Toarcian.

A species of *Kalentera* lived in the Neuquén Basin during the Early Jurassic (Riccardi *et al.*, 1991; Damborenea and Manceñido, 1992; Damborenea, 1993, 1996, 2002). The aims of this paper are to provide a proper description of this species and to dis-

¹ Departamento Paleontología Invertebrados, Museo de Ciencias Naturales La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. CONICET.
sdambore@museo.fcnym.unlp.edu.ar

cuss the palaeobiogeographical significance of the genus. Since it is not possible to understand this bi-valve group without involving both Palaeozoic and Mesozoic taxa, a rather substantial discussion on their systematic position and relationships is also included. It is necessary to point out, though, that there are many species in this group which are too poorly known to be considered in this discussion.

Kalentera appears to be restricted to uppermost Sinemurian-lower Pliensbachian in Argentina, and it was only found in four localities of two widely separated regions (figure 1): arroyos Las Chilcas and Blanco (Codo and La Horqueta), river Atuel region, Mendoza Province; and arroyo Lapa (Charahuilla region, Neuquén Province). The arroyo Las Chilcas section, which yielded most of the specimens, was measured by M. Manceñido and the author in 1983 (see Riccardi *et al.*, 1988, 1991 for details). At this section the species has a well-documented stratigraphical distribution spanning the *Miltoceras* and *Dubariceras* Ammonite Zones (table 1). Only one specimen is yet known from the arroyo Lapa section (also logged by the author and colleagues) in beds of similar age (see Damborenea, 1987 for detailed section). Lanés (2002; in press) measured the Codo del Arroyo Blanco and La Horqueta sections, where she collected further specimens.

Material

Most of the material described here was collected by the author and colleagues in several field trips from 1983 to 2002, and some specimens by S. Lanés during field work related to her doctoral thesis (Lanés, 2002; see also Lanés, in press).

All the specimens from Argentina are housed in the Departamento Paleontología Invertebrados, Museo de Ciencias Naturales La Plata, La Plata, Argentina (MLP). Illustrated material from New Zealand is housed in Department of Geology, University of Otago (OU).

Abbreviations used in text: L= length; H= height; W= width or inflation of single valves; Lhp= length of the posterior portion of the hinge-line; B= both valves; LV= left valve; RV= right valve. In order to facilitate comparisons, the mode of preservation of each measured specimen is indicated as IM= internal mould; EM= external mould or CM= composite mould.

Systematic palaeontology

Superfamily MODIOMORPHOIDEA Miller, 1877

Family KALENTERIDAE Marwick, 1953

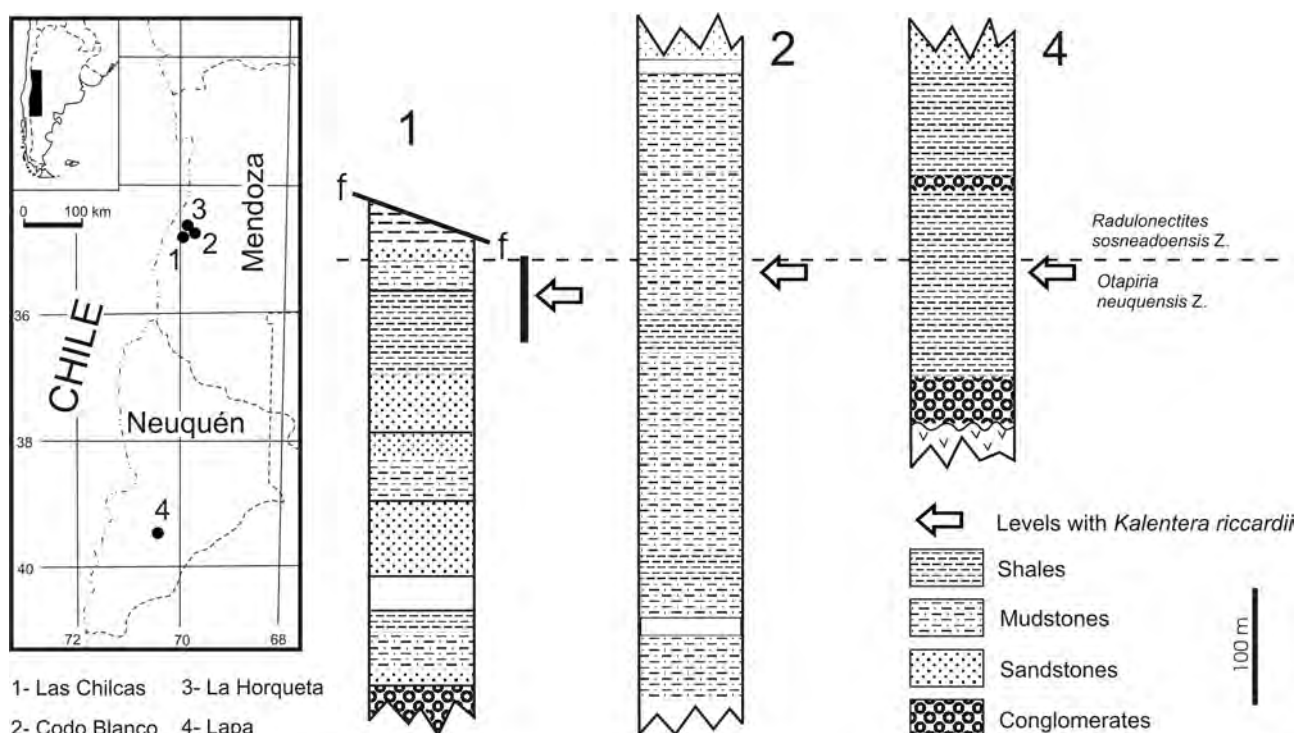


Figure 1. Location map and general sketch of measured sections bearing *Kalentera riccardii* n. sp. Sections levelled to the base of the *Radulonectites sosneadoensis* Zone. 1: Las Chilcas section (personal data), 2: Blanco section (from Lanés, 2002), 4: Lapa section (personal data). / Mapa de ubicación y esquema de los perfiles medidos que contienen *Kalentera riccardii* n. sp. Los perfiles han sido nivelados a la base de la Zona de *Radulonectites sosneadoensis*. 1: perfil de arroyo Las Chilcas (datos personales), 2: perfil del codo del arroyo Blanco Blanco (según Lanés, 2002), 4: perfil de arroyo Lapa (datos personales).

Although this is a relatively well-known group of bivalves, serious controversies are still evident concerning its systematic affinities and phylogenetic relationships. First, it is clear that shell shape and hinge similarities between *Kalentera* and *Permophorus* strongly indicate that they should be placed in the same family (compare figure 2 here with Logan, 1964, pl. 47 and text-fig. 1; Morris *et al.*, 1991, figure 35; or Newell and Boyd, 1999, figs. 1 and 3). The systematic discussion has been largely focused on the Late Palaeozoic representatives of this group, i.e. *Permophorus* and its allies, and involves a combination of problems derived from the poor knowledge of some genera, the artificial grouping of superficially similar genera and the consequently different scope of high rank taxa, the variable emphasis given by different authors to specific shell features and shell structure, and, last but not least, the presence of nomenclatorial complications. The subject has been extensively dealt with by Fang and Morris (1997), who unfortunately did not discuss the Mesozoic genera in detail.

In summary, this group of bivalves has been referred to three bivalve subclasses (in the frame of Pojeta's classification, 1987): the Heterodonta/Palaoheterodonta or Heteroconchia by suspected relations

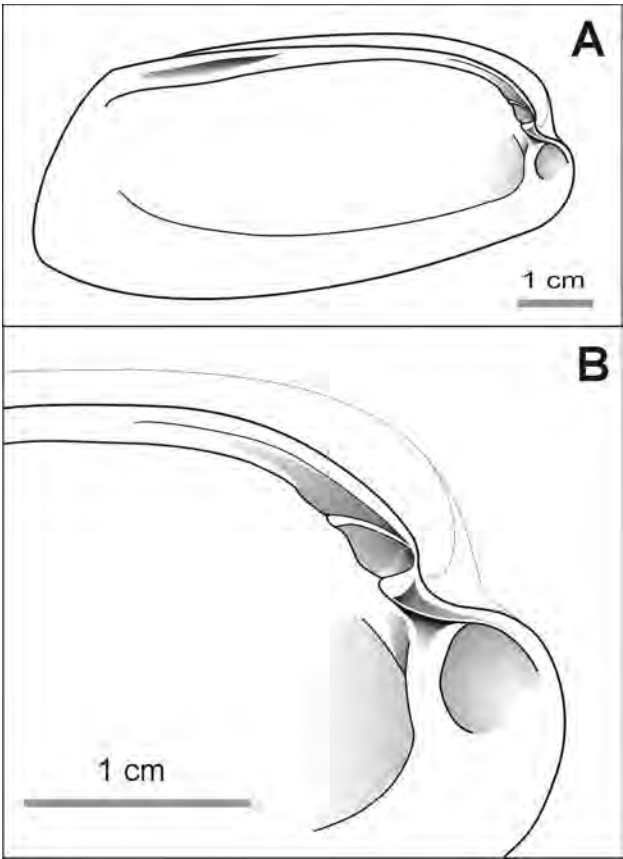



Figure 2. Sketch of *Kalentera riccardii* n. sp. left valve hinge region, mainly based on specimens MLP 13500, 24304 and 24308 / Esquema de la región charnelar de la valva izquierda de *Kalentera riccardii* n. sp., basado en los ejemplares MLP 13500, 24304 y 24308.

Table 1. Stratigraphical range of *Kalentera riccardii* n. sp. in the context of the local ammonite and bivalve zonations (Riccardi *et al.*, 1991, 2000; Damborenea, 1994) / Rango estratigráfico de *Kalentera riccardii* n. sp. en el contexto de las zonaciones locales de amonites y bivalvos (Riccardi *et al.*, 1991, 2000; Damborenea, 1994).

STAGE	AMMONITES		BIVALVES	<i>Kalentera riccardi</i> n. sp.
Toarcian	<i>Dumortieria</i>		<i>Meleagrinnella</i> 	
	<i>Phlyseogrammoceras tenuicostatum</i>		<i>Parvamussium</i> cf. <i>pumilum</i>	
	<i>Phymatoceras</i>			
	<i>Collina chilensis</i>			
	<i>Peronoceras pacificum</i>			
	<i>Peronoceras largaense</i>			
	<i>Dactylioceras hoeldereri</i>			
	<i>Tenuicostatum</i>		<i>Posidonotis cancellata</i>	
Pliensbachian	<i>Fanninoceras</i>	<i>disciforme</i>	<i>Radulonectites</i>	
		<i>fannini</i>	<i>sosneadoensis</i>	
		<i>behrendseni</i>	<i>Otapiria neuquensis</i>	
	<i>Dubariceras</i>			
<i>Tropidoceras</i>				
	<i>Miltoceras</i>		<i>Cardinia</i> cf. <i>listeri</i>	
Sinemurian	<i>Epophioceras</i>			
	?		<i>Otapiria pacifica</i>	
	"Agassicerias"			
"Vermiceras"				
	<i>Badouxia canadensis</i>		<i>Palmoxytoma</i> cf. <i>cygnipes</i>	
Hettangian	"Waelneroceras-Schlotheimia"			
	"Psiloceras"			
	<i>Psiloceras rectocostatum</i>			
	?			

to the carditoids (Newell, 1957; Logan, 1964; Rossi-Ronchetti and Allasinaz, 1965, 1966; Chavan in Cox *et al.*, 1969; Bailey, 1983; Cope, 1995; Newell and Boyd, 1999); the Isofilibranchia due to their alleged resemblance to the mytiloids (Carter, 1990; Kobayashi and Ichikawa, 1950; Pojeta *et al.*, 1986); and, more recently, to the Anomalodesmata (Morris, 1978; Campbell, 1984; Morris *et al.*, 1991; Fang and Morris, 1997; Carter *et al.*, 2000; Cope, 2000) close to the pholadomyiids.

Kalentera was originally related to *Permophorus* by Marwick (1953) and placed in the Cypricardioida. Later the group was referred to the Carditoidea by Newell (1957) and Chavan in Cox *et al.* (1969), on the basis of superficial resemblance of shell shape with some late Cretaceous to Recent carditoids, such as *Beguinia* Röding, and also apparent similarities in the dentition pattern. This opinion has been challenged by many authors (Stanley, 1968, 1972; Carter, 1990; Morris *et al.*, 1991; Fang and Morris, 1997).

On the other hand, *Kalentera*, *Permophorus* and modiomorphids have striking similarities, as pointed

out by Carter (1990). Apart from an overall resemblance in shape and ornamentation pattern, the number, position, and arrangement of "cardinal" teeth (figure 2) are very similar to those present in some Palaeozoic modiomorphids. It should be pointed out now, in order to understand this discussion, that previous to Fang and Morris (1997) the modiomorphoids were a very heterogeneous group, including both Ordovician modiolopsids and Devonian modiomorphids (see for instance Pojeta *et al.*, 1986). Newell (1957) discussed the possible relationships between Kalenteridae, Myoconchidae and Modiolopsidae, which he regarded of family rank. He proposed that Modiolopsidae could have given rise to the Carditoidea, while Pojeta (1978), Carter and Tevesz (1978), Pojeta *et al.* (1986) and Carter (1990) suggested that Modiomorphoidea (which for them included modiolopsids) and Mytiloidea are closely related, based on hinge, ligament and shell microstructure details, and the last author referred the Modiomorphoidea (including Kalenteroidea) to the Isofilibranchia. Waller (1990) challenged this opinion and referred the modiomorphids to the Anomalodesmata.

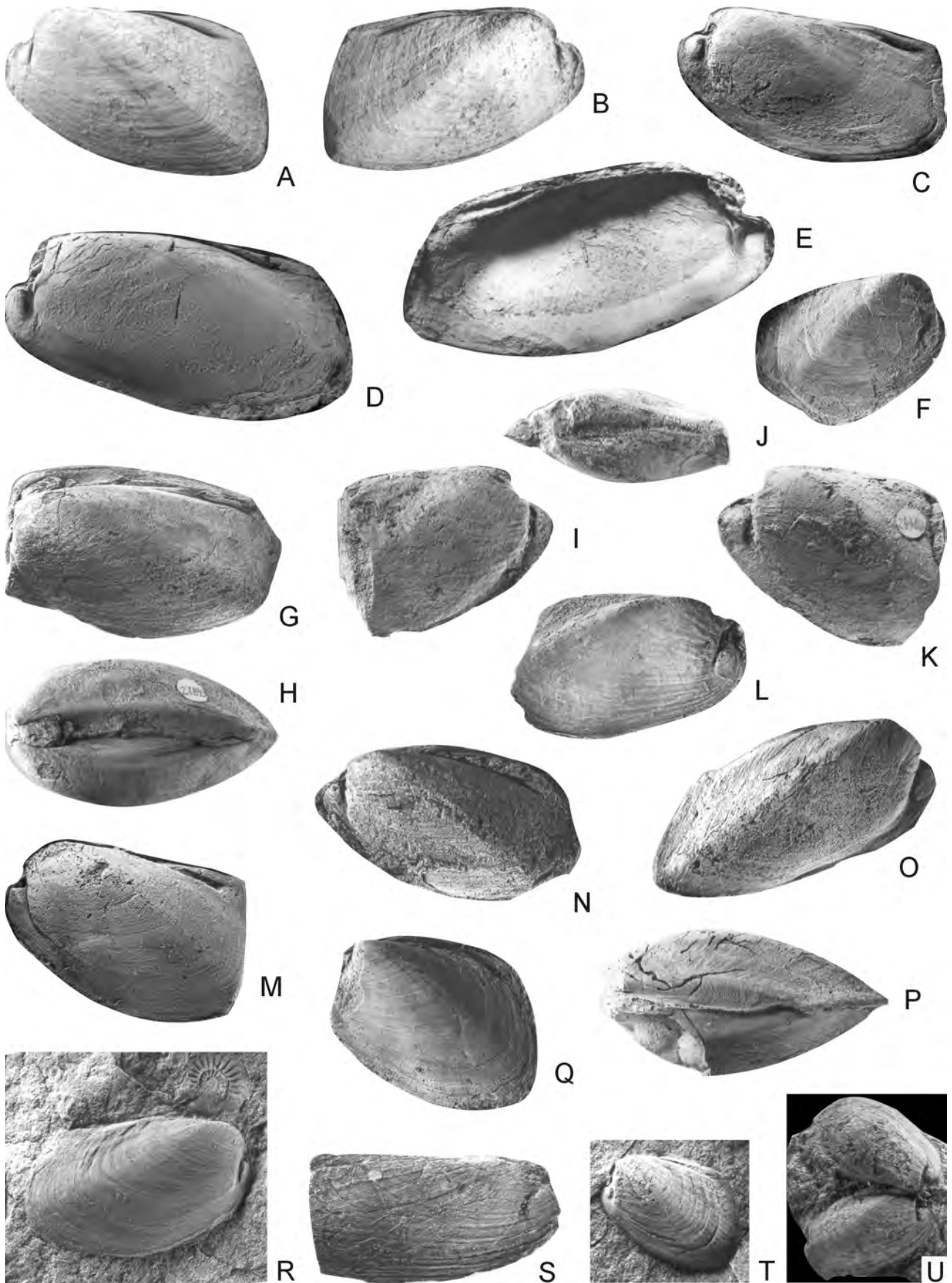
Based on the analysis of late Palaeozoic forms, Morris *et al.* (1991) regarded that the "Permophoridae" should be placed within the Pholadomyoidea of the Subclass Anomalodesmata. They proposed that the similarities in dentition between Carditidae and Permophoridae are the result of convergence, but they did not discuss their similarities with the modiomorphids. According to Carter (1990), modiomorphids appear to be closely related to pholadomyids in shell features and details of shell structure, to the point that common ancestry seems likely. Fang and Morris (1997) regarded the family names Kalenteridae and Permophoridae as junior subjective synonyms of Modiomorphidae (from which they excluded the modiolopsids and the modiolodontids, the latter as a new family within the Mytiloidea), and assigned this family to the Anomalodesmata, as already suggested by Waller (1990), Morris *et al.* (1991) and Johnston (1993).

Concerning shell structure, the Carditoidea have, according to Taylor (1973) a complex crossed-lamellar inner layer, while other morphologically similar groups, such as the Palaeozoic Modiomorphoidea, have a nacreous inner layer (see Carter and Tevesz, 1978; Carter, 1990). Morris (1978; also Morris *et al.*, 1991) indicates that some Mesozoic members of the Modiomorphidae have an homogeneous shell structure with an internal nacreous layer, which is common in several Anomalodesmata. Although no actual shell is preserved in the *Kalentera* specimens described herein, one internal mould shows traces of what appears to be the relicts of a nacreous microstructure, more evident on the region adjacent to the pallial line (figure 4.B).

Fang and Morris (1997) general arrangement is followed here, though maintaining kalenterids as separate from modiomorphids at family level. Thus, three families are recognized here within Modiomorphoidea: Modiomorphidae Miller, 1877 (Ordovician to Permian), Kalenteridae Marwick, 1953 (early Carboniferous to early Jurassic) and Myoconchidae Newell, 1957 (Devonian to late Cretaceous). The Modiomorphidae are restricted to a few Palaeozoic genera, which lack lateral teeth. Good descriptions and illustrations of the type and other species of the genus *Modiomorpha* are in Bailey (1983), Pojeta *et al.* (1986), and Bradshaw (1999). The Myoconchidae are understood as diagnosed in Cox *et al.* (1969), with the addition of *Modiophorus* Fang and Morris (1997). In South American Jurassic faunas this family is represented by several large, thick-shelled species of the genus *Myoconcha*, well-known since the end of the last century (Bayle and Coquand, 1851; Jaworski, 1915; Weaver, 1931; Leanza, 1940; among others).

The Kalenteridae as here understood are basically as diagnosed in Cox *et al.* (1969) under Permophorinae, with the same scope and the addition of *Bowlandia* Morris *et al.* (1991) and tentatively also *Soma-reoides* Skwarko (1983), but probably not *Ouamouia* Campbell (1984, see discussion below).

Figure 3. *Kalentera riccardii* n. sp. from Argentina. All specimens X 1. **A-B.** MLP 24294, holotype, left valve composite mould, lateral view (A) and latex cast (B) / *holotipo, molde compuesto de valva izquierda en vistas lateral (A) y molde de goma (B)*. **C.** MLP 24304, left valve internal mould / *molde interno de valva izquierda*. **D-E.** MLP 24308, left valve internal mould, lateral view (D) and latex cast (E) / *molde interno de valva izquierda en vistas lateral (D) y molde de goma (E)*. **F.** MLP 27829, right valve composite mould / *molde compuesto de valva derecha*. **G-H.** MLP 27843, steinkern, left valve (G) and dorsal (H) views / *steinkern, vistas de valva izquierda (G) y dorsal (H)*. **I-K.** MLP 24302, steinkern, right valve (I), dorsal (J) and left valve (K) views / *steinkern, vistas de valva derecha (I), dorsal (J) y valva izquierda (K)*. **L.** MLP 24298, right valve incomplete composite mould / *molde compuesto incompleto de valva derecha*. **M.** MLP 13500, composite mould of left valve / *molde compuesto de valva izquierda*. **N.** MLP 27837, steinkern, lateral view of left valve / *steinkern, vista lateral de valva izquierda*. **O-P.** MLP 13497, steinkern, right valve (O) and dorsal (P) views / *steinkern, vistas de valva derecha (O) y dorsal (P)*. **Q.** MLP 24300, left valve incomplete composite mould / *molde compuesto incompleto de valva izquierda*. **R.** MLP 24306, right valve composite mould / *molde compuesto de valva derecha*. **S.** MLP 13362, right valve composite mould / *molde compuesto de valva derecha*. **T.** MLP 13496, left valve composite mould / *molde compuesto de valva izquierda*. **U.** MLP 27832-b, internal mould of both valves / *molde interno de ambas valvas preservadas abiertas*. All specimens from Arroyo Las Chilcas (Mendoza) except M, O-P= La Horqueta (Mendoza), S= Codo del Arroyo Blanco (Mendoza), and T= Arroyo Lapa (Neuquén). Todos los ejemplares de arroyo Las Chilcas (Mendoza), excepto M, O-P= La Horqueta (Mendoza), S= Codo del Arroyo Blanco (Mendoza), y T= Arroyo Lapa (Neuquén)



A few nomenclatorial comments on the family name must be added. Since *Pleurophoridae* Dall, 1895 was invalidated by homonymy of its type genus

(as already pointed out by Marwick, 1953: 69; Logan, 1964; and Nevesskaya *et al.*, 1971), it must be replaced by the oldest available name from among its syn-

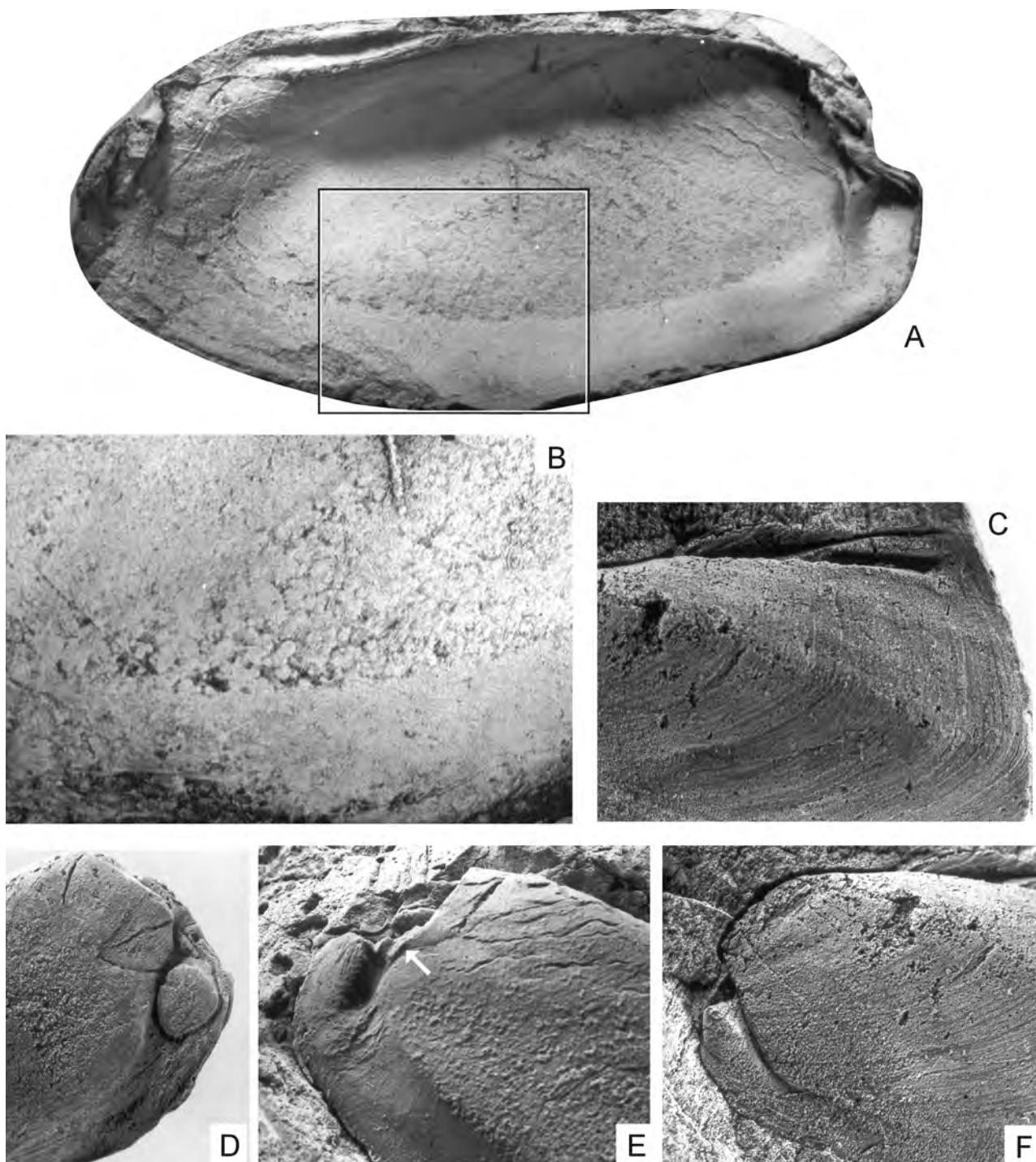


Figure 4. *Kalentera riccardii* n. sp. from Argentina. **A-B, E.** MLP 24308: **A.** Latex cast of complete internal mould / molde de goma de un molde interno completo, X 2; **B.** Detail of pallial line region / detalle de la región de la línea paleal, X 3; **E.** Detail of anterior region of natural internal mould showing deep anterior adductor muscle scar, oblique buttress and probable pedal retractor pit (white arrow) / detalle de la región anterior del molde interno natural mostrando la profunda impresión del músculo aductor anterior, el soporte oblicuo y la impresión del retractor pedal (flecha blanca), X 2. **C, F.** MLP 13500, composite mould / molde compuesto, **C.** Posterior region showing strong posterior lateral tooth and faint radial ribs / región posterior mostrando el fuerte diente lateral posterior y suaves costillas radiales, X 2; **F.** Anterior region showing anterior adductor muscle scar and oblique buttress / región anterior mostrando la impresión del músculo aductor anterior y el soporte oblicuo, X 2. **D.** MLP 13497, anterior region of internal mould with strong buttress and anterior adductor muscle scar / región anterior de un molde interno con soporte fuerte e impresión del músculo aductor anterior, X 2.

onyms (ICZN, 1999, Art. 39). Following the arrangement of genera proposed by Chavan (in Cox *et al.*, 1969), these names are Kalenteridae Marwick, 1953, and Permophoridae van de Poel, 1959. Thus the correct valid family-group name to be used is Kalenteridae Marwick, 1953 and not Permophoridae as used by van de Poel (1959: 11) and Chavan (in Cox *et al.*, 1969: 543), despite the fact that *Pleurophorus* King, 1844 (*non* Mulsant, 1842, *fide* Neave, 1940, Coleoptera) was objectively replaced by *Permophorus* Chavan, 1954. This last author (in Cox *et al.*, 1969) wrongly referred to Art. 40 of ICZN (1961 Code) in an attempt to justify the adoption of Permophoridae and its date-authorship citation. This article deals exclusively with synonymy of the type genus, which is a completely different situation. Hence, even under that version of the Code, he ought to have applied Art. 39 instead, and strictly follow the principle of priority ICZN (1961). Unfortunately, this erroneous use became rather widespread in post-Treatise literature, except perhaps for few authors who maintained the correct name (Grant-Mackie, 1960). Carter (1990) regarded Kalenteridae and Permophoridae as separate families but he correctly referred to the superfamily as Kalenteroidea (see also Ivimey-Cook *et al.*, 1999; Hodges, 2000). On the other hand, Fang and Morris (1997) state that this nomenclatorial decision "is not the right one", without further comments.

Genus *Kalentera* Marwick, 1953

Type species. *Kalentera mackayi* Marwick, 1953, from the Aratauran (Hettangian-Sinemurian) of New Zealand, original designation.

The more closely related genera are *Triaphorus* Marwick, *Pleurophorella* Girty, *Curionia* Rossi-Ronchetti and Allasinaz, *Permophorus* Chavan and *Bowlandia* Morris, Dickins and Astafieva-Urbaitis. It is interesting to note that none of the revisions of the late Palaeozoic genera has discussed in detail the Mesozoic representatives of the same family, and a first comparison suggests that relationships are closer than previously thought, perhaps to the point of needing re-definition of the scope of some genera and their stratigraphical distribution.

Permophorus is very similar to *Kalentera* in shell shape, ornamentation and even details of hinge and muscular patterns (see Cox *et al.*, 1969, fig. E44.1; Morris *et al.*, 1991, fig. 35; and species comparisons here), but *Kalentera* has a more modioliform shape due to a shorter anterior region. *Pleurophorella* differs from *Kalentera* by having lunule and being "more or less edentulous" (Morris *et al.*, 1991). *Bowlandia* is similar to *Kalentera* in shell shape but has a stronger umbonal carina; details of dentition are not adequately known to compare it (Morris *et al.*, 1991, figs. 43-44). Marwick (1953) already compared *Kalentera*

and *Triaphorus*, which differ in hinge details and general shell shape.

Somareoides Skwarko (1983), a late Triassic genus from Papua New Guinea, has a more elongated shell with longer anterior region and lacks the myophoric buttress. *Curionia* Rossi-Ronchetti and Allasinaz (1965), a widely distributed Triassic genus, has a well-developed lunule.

The monotypic genus *Ouamouia* Campbell (1984), originally referred to this subfamily, is quite different from *Kalentera*. The former has a very large and thick shell with a deep lunule and a massive hinge-plate, and a posteriorly notched pallial line. All these characters and also details of the dentition resemble those of cardinid bivalves.

Kalentera riccardii n. sp.

Figures 3.A-U, 4.A-F

1991 *Kalentera* sp. Damborenea; in Riccardi *et al.*, p. 166.

? 1991 *Kalentera* sp. Covacevich *et al.*, p. 69, fig. 3.

1992 *Kalentera* n. sp. Damborenea; in Damborenea and Manceñido, p. 133-134, pl. 1, fig. 4a.

1992 *Kalentera* n. sp. Damborenea; in Damborenea *et al.*, p. 304.

1992 *Kalentera* n. sp. Damborenea, pl. 115, figs. 7, 8.

2002 *Kalentera* nov. sp. Damborenea, fig. 2.E.

Derivation of name. Dedicated to Dr. A.C. Riccardi.

Material. *Holotype*: a composite mould of a left valve: MLP 24294 (figures 3.A-B). *Paratypes*: 13 steinkerns, 17 left valves and 12 right valves, preserved as internal or composite moulds: MLP 13362, 13496 to 13502, 24293, 24295 to 24308, 27828, 27829, 27832, 27834, 27837, 27838, 27843 (many from author's collection, and some specimens collected by S. Lanés). Most specimens from uppermost Sinemurian-lower Pliensbachian beds (*Miltoceras* and *Dubariceras* Zones), at Arroyo Las Chilcas, Mendoza, some from La Horqueta, one deformed steinkern from Codo del Arroyo Blanco, and one left valve from Arroyo Lapa, Neuquén.

Diagnosis. Sub-trapezoidal equivalve shells, with almost straight posterior margin and conspicuous umbonal carina. Prosogyrous umbones placed near anterior end. Escutcheon long and deep. Growth-lines grouped in shallow folds and 8 to 11 faint radial ribs on the posterior region. Anterior adductor scar deeply impressed, posteriorly limited by strong buttress, well-impressed pallial line; posterior adductor muscle scars not evident. Small pedal retractor pit just below umbones. Left valve with two posterior cardinal teeth, a narrow and long dorsal one and short ventral one, separated by a triangular socket. Strong posterior lateral tooth on the left valve. Short external opisthodontic parivincular ligament.

Description. Medium-sized, thick equivalve shells, shell outline very variable, though mostly subtrapezoidal to oblong, anteriorly narrow with greatest shell height posteriorly placed. There is an evident

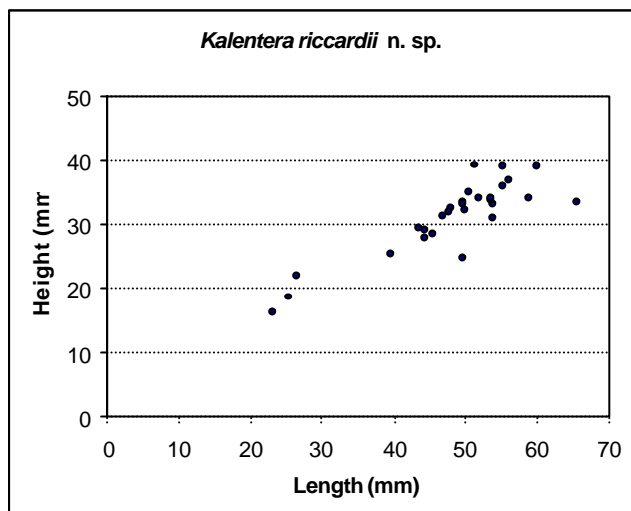


Figure 5. Scatter diagram of length vs. height of *Kalentera riccardii* n. sp. (n=29) / Diagrama bivariado largo/alto de *Kalentera riccardii* n. sp.

change in shell shape and proportions with size due to anisometric growth (figure 5): small shells are relatively shorter and more trapezoidal (figure 3.T) than large ones (figure 3.D), which are oblong and relatively longer. Umbones broad and low, prosogyrous, placed at about 1/8 of total shell length from anterior end. Dorsal margin long and only very slightly arched, meeting posterior margin at an obtuse angle (about 110°). Posterior margin nearly straight in some specimens to rounded, ventral margin evenly convex, forming a rounded postero-ventral corner. Anterior margin short and rounded. A distinct umbonal carina extends from the umbo to the postero-ventral corner of the shell (figures 3.A, L-O). Area anterior to the carina gently convex, posterior area flat. Escutcheon long and narrow, limited by sharp ridges (figures 3.H, P). Inflation of shell moderate to strong, dorsally placed.

The shell has a variable number (8 to 11) of faint radial ribs. These ribs are narrow, separated by wide interspaces, and are mostly restricted to the area posterior to the carina, only two or three ribs are found anterior to the carina and near it. The whole shell surface is also covered by commarginal growth-lines which have a tendency to form series separated by groups of closely-packed lines, which may even correspond to slight commarginal depressions.

The inner shell surface is smooth, with a conspicuous and entire pallial line (figures 3.E, 4.A). The anterior adductor muscle scar is deeply impressed and situated anteriorly to the beak. In internal moulds this scar has a conical shape (figures 4.D-F). A strong oblique buttress extends from below the umbo and posteriorly limits the anterior muscle scar. This buttress forms with the dorsal

margin of the shell an angle of about 90°. Just below the umbo and postero-dorsal to the buttress there is a deep small depression interpreted by Marwick as a pedal retractor pit (figure 4.E). The posterior adductor does not leave any impression on the inner shell surface.

The hinge plate is narrow and curved with cardinal and posterior lateral teeth (figures 2, 3.E, 4.A). The left valve has two cardinal teeth, both posterior to the umbones, a posterior one which is long, narrow and parallel to the dorsal margin, and an anterior one short and stout, oblique to the hinge-line. The teeth are separated by a triangular socket which bears a low crest. The right valve hinge is not adequately preserved in any specimen, but, according to the left valve morphology and one incomplete specimen, it had one subtriangular and probably slightly bifid (at least grooved) cardinal tooth. The left valve also bears a strong posterior lateral tooth, which is straight and long but widely separated from the cardinals. Apparently, no posterior lateral teeth are present in the right valve, though a marginal thickening probably occurs, since the posterior lateral of the left valve is separated from the dorsal margin by a deep furrow. The ligament was opisthodontic parivincular and probably external, its length apparently not reaching half of the posterior hinge length, as shown in specimens preserved with the valves flatly open (figure 3.U).

The inner shell surface just dorsal to the pallial line shows a hexagonal dissolution pattern which can be interpreted as a relict trace of a simple nacreous aragonitic structure for the inner shell layer (figure 4.B).

Measurements. See table 2 for measurements in mm of figured specimens. See also scatter diagram on figure 5.

Table 2. Measurements in mm of complete figured specimens of *Kalentera riccardii* n. sp. (abbreviations in Introduction) / Medidas en mm de los ejemplares completos figurados de *Kalentera riccardii* n. sp. (abreviaturas en Introducción).

SPECIMEN	Material		L	H	W	Lhp
MLP 13496	LV	CM	26.5	21.8	4.5	19.3
MLP 13497	BV	CM	53.9	31.0	13.6	36.0
MLP 13500	LV	CM	50.0	32.2	6.5	35.3
MLP 24294	LV	CM	44.6	29.1	7.0	32.0
MLP 24298	BV	CM	44.6	27.7	6.5	33.4
MLP 24304	LV	IM	49.7	24.8	5.5	38.8
MLP 24306	RV	CM	39.6	25.5	5.2	29.5
MLP 24308	BV	IM	65.6	33.4	9.5	47.5
MLP 27832-b	BV	IM	25.4	18.5	3.9	17.3
MLP 27837	BV	IM	49.7	33.4	11.5	33.6
MLP 27843	BV	IM	50.6	35.2	13.4	42.5

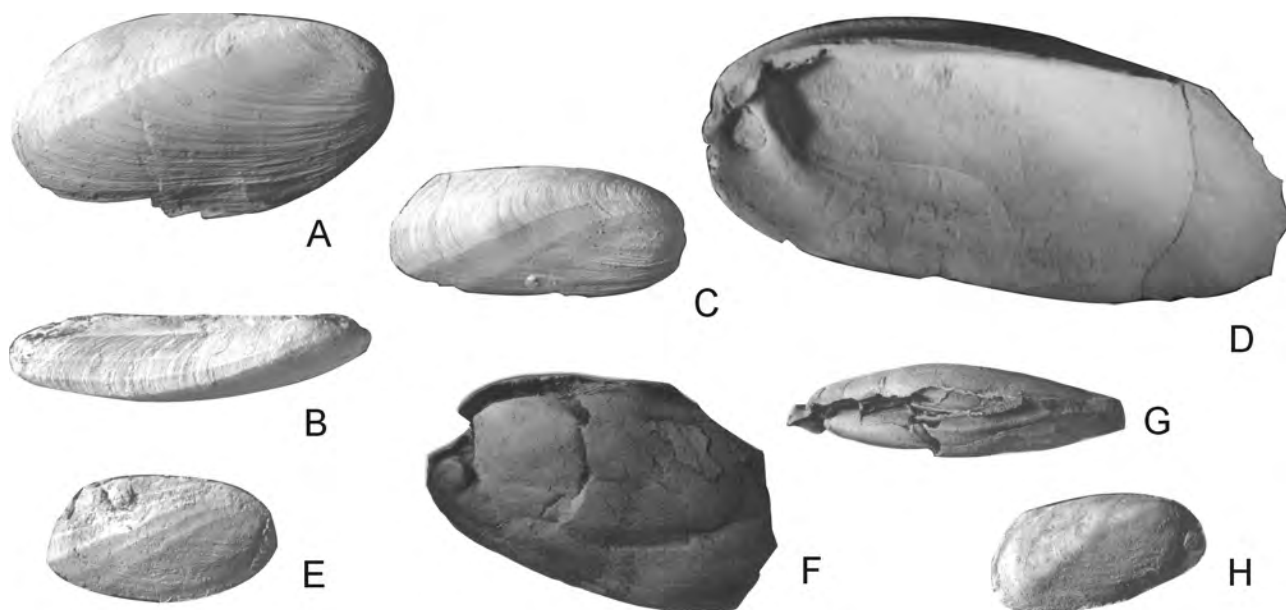


Figure 6. Some *Kalentera* and *Triaphorus* species from New Zealand. All specimens X 1 except D: X 2. / *Algunas especies de Kalentera y Triaphorus de Nueva Zelanda*. Todos los ejemplares X 1 excepto D: X 2. **A-D.** *Triaphorus zealandicus* (Trechmann), **A-B.** OU 14352, topotype (F45/f8897, J. Grant-Mackie collection), right valve in lateral and dorsal views / *topotipo, valva derecha en vistas lateral y dorsal*. **C-D.** OU-CP 136, Otamita stream (S169/f816, J.D. Campbell collection), right valve / *valva derecha*, **C.** external view / *vista externa*; **D.** internal view / *vista interna*. **E.** *Kalentera marwicki* Grant-Mackie, OU 14465, Kiritehere beach, D. MacFarlan collection, right valve / *valva derecha*. **F-H.** *Kalentera mackayi* Marwick, **F-G.** MLP 24873, north face of Ben Bolt, Hokonui Hills (S169/f676), steinkern in left lateral and dorsal views / *steinkern en vistas lateral izquierda y dorsal*. **H.** OU-CP 1382, internal mould of right valve / *molde interno de valva derecha*.

Affinities. The small left valve composite mould from the Pan de Azúcar Formation, Sinemurian of northern Chile, figured by Covacevich *et al.* (1991) as *Kalentera* sp. can belong either to *Kalentera riccardii* n. sp. or to *K. flemingi* Marwick (1953, pl. 11, figs. 14, 16). It differs from the Argentine specimens by the fewer (5-6) radial costae, but this character may be related to the small size of the Chilean specimen.

The most closely related species to *K. riccardii* n. sp. is *K. flemingi* Marwick (1953, pl. 11, figs. 14, 16; Speden and Keyes, 1981, pl. 17, figs. 5, 8), from the upper Ururoan (Toarcian ?) of New Zealand. The general shape and external ornamentation pattern are similar, though the Andean species has more radial ribs. The internal morphology of *K. flemingi* is unknown.

The type species, *K. mackayi* Marwick (1953, pl. 13, figs. 5, 8, 9, 12; Cox *et al.*, 1969, fig. E46/4a-b; Speden and Keyes, 1981, pl. 17, figs. 4, 7, 9-11; figure 6.F-H here), from the Aratauran (early Lower Jurassic) of New Zealand has a much more oblong shape with rounded posterior margins and less defined umbonal carina, but is comparable to *K. riccardii* on hinge details. *Kalentera marwicki* Grant-Mackie (1960, figs. 3-6; Speden and Keyes, 1981, pl. 11, fig. 16; figure 6.E here) from the Otapirian (Upper Triassic) of New Zealand and New Caledonia, has a sub-oval outline and fewer and stronger radial ribs. It also differs

from *K. riccardii* by details of hinge morphology.

Kalentera? lawsi Taylor and Guex (2002, pl. 1, figs. 5-7, 12, 13), from the Triassic-Jurassic boundary beds of Nevada, has a small lunule and the radial ribs restricted to the umbonal region. *Kalentera brodnayaensis* Milova (1988, pl. 12, fig. 19, pl. 13, figs. 8, 9), from the Late Pliensbachian of NW Siberia, has a more oval adult shell shape, with short anterior and posterior regions.

Kalentera riccardii n. sp. has also affinities with some Triassic species referred to *Triaphorus*, though most of them have a more oblique anterior buttress, which forms an acute angle with the dorsal margin. *Triaphorus trapezoidalis* (Kobayashi and Ichikawa, 1950, pl. 1, figs. 11-13), from the Carnian of Japan, has a more ovoid shape, less defined umbonal carina, and apparently lacks radial ribs. *Triaphorus multiformis* Kiparisova (in Kiparisova *et al.*, 1966, tabl. 31, figs. 5-6), from the upper Triassic of northern Russia, is also ovoid and lacks a defined carina, but has faint radial riblets like *K. riccardii*. On the other hand the type species of *Triaphorus*, *T. zealandicus* (Trechmann, 1918, pl. 21, fig. 6; Wilckens, 1927, pl. 1, fig. 8; Marwick, 1953, pl. 3, figs. 8-9; Speden and Keyes, 1981, pl. 12, figs. 28-29; figure 6.A-D here) has, apart from these differences in shape, a more anterior umbo with a reduced anterior region, different hinge details and a more oblique myophoric buttress.

Hinge details are strikingly similar to those of some *Permophorus* species, such as *P. cf. albequius* (Beede) as illustrated by Cox *et al.* (1969, fig. E44.1) and Morris *et al.* (1991, fig. 35), they only differ by a greater angle of the cardinal teeth with the dorsal line in *K. riccardii*, and a more oblique myophoric buttress in *Permophorus*.

Taphonomy and autecology

Kalentera riccardii n. sp. is found in very fine-grained sandstones and siltstones of southern Mendoza and central Neuquén. There are almost equal numbers of whole steinkerns and of complete isolated valves preserved as internal or composite moulds. Most specimens appear with both valves closed, but occasionally the "butterfly" preservation occurs (figure 3.U). Although at Arroyo Las Chilcas they occur along a thickness of about 60 m spanning two ammonite Zones, they are not abundant at any level. They are associated to *Grammatodon costulatus* (Leanza), *Otapiria neuquensis* Damborenea, *Palaeonucula* n. sp., other bivalves (pectinids and limids), brachiopods (*Spiriferina*) and ammonoids (figure 3.R), in a low-diversity soft-bottom community. Grant-Mackie (1960) pointed out that "none of the members of the family occurs plentifully at any one locality", and this is true as well for the Argentine occurrences. Neither borings of endolithic biota nor encrusting organisms were observed, but a few steinkerns show nucleocavities traces (figures 3.O-P).

According to Lanés (in press), the sediments were deposited in an offshore-shoreface transition palaeo-environment. This occurrence agrees to every detail to the known conditions in which other species of this genus are known to occur in New Zealand (Grant-Mackie 1960), Chile (Covacevich *et al.*, 1991) and Nevada (Laws, 1982; Taylor *et al.*, 2000). Grant-Mackie (1960) adequately summarized characteristics of the likely environment as a "relatively flat area of the sublittoral zone of the continental shelf with fairly uniform bottom conditions". On the other hand Laws (1982) stated that the *Curionia* association developed in a near-shore high-stress environment. Type and stability of substrate seem to have been definite factors controlling distribution of these species. Despite its stratigraphical range, in southern Mendoza *K. riccardii* is restricted to only three localities, and it is not known from nearby areas where sediments of equivalent age are either coarser-grained or deposited by storms and/or turbiditic flows, such as those from arroyo del Portezuelo Ancho, which contain large *Myoconcha neuquena* Leanza instead.

Shell morphology suggests a semi-infaunal (shallow burrower) mode of life for *Kalentera* species

(Grant-Mackie, 1960; Campbell, 1984), similar to postulated life habits of modiomorphids (Stanley, 1972; Bradshaw, 1999). As occurs in New Zealand, the associated fauna is dominated by shallow burrowers and epifaunal bivalves.

Palaeobiogeography

Since Marwick (1953) named this peculiar bivalve genus, it was regarded as a Maorian endemic taxon (Grant-Mackie, 1960; Hallam, 1977; Stevens and Speden, 1978: 311; Campbell *et al.*, 1985). Although Grant-Mackie (1960) expected it to occur at least in other parts of the Papuan Geosyncline, it was only known from New Zealand-New Caledonia, where it is restricted to Uppermost Triassic - Lowest Jurassic deposits. The genus was traditionally regarded as endemic to the Maorian Province during late Triassic and early Jurassic times (Grant-Mackie, 1960; Grant-Mackie *et al.*, 2000).

Nevertheless, other forms of this group were later found elsewhere, notably around the northern circum-Pacific margins (figure 7). These occurrences in no way weaken the concept of a Maorian Province, but rather help to adequately define this austral biogeochorema and its regional extension on a sound basis

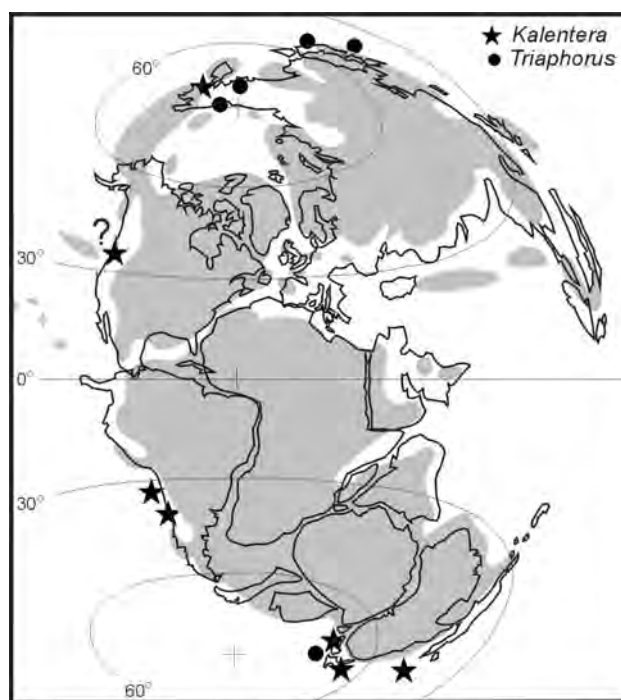


Figure 7. Palaeogeographic distribution of *Kalentera* and *Triaphorus*. Base map for Early Jurassic, continent palaeopositions based on Smith and Briden (1977) and Scotese (1991, 1997), palaeogeography compiled from various sources / Distribución paleobiogeográfica de *Kalentera* y *Triaphorus*. Mapa base para el Jurásico temprano, paleopositiones de los continentes basadas en Smith y Briden (1977) y Scotese (1991, 1997), paleobiogeografía compilada de varias fuentes.

(Grant-Mackie *et al.*, 2000; Damborenea, 2002). During Late Triassic times several species referred to the closely related genus *Triaphorus* Marwick lived in northeastern Russia (Kiparisova *et al.*, 1966) and Japan (Kobayashi and Ichikawa, 1950; Hayami, 1975). In fact some species which do not have all hinge details completely preserved are difficult to assign either to *Kalentera* or to *Triaphorus*. On the other hand, a couple of species from NW China doubtfully referred to *Triaphorus* (Zhang *et al.*, 1979), namely *T. ? qinghaiensis* Chen and Lu and *T. ? yushuensis* Chen and Lu, do not belong to this genus and should even be excluded from this family. It appears, though, that the genus is indeed present in China (J.D. Campbell, personal communication, 1990).

In western USA (Nevada) *Kalentera*? has been recognized as a by-product of a pre-congress field trip organized during the 5th International Symposium on the Jurassic System. Its presence in the Muller Canyon Member of the Gabbs Formation (Triassic-Jurassic boundary beds) had previously been recorded as *Curionia* sp. (Laws, 1982; Taylor, 1998), and was subsequently reported as *Kalentera*? sp. (Taylor *et al.*, 2000, 2001) and *Kalentera? lawsi* Taylor and Guex, 2002.

Occurrence of the genus *Kalentera* in late Pliensbachian beds from northeastern Siberia (Omolon massif) is documented with descriptions and illustrations provided by Milova (1988).

The genus was represented during the Early Jurassic by very few species which probably had rather strict palaeoenvironmental requirements, especially regarding substrate conditions (see Grant-Mackie, 1960 and previous discussion). These species are *K. mackayi* Marwick (1953) from the Aratauran (Hettangian - Sinemurian) of New Zealand; the species here described from latest Sinemurian-earliest Pliensbachian of western Argentina; *K. brodnayaensis* Milova (1988) from the late Pliensbachian of NE Siberia; and the poorly known *K. flemingi* Marwick (1953) from the upper Ururoan (Toarcian) of New Zealand. This genus is not known in younger deposits.

The discovery of a species clearly referable to *Kalentera* in Lower Jurassic sediments of western Argentina and Chile (Riccardi *et al.*, 1991; Covacevich *et al.*, 1991) is, thus, of great interest from the palaeobiogeographic point of view. *Kalentera* was endemic to the Maorian Province in Late Triassic times but became bipolar around the Triassic-Jurassic boundary (Damborenea, 2002). *Kalentera riccardii* n. sp. extends the palaeolatitudinal range of the genus in the southern hemisphere to around 35° (see figure 6). No species is known below 30° in either hemisphere.

Kalentera is one of the characteristic elements of the maorian-austral biochorema of the South Pacific Realm as recognized on the basis of bivalve distribution during the Early Jurassic (Damborenea, 1996,

2002, 2003). This biogeographic unit developed in high latitude regions and extended to central Argentina and Chile during early Pliensbachian times, as indicated by the presence in the Neuquén basin of several high latitude bivalve genera, such as *Kalentera*, *Otapiria*, *Kolymonectes*, *Agerchlamys* and *Harpax*.

Conclusions

The genus *Kalentera* is represented in Argentina by a new species, *K. riccardii*, found in southern Mendoza and Neuquén provinces, Neuquén basin. The species probably had a semi-infaunal life habit restricted to fine-grained sandy and muddy bottoms.

Kalentera belongs to a bivalve group which was diversified during late Palaeozoic times and survived the Permo-Triassic extinction. During the Late Triassic *Kalentera* had a high-latitude austral distribution, restricted to New Zealand and characteristic of the Maorian Province, while the closely related genus *Triaphorus* was clearly bipolar. From the Triassic/Jurassic boundary onwards, the distribution of *Kalentera* becomes bipolar, present only at palaeolatitudes higher than 30°, being apparently absent from Tethys. *Kalentera* is regarded as a conspicuous member of the austral biogeographic unit which included New Zealand/New Caledonia and extended towards the north to central Argentina and Chile during early Pliensbachian times.

The stratigraphical distribution of *Kalentera riccardii* n. sp. spans the *Otapiria neuquensis* Association Zone in western Argentina (*Miltoceras* to lower *Fanninoceras* Zones), i.e. topmost Sinemurian and early Pliensbachian.

Acknowledgements

M. Manceñido and A. Riccardi greatly assisted in all stages of research, from the logging of the sections and collection of material to fruitful discussions on the conclusions. S. Lanés collected part of the material described herein and provided stratigraphical data of the Codo del Arroyo Blanco and La Horqueta sections. A visit to New Zealand in early 1990, financed by the Royal Society of New Zealand and the La Plata Museum Foundation, allowed the direct comparison with type material housed in Otago University Museum, New Zealand Geological Survey and University of Auckland Museum. I am grateful to J.A. Grant-Mackie (Auckland) and the late J.D. Campbell (Dunedin) for the opportunity to visit the type localities of New Zealand species and extensively discuss about the relationships of the material from Argentina. I also thank C. McRoberts and J. Grant-Mackie who reviewed the manuscript and provided useful comments. Field work was partly financed with PID CONICET 3340900-92/93.

References

- Bailey, J.B. 1983. Middle Devonian Bivalvia from the Solsville Member (Marcellus Formation), Central New York State. *Bulletin, American Museum of Natural History* 174: 193-326.

- Bayle, E. and Coquand, H. 1851. Mémoire sur les Fossiles recueillis dans le Chili par M. Ignace Domeyko et sur les terrains auxquels ils appartiennent. *Mémoire de la Société Géologique de France* ser. 2, 4: 1-47.
- Bradshaw, M.A. 1999. Lower Devonian bivalves from the Reefton Group, New Zealand. *Memoir of the Association of Australasian Palaeontologists* 20: 1-171.
- Campbell, H.J. 1984. New records and taxa of Permian and Triassic fossils from New Caledonia and New Zealand. *Alcheringa* 8: 151-167.
- Campbell, H.J., Grant-Mackie, J.A. and Paris, J.P. 1985. Geology of the Moindou-Téremba area, New Caledonia. Stratigraphy and structure of Téremba Group (Permian-Lower Jurassic) and Baie de St. Vincent Group (Upper Triassic-Lower Jurassic). *Géologie de la France* 1: 19-36.
- Carter, J.G. 1990. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorpha and Isofilibranchia (Bivalvia: Mollusca). In: J.G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends*. Volume 1. Van Nostrand Reinhold, New York, pp. 135-296.
- Carter, J.G. and Tevesz, M.J.S. 1978. Shell microstructure of a Middle Devonian (Hamilton Group) bivalve fauna from central New York. *Journal of Paleontology* 52: 859-880.
- Carter, J.G., Campbell, D.C. and Campbell, M.R. 2000. Cladistic perspectives on early bivalve evolution. In: E.M. Harper, J.D. Taylor and J.A. Crame (eds.), *The Evolutionary Biology of the Bivalvia*. The Geological Society, London, Special Publication 177, pp. 47-79.
- Chavan, A. 1954. Les *Pleurophorus* et genres voisins. *Cahiers Géologiques de Thoiry* 22: 200.
- Cope, J.C.W. 1995. The early evolution of the Bivalvia. In: J.D. Taylor (ed.), *Origin and Evolutionary Radiation of the Mollusca*. Centenary Symposium of the Malacological Society of London. Oxford University Press, Oxford, pp. 361-370.
- Cope, J.C.W. 2000. A new look at early bivalve phylogeny. In: E.M. Harper, J.D. Taylor and J.A. Crame (eds.), *The Evolutionary Biology of the Bivalvia*. The Geological Society, London, Special Publication 177, pp. 81-95.
- Covacevich, V., Pérez, E. and Escobar, F. 1991. Presencia del género *Kalentera* Marwick, 1953 (Mollusca: Bivalvia) en el Sinemuriano al Sur de Taltal, Chile. *Sexto Congreso Geológico Chileno* (Viña del Mar), Actas 1: 68-71.
- Cox, L.R., Newell, N.D., Boyd, D.W., Branson, C.C., Casey, R., Chavan, A., Coogan, A.H., Dechaseaux, C., Fleming, C.A., Haas, F., Hertlein, L.G., Fauflnab, E.G., Keen, A.M., Larocque, A., McAlester, A.L., Moore, R.C., Nuttall, C.P., Perkins, B.F., Puri, H.S., Smith, L.A., Soot-Ryen, T., Stenzel, H.B., Trueman, E.R., Turner, R.D. and Weir, J. 1969. Mollusca 6. Bivalvia. In: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology. Part N-1*. University of Kansas Press and Geological Society of America. Kansas, 489 pp.
- Dall, W.H. 1895. Report on Mollusca and Brachiopoda dredged in deep waters, chiefly near the Hawaiian Islands with illustrations of hitherto unfigured species from North West America. *Proceedings of the United States National Museum* 17: 675-753.
- Damborenea, S.E. 1987. Early Jurassic Bivalvia of Argentina. Part 1: Stratigraphical Introduction and Superfamilies Nuculanacea, Arcacea, Mytilacea and Pinnacea. *Palaeontographica A* 199: 23-111.
- Damborenea, S.E. 1992. South American Jurassic bivalves. In: Westermann, G.E.G. (Ed.): *The Jurassic of the Circum-Pacific*. Cambridge University Press, Cambridge, pp. 610-619.
- Damborenea, S.E. 1993. Early Jurassic South American pelecypods and circum-Pacific palaeobiogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 100: 109-123.
- Damborenea, S.E. 1994. Circum-Pacific correlation of Argentine Early and Middle Jurassic bivalve zones. 3rd International Symposium on Jurassic Stratigraphy (Poitiers, France, Sept. 22-29, 1991). *Geobios, Mémoire Spécial* 17: 141-147.
- Damborenea, S.E. 1996. Palaeobiogeography of Early Jurassic bivalves along the southeastern Pacific margin. 13º Congreso Geológico Argentino y 3º Congreso de Exploración de Hidrocarburos (Buenos Aires), Actas 5: 151-167.
- Damborenea, S.E. 2002. Jurassic evolution of Southern Hemisphere marine palaeobiogeographic units based on benthonic bivalves. *Geobios* 35, *Mémoire Spécial* 24: 51-71.
- Damborenea, S.E. 2003. Unidades paleobiogeográficas marinas jurásicas basadas sobre moluscos bivalvos: una visión desde el hemisferio sur. *Anales de la Academia Nacional de Ciencias Exactas, Físicas y Naturales* (Buenos Aires) 53: 141-160.
- Damborenea, S.E. and Manceñido, M.O. 1992. A comparison of Jurassic marine benthonic faunas from South America and New Zealand. *Journal of the Royal Society of New Zealand* 22: 131-152.
- Damborenea, S.E., Polubotko, I.V., Sey, I.I. and Paraketsov, K.V. 1992. Bivalve zones and assemblages of the circum-Pacific region. In: G.E.G. Westermann (ed.), *The Jurassic of the Circum-Pacific*. Cambridge University Press. Cambridge, pp. 300-307.
- Fang, Zong-jie and Morris, N.J. 1997. The genus *Pseudosanguinolites* and some modioliform bivalves (mainly Palaeozoic). *Palaeoworld* (Laboratory of Paleobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Academia Sinica) 7: 49-74.
- Grant-Mackie, J.A. 1960. On a new *Kalentera* (Pelecypoda: Cypricardiacea) from the Upper Triassic of New Zealand. *New Zealand Journal of Geology and Geophysics* 3: 74-80.
- Grant-Mackie, J.A., Aita, Y., Balme, B.E., Campbell, H.J., Challinor, A.B., MacFarlan, D.A.B., Molnar, R.E., Stevens, G.R. and Thulborn, R.A. 2000. Jurassic palaeobiogeography of Australasia. In: A.J. Wright, G.C. Young, J.A. Talent and J.R. Laurie (eds.), *Palaeobiogeography of Australasian faunas and floras*. *Memoir of the Association of Australasian Palaeontologists* 23: 311-353.
- Hallam, A. 1977. Jurassic bivalve biogeography. *Paleobiology* 3: 58-73.
- Hayami, I. 1975. A systematic survey of the Mesozoic Bivalvia from Japan. *Bulletin University Museum, University of Tokyo* 10: 1-249.
- Hodges, P. 2000. The Early Jurassic Bivalvia from the Hettangian and Lower Sinemurian of south-west Britain. *Monograph of the Palaeontographical Society* (London) 614: 1-64, i-vii, pl. 1-6.
- Ivimey-Cook, H. C., Hodges, P., Swift, A. and Radley, J. D. 1999. Bivalves. In: A. Swift and D. M. Martill (eds.), *Fossils of the Rhaetian Penarth Group*. Palaeontological Association (London) Field Guides to Fossils 9: 83-127.
- Jaworski, E. 1915. Beiträge zur Kenntnis des Jura in Süd-Amerika. Teil II. Spezieller, paläontologischer Teil. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie B.B.* 40: 364-456.
- Johnston, P.A. 1993. Lower Devonian Pelecypoda from southeastern Australia. *Memoirs of the Association of Australasian Palaeontologists* 14: 1-134.
- King, W. 1844. On a new genus of Palaeozoic shells. *Annals and Magazine of Natural History* 1: 313-317.
- Kiparisova, L.D., Bychkov, Yu.M. and Polubotko, I. 1966.

- Pozdnetriyasovye dvustvorchatye mollyuski Severo-Vostoka SSSR. *Sev.-Vost. Geol. Uprav. (VSEGEI)* Magadan, 312 pp. (In Russian).
- Kobayashi, T. and Ichikawa, K. 1950. On the Upper Triassic Kochigatani Series in the Sakawa Basin in Japan, and its Pelecypod-Faunas. 2. Late Triassic *Mytilus*, *Volsella*, *Pleurophorus* and *Myoconcha* from the Sakawa Basin in Shikoku, Japan. *Journal of the Faculty of Sciences, University of Tokyo*, sec. 2, *Geol., Mineralogy, Geography, Seismology* 7: 207-215.
- Lanés, S. 2002. [Paleoambientes y paleogeografía de la primera transgresión en Cuenca Neuquina, Sur de Mendoza]. Tesis Doctoral, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales. 403 pp. Unpublished].
- Lanés, S. in press. Late Triassic to Early Jurassic in northern Neuquén Basin, Argentina: Tectosedimentary evolution of the first trasgression. *Geologica Acta*.
- Laws, R.A. 1982. Late Triassic depositional environments and molluscan associations from west central Nevada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37: 131-148.
- Leanza, A.F. 1940. *Myoconcha neuquena* n. sp. del Lias de Piedra Pintada, en el Neuquén. *Notas del Museo de La Plata, Paleontología* 5: 123-131.
- Logan, A. 1964. The dentition of the Durham Permian pelecypod *Permophorus costatus* (Brown). *Palaeontology* 7: 281-285.
- Marwick, J. 1953. Divisions and Faunas of the Hokonui System (Triassic and Jurassic). *Palaeontological Bulletin, New Zealand Geological Survey* 21: 1-142.
- Milova, L.V. 1988. *Ranneyurskie dvustvorchatye Mollyuski Severo-Vostoka SSSR*. Akademiya Nauk SSSR. Dal'nevostochnoe Otdelenie, Severo-Vostochnyy Kompleksnyy Nauchno-Issledovatel'skiy Institut. Vladivosok, pp. 1-24. [In Russian]
- Morris, N.J. 1978. The infaunal descendants of the Cycloconchidae: an outline of the evolutionary history and taxonomy of the Heteroconchia, superfamilies Cycloconchacea to Chamacea. *Philosophical Transactions of the Royal Society of London*, B 284: 259-275.
- Morris, N.J., Dickins, J.M. and Astafieva-Urbaitis, K. 1991. Upper Palaeozoic Anomalodesmatan Bivalvia. *Bulletin of the British Museum (Natural History), Geology* 47: 51-100.
- Neave, S.A. 1940. *Nomenclator Zoologicus*. Volume III (M-P). The Zoological Society of London, London, 1065 pp.
- Nevesskaya, L.A., Scarlato, O.A., Starobogatov, Y.I. and Eberzin, A.G. 1971. New ideas on bivalve systematics. *Palaeontological Journal* 1971: 141-155.
- Newell, N.D. 1957. Notes on certain primitive heterodont pelecypods. *American Museum Novitates* 1857, 14 pp.
- Newell, N.D. and Boyd, D.W. 1999. A new Lower Triassic *Permophorus* from the central Rocky Mountains. *American Museum Novitates* 3263: 1-5.
- Pojeta, J. 1978. The origin and early taxonomic diversification of pelecypods. *Philosophical Transactions of the Royal Society of London* B 287: 363-379.
- Pojeta, J. 1987. Class Pelecypoda. In: R.S. Boardman, A.H. Cheetham and A.J. Rowell (eds.), *Fossil Invertebrates*. Blackwell Scientific Publications, Palo Alto, pp. 386-435.
- Pojeta, J., Zhang, R. and Yang, Z. 1986. Systematic paleontology of Devonian pelecypods of Guangxi and Michigan. In: J. Pojeta (ed.), *Devonian Rocks and Lower and Middle Devonian Pelecypods of Guangxi, China, and the Traverse Group of Michigan*. U.S. Geological Survey Professional Paper 1394 G: 57-108.
- Riccardi, A.C., Damborenea, S.E., Manceñido, M.O. and Ballent, S.C. 1988. Hettangiano y Sinemuriano marinos en Argentina. 5º Congreso Geológico Chileno (Santiago), *Actas* 2: C359-C373.
- Riccardi, A.C., Damborenea, S.E., Manceñido, M.O. and Ballent, S.C. 1991. Hettangian and Sinemurian (Lower Jurassic) biostratigraphy of Argentina. *Journal of South American Earth Sciences* 4: 159-170.
- Riccardi, A.C., Damborenea, S.E., Manceñido, M.O. and Ballent, S.C. 2000. El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. 3. Bioestratigrafía. In: R. Caminos (ed.), *Geología Argentina. Anales Servicio Geológico Minero Argentino* (Buenos Aires) 29 [for 1999]: 419-432.
- Rossi-Ronchetti, C.R. and Allasinaz, A. 1965. Il Trias in Lombardia (Studi geologici e paleontologici). XI. *Curionia*, nuovo genere di Lamellibranco Eterodonte triassico. *Rivista Italiana di Paleontologia* 71: 351-412.
- Rossi-Ronchetti, C.R. and Allasinaz, A. 1966. Il Trias in Lombardia (Studi geologici e paleontologici). XX. *Pseudomyoconcha*, nuovo genere triassico di Lamellibranchi Eterodonte. *Rivista Italiana di Paleontologia* 72: 1083-1132.
- Scotese, C.R. 1991. Jurassic and Cretaceous plate tectonic reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 87: 493-501.
- Scotese, C.R. 1997. *Paleogeographic Atlas*. PALEOMAP Progress Report 90-0497, Department of Geology, University of Texas at Arlington, Arlington, Texas, 37 pp.
- Skwarko, S.K. 1983. *Somareoides hastatus* (Skwarko), a new Late Triassic bivalve from Papua New Guinea. *Bulletin of the Bureau of Mineral Resources (Australia)* 217: 67-71.
- Smith, A.G. and Briden, J.C. 1977. *Mesozoic and Cenozoic paleocontinental maps*. Cambridge University Press, Cambridge, 63 pp.
- Speden, I.G. and Keyes, I.W. 1981. *Illustrations of New Zealand Fossils*. New Zealand Dep. Sci. and Indust. Res. DSIR Information Series 150, Wellington, 109 pp.
- Stevens, G.R. and Speden, I.G. 1978. New Zealand. In: M. Moullade and A. Nairn (eds.), *The Phanerozoic Geology of the World. II. The Mesozoic*, A. Elsevier, Amsterdam, pp. 251-328.
- Stanley, S.M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs - a consequence of mantle fusion and siphon formation. *Journal of Paleontology* 42: 241-229.
- Stanley, S.M. 1972. Functional morphology and evolution of byssally attached bivalve molluscs. *Journal of Paleontology* 46: 165-212.
- Taylor, D.G. 1998. Field trip A2: Nevada. In: P.L. Smith (ed.), *Field Guide for the Fifth International Symposium on the Jurassic System*, The Geological Survey of Canada, Vancouver, pp. 104-125.
- Taylor, D.G. and Guex, J. 2002. The Triassic/Jurassic System boundary in the John Day Inlier, east-central Oregon. *Oregon Geology* 64: 3-28.
- Taylor, D.G., Boelling, K. and Guex, J. 2000. The Triassic/Jurassic System in the Gabbs Formation, Nevada. In: R.L. Hall and P.L. Smith (eds.), *Advances in Jurassic Research 2000*. *GeoResearch Forum* 6: 225-236.
- Taylor, D.G., Guex, J. and Rakus, M. 2001. Hettangian and Sinemurian Ammonoid Zonation for the Western Cordillera of North America. *Bulletin de la Société Vaudoise des Sciences Naturelles* 87: 381-421. [also as *Bulletin des Laboratoires de Géologie, Minéralogie, Géophysique et de Musée Géologique de l'Université de Lausanne* 350].
- Taylor, J.D. 1973. The structural evolution of the bivalve shell. *Palaeontology* 16: 519-534.
- Trechmann, C.T. 1918. The Trias of New Zealand. *Quarterly Journal of the Geological Society (London)* 73: 165-246.
- van de Poel, L. 1959. Faune malacologique du Hervien.

- Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 35(15): 1-26; (16): 1-28.
- Waller, T.R. 1990. The evolution of ligamental systems in the Bivalvia. In: B. Morton (ed.), *The Bivalvia. Proceedings of a Symposium in Honour of Sir Charles Maurice Yonge*. Hong Kong University Press, Hong Kong, pp. 49-71.
- Weaver, C. 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina. *Memoir University of Washington* 1: 1-469.
- Wilckens, O. 1927. Contribution to the Palaeontology of the New Zealand Trias. *Palaeontological Bulletin, Geological Survey of New Zealand* 12: 1-65.
- Zhang, Z., LU, and Wen, S. 1979. Lamellibranchiata. In: *Palaeontological Atlas of Northwest China (Fascicle Qinghai)* (I). Nanjing Institute of Geology and Palaeontology and Qinghai Institute of Geosciences. Geology Publishing House, Beijing, pp. 218-314, 370-393, pl. 58-96. [In Chinese].
- Recibido:** 8 de mayo de 2003.
Aceptados: 16 de octubre de 2003.