Journal of Paleontology, 93(5), 2019, p. 925–944
Copyright © 2019, The Paleontological Society
0022-3360/19/1937-2337
doi: 10.1017/jpa.2019.12

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

Early Jurassic protobranch bivalves from Chubut, Argentina

Susana E. Damborenea[1,2] and María Alejandra Pagani[1,3]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (CONICET)
[2]Departamento Paleontología Invertebrados, Museo de Ciencias Naturales La Plata, 1900 La Plata, Argentina <sdambore@fcnym.unlp.edu.ar>
[3]Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut, Argentina <apagani@mef.org.ar>

Abstract.—Knowledge on Early Jurassic marine fossil invertebrates from Argentina is very uneven. Particularly, faunas from Chubut Province received less attention and were thought to be poorer than those from the Neuquén Basin. Nevertheless, an updated revision of bivalves shows that some groups, such as the Protobranchia, were relatively more diverse in Chubut than in Neuquén during late Pliensbachian–early Toarcian times. Only four species are known from the southern areas of the Neuquén Basin, while seven species (three of them new) are here described from Chubut, belonging to the families Nuculidae, Nuculanidae, Polidevciidae, and Malletiidae. The new species are: *Palaeonucula feruglioi* n. sp., *Ryderia tehuelchana* n. sp., and *Phaenodesmia*? *piatnitzkyi* n. sp. The material is well preserved and allows a detailed analysis of their hinge regions and other internal characters. The presence in Chubut of *Palaeoneilo*? *patagonidica* (Leanza) is confirmed, which, along with *Praesaccella ovum* (Sowerby), are the only two species in common with the Neuquén Basin. The new species *Ryderia tehuelchana*, belonging to a genus that had a wide global distribution between Rhaetian and Toarcian times, but which was known from South America only for upper Triassic deposits, is of special paleobiogeographic interest. These bivalves are restricted to normal marine environments, and due to their detritivorous feeding habits they only live in organic-rich bottoms as very active shallow burrowers.

UUID: http://zoobank.org/41225cf2-b7de-4ff0-ad20-ce0d738799a9

Introduction

Protobranch bivalves are common elements in fossil assemblages throughout the whole Phanerozoic, but despite their local abundance, they are usually difficult to identify on shell characters alone due to a combination of conservativeness of the shell form and homeomorphy between members of different families (Allen, 1978). There is consensus that the Nuculida are the most primitive living Bivalvia. On the other hand, the Nuculanida have specialized feeding mechanisms with a posterior inhalant current (Yonge, 1939), and highly modified ctenidia for pumping water, and "there is nothing remotely primitive about them" (Yonge, 1959, p. 211). Early Paleozoic radiation produced all protobranch superfamilies (Waller, 1990), but diversification within extant clades occurred after the end-Permian mass extinction during the early Mesozoic (Sharma et al., 2013). In this context, new knowledge about this critical period becomes of great interest to understand the phylogeny of the group.

This paper includes all Early Jurassic protobranch bivalve specimens available from Chubut. Although the Early Jurassic bivalve faunas from Chubut are very similar to those from the Neuquén Basin (only somewhat less diverse), protobranchs are more diverse than in Neuquén (Damborenea et al., 2013; Damborenea and Echevarría, 2015, see Table 1 here). Nevertheless, there were only few previous mentions to protobranch bivalves from Chubut (Levy, 1966; Franchi and Page, 1980, p. 217; Damborenea, 1987a, p. 54), the last one based on specimens collected by Piatnitzky and housed at the La Plata Museum. On the other hand, the specimens referred to by Franchi and Page (1980) and examined by Levy de Caminos (1978) could not be located in the collections of the National Geological Survey in Buenos Aires.

Extensive personal collections with accurate stratigraphic and geographical location were made with the purpose of updating the knowledge of Early Jurassic bivalve faunas from Chubut, which is of great potential interest from a paleobiological point of view because that was a time of phylogenetic diversification for most bivalve clades. This study is the first of a series of systematic analyses that attempt to review old identifications and describe newly collected material, with the purpose to obtain an updated picture of marine bivalve diversity in the Chubut Early Jurassic basin. Ammonites from the same or nearby levels provided the key to the stratigraphy according to the biostratigraphic zonation in use (Riccardi et al., 2000; Riccardi, 2008a, b).

Previous research

Early Jurassic marine deposits from Chubut Province have been known since the accounts made by Roth (1908) of a trip to the Tecka River region and by Keidel (1917) to Nueva Lubecka. This last region provided a particularly diverse invertebrate fauna, and its most conspicuous elements were described by Feruglio (1934) and later by Wahnish (1942). Furthermore, early geological surveys of central and western Chubut provided lists of fossils that clearly indicate a varied benthic fauna with bivalves, gastropods, corals, and brachiopods (Piatnitzky, 1936; Perrot, 1961; Levy, 1966; Franchi and Page, 1980;

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Table 1. Regional distribution of protobranch species recorded from Early Jurassic deposits in South America.

	Taxon	N Chile	N Neuquén Basin	S Neuquén basin	Chubut
Nuculoidea	*Palaeonucula cuevitana* Aberhan	L Hett			
	Palaeonucula feruglioi n. sp.				Pli-Toa
	Palaeonucula sp.				Pli/Toa
	Palaeonucula? sp.		(?) L Pli		Pli/Toa
Nuculanoidea	*Nuculana ovum* (J. de C. Sowerby)	L Pli–L Toa	U Pli–L Toa	U Pli	Pli/Toa
	Ryderia tehuelchana n. sp.				Pli/Toa
	Phaenodesmia piatnitzkyi n. sp.				Pli/Toa
	Palaeoneilo patagonidica (Leanza)		U Pli	U Pli	Pli/Toa
	Palaeoneilo galatea (d´Orbigny)			U Pli	
	Malletiidae indet.			U Pli	

Turner, 1982; Nullo, 1983). Gastropods have been recently revised (Ferrari, 2013 and references therein), and a new decapod crustacean was described (Pagani et al., 2011), but bivalves were not systematically updated. Ammonites were also recorded (Musacchio and Riccardi, 1971; Blasco et al., 1979; Vizán, 1989; Massaferro, 2001; Pagani et al., 2012), and, although they need revision, they indicate an age range from late Pliensbachian to early Toarcian for most deposits.

Early Jurassic bivalve faunas from the Neuquén Basin in Argentina and Chile are relatively well known as a result of several systematic revisions (Damborenea, 1987a, 1987b, 2002; Aberhan, 1994, 2004; Pérez et al., 2008). Their systematic study allowed the development of a biostratigraphic zonation for the region based on bivalves, which complements those based on ammonites and brachiopods (Damborenea in Riccardi et al., 1990; Damborenea, 1993, 1994, 2002). Nevertheless, only a few bivalves from Chubut Province were included in those systematic revisions, and their systematic knowledge has become largely outdated since the pioneer studies from the first half of the 20th century (Feruglio, 1934; Wahnish, 1942; Levy, 1966). Only few additions were made later, some in comprehensive papers dealing with Early Jurassic bivalves (Damborenea, 1987a, 1987b, 1993, 2002), and most in lists related to geological mapping (Franchi and Page, 1980; Turner, 1982; Nullo, 1983) or isolated figures in geological studies of localized areas (Vizán, 1989; Massaferro, 2001; Pagani et al., 2012; Ferrari and Bessone, 2015).

Geological setting and localities

In central and western Chubut Province there are extensive outcrops of Jurassic beds, mostly deposited in terrestrial environments. Marine beds are occasionally intercalated and laterally interdigitated with Early Jurassic volcanoclastic and coarse-grained clastic sediments, and although outcrops are scattered over a wide geographical area (Fig. 1), they show frequent lateral facial changes. In the Pampa de Agnia-Cañadón Puelman region of central Chubut, the marine sediments are referred to the Osta Arena Formation (Musacchio in Herbst, 1966) or Lomas Chatas Formation (Robbiano, 1971), previously known as "Sedimentos Liásicos Marinos" in Feruglio (1949). Farther southwest, in the Nueva Lubecka-Ferrarotti area, Early Jurassic marine beds are known as Mulanguiñeu Formation (Fernández Garrasino, 1977; see Cortiñas, 1984 and references therein). The southwesternmost outcrops with marine fossils were reported from the Lake Fontana region (Blasco et al., 1980). Contrary to Wahnish´s (1942, p. 22, 67) assumption of a complete Early Jurassic marine sequence in Chubut, most marine beds seem to have been deposited during the short interval of the late Pliensbachian to early Toarcian. Ammonites were reported by Musacchio and Riccardi (1971), Blasco et al. (1979, 1980), and Massaferro (2001).

Material from four localities, which can be grouped in eastern and southwestern areas of the Chubut Basin, was examined (see A to D, Figure 1.2 and synthesis of faunal contents in Table 2). Protobranchs were also reported by Franchi and Page (1980, p. 217) from Quichaura (locality E on Fig. 1), but their material was not available for examination.

Pampa de Agnia area.—At Sierra de Pampa de Agnia region (Fig. 1.2.2), better known as Sierra del Cerro Negro, according to Robbiano (1971), there are extensive outcrops of an Early Jurassic volcanoclastic complex referred to the El Córdoba Formation (Robbiano, 1971). These beds show a complex facial arrangement (Musacchio and Riccardi, 1971; Musacchio, 1975, 1981) and are intercalated with and laterally transitional to sedimentary (mostly marine) beds of the Osta Arena Formation. This unit includes tuffs, fine-grained sandstones, thin conglomerates, and shales. At some levels, late Pliensbachian to early Toarcian ammonites are locally abundant and include dactylioceratids (described by Blasco

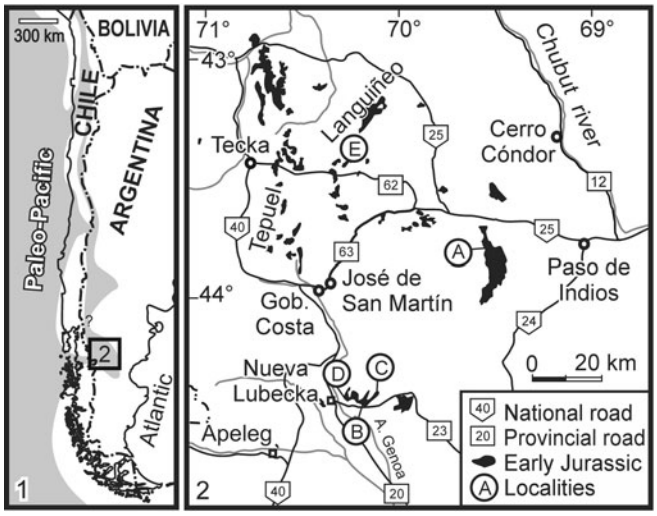


Figure 1. Location map. (**1**) General paleogeographical regional context for the early Toarcian, modified from Vicente, 2005; area marked by 2 in rectangle indicates area enlarged in Figure 1.2; (**2**) Early Jurassic localities in central Chubut Province. Localities mentioned in text: A Puesto Currumil-Quebrada El Córdoba, Pampa de Agnia region; B Aguada Loca; C Betancourt; D Loma de Plate; E Quichaura.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Table 2. Distribution and abundance of the species described here in the sampled localities, and associated fauna. Numbers correspond to number of specimens in each sample. Also listed the associated fauna at the same levels and localities.

LOCALITIES	Quichaura	Pampa de Agnia				Aguada Loca				Betancourt	Aguada de Plate
Samples		PA01	PA02	PA06	PA07	AL35 + 36	AL37	AL39	AL40	Bet 33	
Palaeonucula feruglioi n. sp.			9	2	4	5	2	7	2		
Palaeonucula sp.						15	3	6	2		
Palaeonucula? sp.		1				19	6	7	6	1	
Praesaccella ovum (Sowerby)			1			5	2		2		
Ryderia tehuelchana n. sp.			1			11	7	4	3		
Phaenodesmia? piatnitzkyi n. sp.				1	2			2	1		
Palaeoneilo? *patagonidica* (Leanza)	?	1		1		13		2	1	2	3
Grammatodon costulatus (Leanza)		x			x	x	x	x	x		
Parallelodon sp.								x			
Parainoceramya apolo (Leanza)		x							x		
Pteriidae indet.						x					
Kolymonectes weaveri Damborenea	?	x				x		x	x	x	
Agerchlamys wunschae (Marwick)?		x					x	x	x		
Radulonectites sosneadoensis (Weaver)?						x					
Praechlamys sp.	?	x					x				
Pseudolimea sp.						x					
Myophorella? sp.						x					
Frenguelliella chubutensis (Feruglio)										x	
Ostreidae indet.				x							
Lucinidae indet.						x					
Astartidae indet.						x	x			x	
Dactylioceratidae ammonoids			x	x	x	x		x	x		
Hildoceratidae ammonoids				x							
Gastropods				x	x	x	x	x	x	x	
Serpulids						x	x		x	x	
Echinoids									x		
Crinoids						x					
Mecochirus robbianoi Pagani et al.				x							

et al., 1979). Bivalves are also common, but only a few have been formally described (Levy, 1966; Damborenea, 1987a, 1987b, 1998, 2002). The material described here was collected at Puesto Currumil-Quebrada El Córdoba (Fig. 2; see logged section in Pagani et al., 2011, fig. 1).

The material mentioned by Franchi and Page (1980, p. 217) was probably collected near Pocitos de Quichaura (NW of Pampa de Agnia, locality E on Fig. 1.2), in deposits also referable to the Osta Arena Formation, characterized by their high volcanoclastic content, scarcity of invertebrate fossils, and lack of ammonites.

Betancourt area.—To the southwest of the previous region, Early Jurassic marine deposits show less volcanic content, and were deposited in a diversity of near-shore environments. They are referred by most authors to the Mulanguiñeu Formation, and, as can be seen at Betancourt (Fig. 1.2.C), Nueva Lubecka, and Cerro La Trampa, they rest unconformably on top of late Palaeozoic, mostly marine, deposits.

No protobranch bivalves were recovered from the shallow-water deposits at Lomas Occidentales, just west of Nueva Lubecka, River Genoa region, which bear a diverse bivalve, gastropod, coral, and brachiopod fauna, typical of a high-energy sublittoral environment. Depth increased and energy decreased to the east, and at Aguada Loca (see logged section in Fig. 2.2) and Betancourt localities (Fig. 2.3; logged section in Pagani et al., 2012, fig. 1), protobranchs were particularly abundant and diverse. At these last two localities, fine- and medium-grained sandstones prevail, and bear a far less diverse bivalve and gastropod fauna, with frequent ammonoids, locally dominated by pectinoideans, astartids, or protobranchs. At Aguada Loca, all the species described here are present, and both diversity and abundance of protobranch bivalves are particularly high in two extremely bioturbated levels towards the top of the logged section.

Lomas de Plate is located to the west of Aguada Loca. This locality was mentioned for the first time by Ugarte (1966). There, the Early Jurassic deposits rest unconformably on top of late Paleozoic sediments. The beds include slates and calcareous breccias with corals. This locality was not sampled by the authors. The material described here belongs to Piatnitzky collection.

Material, terminology and measurements

The species synonymy lists contain only the original reference and those strictly referring to material from Chubut. Other records are discussed in the text. The systematic arrangement follows Bouchet and Rocroi (2010) and Carter et al. (2011), with the emendations proposed by Carter et al. (2015). The interpretation of hinge details and muscle scars was based on Driscoll (1964), Bradshaw and Bradshaw (1971), and Bradshaw (1999). Terminology of dentition follows Carter et al. (2012).

Linear measurements were made with Vernier calipers to an accuracy of 0.1 mm. For orientation of specimens for measurements, see Figure 3. Abbreviations: AL = anterior length, H = height, L = length, PL = posterior length, W = inflation, nAT = number of anterior teeth, nPT = number of posterior teeth.

Repositories and institutional abbreviations.—All newly collected material is deposited in the Invertebrate Paleontology collections of the Museo Paleontológico Egidio Feruglio, Trelew, Chubut (MPEF-PI). Old collections were seen at the Museo de Ciencias Naturales, La Plata (MLP), and Servicio Nacional Geológico y Minero, Buenos Aires (SNGM).

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

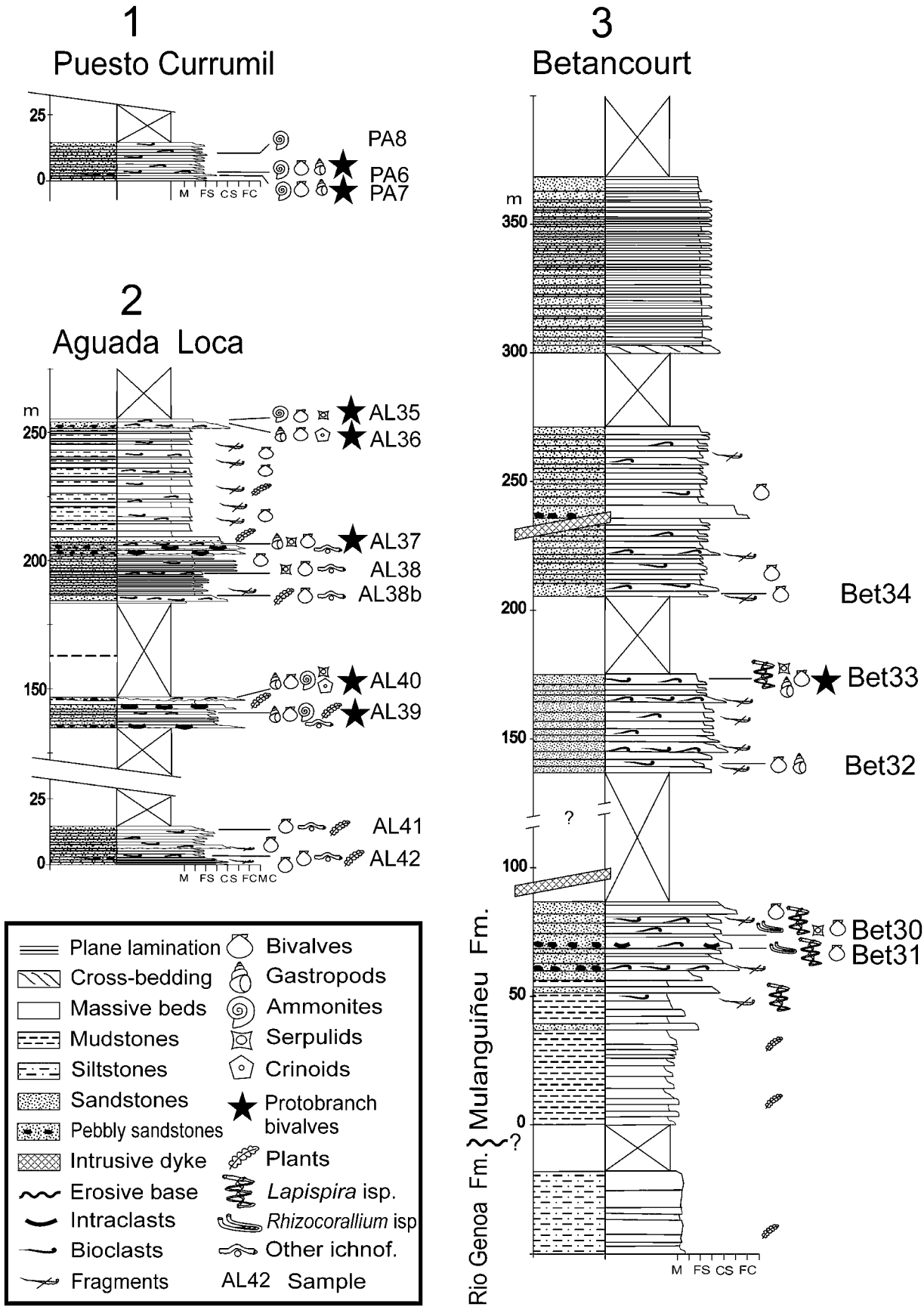


Figure 2. Logged sections (by S. Damborenea and A. Pagani) at (**1**) Puesto Currumil, Pampa de Agnia region, (**2**) Aguada Loca, and (**3**) Betancourt, the main three localities with abundant and diverse Protobranchia in central Chubut.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

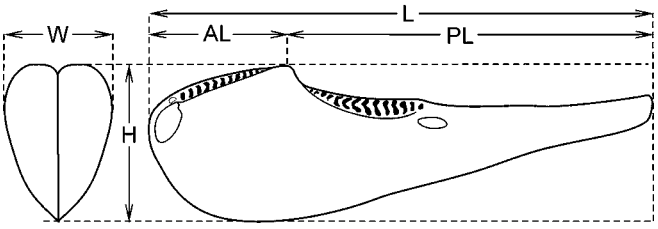


Figure 3. Measurements taken, shown on a sketch of *Ryderia tehuelchana* new species internal mold. AL: anterior length, H: height, L: length, PL: posterior length, W: inflation.

Systematic paleontology

Subclass Protobranchia Pelseneer, 1889 (= Palaeotaxodonta Korobkov, 1954)
Order Nuculida Dall, 1889
Superfamily Nuculoidea Gray, 1824
Family Nuculidae Gray, 1824

Remarks.—Nuculidae shells are characterized by their small to medium size, nacreous shell portions, opisthogyrate beaks, and an internal lamellar ligament in a resilifer. This family has a long record (since the Ordovician), and Jurassic species are mostly referred to *Palaeonucula* Quenstedt and *Nuculoma* Cossmann. The shell characters of both are very similar to the extant *Nucula* Lamarck. All living species are shallow burrowers and deposit feeders, and the same is inferred for extinct species of this family.

On the basis of shell microstructure, Carter (2001) defined the subfamily Palaeonuculinae for nuculids with a largely non-nacreous adult shell, including the genera *Palaeonucula* Quenstedt, 1930 (late Carboniferous to Jurassic) and *Condylonucula* Moore, 1977 (Recent). Carter restricted Nuculinae to mostly nacreous shells with marginal denticulations, extended in time from Cretaceous (or Carboniferous?) to Recent (Carter, 2001). This microstructure criterion is very difficult to apply in most fossil material due to imperfect preservation of the shell.

The abundant material from Chubut referable to this family has a wide range of shell sizes and shapes, and at least three taxa can be recognized, which are all left in open nomenclature.

Genus *Palaeonucula* Quenstedt, 1930

Type species.—*Nucula hammeri* Defrance, 1825, p. 217, from the Early Jurassic of France, original designation.

Remarks.—This taxon was regarded as a subgenus of the late Paleozoic genus *Nuculopsis* Girty by Schenck (1934, 1939). A clear and lucid discussion on the systematic relationships of *Palaeonucula* was provided by Cox, who first considered it as a subgenus of *Nucula* Lamarck (Cox, 1940) and later of *Nuculoma* Cossmann (Cox, 1965). McAlester in Cox et al. (1969) regarded it as a separate genus, and later Duff (1978, pp. 22–23) extensively discussed previous references and argued in support of this. An up-dated diagnosis was provided by Hodges (2000) and its paleogeographic distribution was summarized by Ros et al. (2014, fig. 1). Although no Early Jurassic species from Argentina had been formally assigned to this genus, material described as *Nucula leufuensis* Weaver (1931, p. 183), from Middle Jurassic deposits of the Neuquén Basin, is referable to *Palaeonucula*. Here we describe two Early Jurassic species referred to this genus.

The general shell morphology of *Palaeonucula* is similar to *Nucula* Lamarck, but shell is non-nacreous and has a smooth margin. Species of *Palaeonucula* were probably also deposit feeders, living as shallow burrowers in soft substrate.

Palaeonucula feruglioi new species
Figures 4.1–4.4, 7.1

Holotype.—MPEF-PI 6495, an internal mold of a left valve.

Diagnosis.—Small- to medium-sized *Palaeonucula*, with inflated subtrapezoidal shells. Hinge gradidentate with convexodont teeth, hinge plate with a small, anteriorly directed, triangular resilifer, anterior part of hinge longer than posterior, both slightly dorsally convex. Posterior adductor in a shallow depression. Exterior of shell with regular commarginal threads, inner margin smooth.

Occurrence.—Aguada Loca, Tehuelches Department, Chubut Province (sample levels AL37, AL39, AL40), Pampa de Agnia, Paso de Indios Department, Chubut Province (sample levels PA02, PA06, PA07); see Figure 2.

Description.—Nuculiform, small- to medium-sized subtrapezoidal shell, inequilateral, valves inflated, longer than high (L/H ~1.6). Umbos wide, opisthogyrate, placed posteriorly to mid-length, at about 1/3 of total length from posterior end. Antero-dorsal margin slightly dorsally convex, postero-dorsal margin nearly straight. Anterior, ventral, and posterior margins rounded, with a marked antero-dorsal angle (Fig. 4.1, 4.2). No distinct lunule or escutcheon. Maximum shell height posteriorly placed.

Hinge gradidentate with convexodont teeth, anterior part of hinge longer than posterior, with ~25 narrow, chevron-shaped teeth and sockets decreasing in size towards umbo. Posterior teeth ~10, also decreasing in size towards umbo. All teeth are narrow and tall, triangular, slightly inclined towards umbo, and larger ones are clearly diconvexodont, with a wide M-shaped section. Each tooth shows a shallow but distinct central fold flanked by a shallow sulcus at each side on their external face, and the opposite (central sulcus and two lateral folds) on their umbonal face. Posterior teeth are taller at the middle of the series. There is a small, anteriorly directed, triangular resilifer (Fig. 4.4), placed below the very narrow five or six central anterior teeth.

Posterior adductor muscle scar oval in shape and placed in a very shallow depression, situated below the three posteriormost teeth, and anteriorly limited by a very low ridge (Fig. 4.1, 4.2); anterior adductor muscle scar only slightly impressed, oval in shape. No other muscle scars could be recognized.

External surface with regular, thread-like faint growth lines, ~6 per mm on the central part of the shell. Inner margin smooth.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

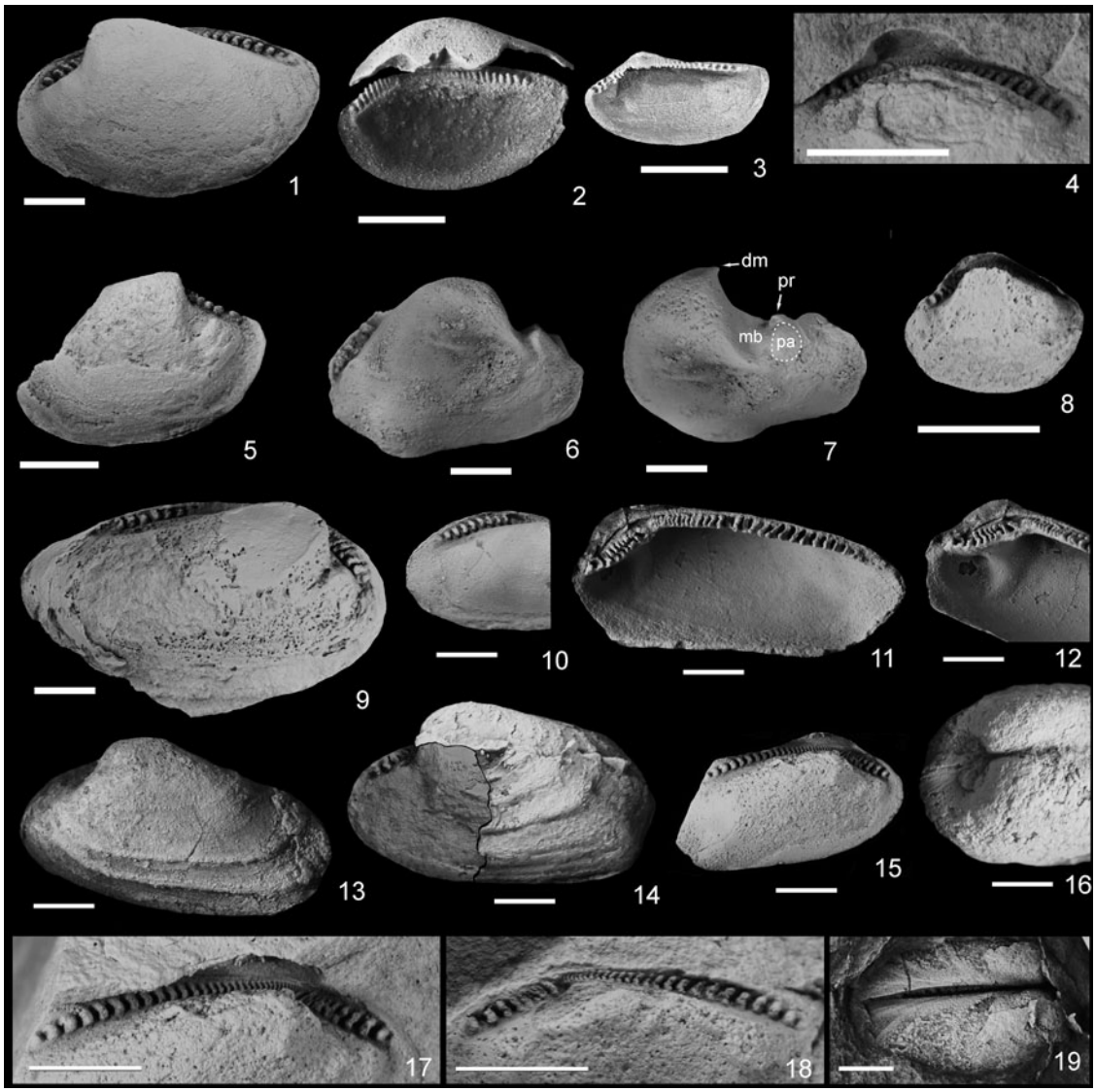


Figure 4. (**1–4**) *Palaeonucula feruglioi* new species; (**1**) MPEF-PI 3149, paratype, right valve internal mold; (**2**) MPEF-PI 3897, paratype, latex cast of specimen with valves half open, showing interior of left valve and fragment of right valve shell and detail of external ornamentation; (**3**) MPEF-PI 6495, holotype, latex cast of left valve internal mold; (**4**) MPEF-PI 3898, paratype, internal mold of right valve, oblique view showing hinge. (**5–8**) *Palaeonucula* sp.; (**5**) MPEF-PI 2843, left valve internal mold; (**6, 7**) MPEF-PI 2932, left valve internal mold of deformed specimen in lateral and dorsally oblique views to show muscle scars; (**8**) MPEF-PI 5763, juvenile specimen, right valve internal mold. Abbreviations: dm = dorsomedian muscle scar; mb = myophoric buttress; pa = posterior adductor muscle scar; pr = posterior retractor muscle scar. (**9–19**) *Palaeonucula*? sp.; (**9**) MPEF-PI 3369, left valve internal mold; (**10**) MPEF-PI 2920, detail of anterior part of left valve; (**11, 12**) MPEF-PI 3144, latex cast of left valve internal mold, inner view and tilted view to show posterior adductor muscle scar; (**13**) MPEF-PI 3371, latex cast of external mold; (**14**) MPEF-PI 3372, right valve internal mold and latex cast of external mold; (**15**) MPEF-PI 2978, left valve internal mold, tilted view showing hinge; (**16**) MPEF-PI 5767, dorsal view of posterior part of complete specimen with closed valves, showing escutcheon, latex cast; (**17**) MPEF-PI 2978, left valve internal mold, tilted view showing hinge; (**18**) MPEF-PI 5765, right valve internal mold and latex cast; (**19**) MPEF-PI 3364, dorsal view of closed valves, latex cast. Scale bars = 5 mm.

Etymology.—Dedicated to Dr. Egidio Feruglio, Italian geologist who made substantial contributions to the geology and paleontology of Patagonia.

Materials.—Two specimens with valves open (one of them in butterfly position), plus 27 isolated right and left valves, most of them preserved as internal molds: MPEF-PI 2964, 2981, 3149 (paratype), 3897 (paratype), 3898 (paratype), 5768, 5771, 6454, 6456, 6457, 6461, 6462, 6463, 6465, 6466, 6467, 6469, 6470, 6471, 6476, 6477, 6487, 6495 (holotype), 6499, 6554, 6555, 6560.

Measurements.—See Table 3.

Remarks.—The type material of *P. cuevitana* Aberhan (1994, pl. 1, figs. 1–4), from the Hettangian of Chile, has a similar shell outline, umbo position, and lack of lunule and escutcheon, but differences include a smaller and shorter shell, more concave postero-dorsal margin, fewer anterior teeth, and lack of regular external ornamentation in the Chilean material.

The type species of the genus, *Palaeonucula hammeri* (Defrance, 1825) (Quenstedt, 1851, p. 527, pl. 44, figs. 4, 5; 1856, p. 313, pl. 43, figs. 7–12; Schenck, 1934, p. 35, pl. 2,

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Table 3. Measurements (in mm) of *Palaeonucula feruglioi* new species. Lines/mm = number of commarginal lines per mm in central part of shell.

MPEF-PI	L	H	AL	nAT	nPT	Lines/mm
2964	10.5+	6.8		26+	12	
3149 (Paratype)	24	15.2	17.1	20+	8+	
3897 (Paratype)	13.1	7	7.6	19	11	6
3898 (Paratype)	11.8	6.4	7.8	21	8	
6457	11.1	6.7	6.6			
6462	10.9	6.9	7.7	20+	13	
6463	10.5	6.4	6.3			
6465	9.6	6.3	4.5			
6467-1	9.3	6.2	6.7			
6467-2	12.8	13	6.9			
6469	13.5	7.8	7			
6471	7.7	4.6	4.8			6
6495 (Holotype)	11	6.5	8.4	18+	10+	7
6560	10.4	7	7			

fig. 20, pl. 4, fig. 1), from the Toarcian-Bajocian of Europe, has a subrectangular, inflated shell, with wider umbones that are more posteriorly placed. The same applies to the possible synonym (see Schenck, 1934, p. 37; Aberhan, 1998, p. 64), *Palaeonucula hausmanni* (Roemer, 1836, p. 98, pl. 6, figs. 12a–12d; Kuhn, 1935, p. 120, pl. 8, figs. 33a–33b, 41a–4d).

Palaeonucula saigonensis Hayami (1972, pl. 33, figs. 1–3, pl. 38, figs. 1, 2), from the Early Jurassic of Saigon, has a similar shell shape to the species here described, but the Asian species has fewer teeth and muscle scars are more strongly impressed. The species here described is also similar in general shape to *P.* sp. B from the Toarcian of Canada (Aberhan, 1998, pl. 1, figs. 1–4), but the specimens from Chubut lack lunule and escutcheon (mentioned for the Canadian material, although all specimens are internal molds), have less-prominent umbos, and have a less-impressed anterior adductor muscle scar.

The shell shape of *Palaeonucula feruglioi* n. sp. is reminiscent of material referred to *Palaeoneilo galatea* (d´Orbigny, 1850), as do the specimens figured by Aberhan et al. (2011, pl. 1, figs. 3, 4) from Europe and those from southern Neuquén (Damborenea, 1987a, pl. 1, fig. 4).

Palaeonucula menkei (Roemer, 1836) in Fürsich and Werner (1988, pl. 1, fig. 2) and Sha et al. (1998, pl. 1, fig. 1), Middle and Late Jurassic from Europe and Asia, is smaller and has fewer teeth.

This species clearly differs from *Palaeonucula* sp. described below, from the same locality, by its longer shell with less-prominent umbos, marked antero-dorsal angle, adductor scars not impressed, and more numerous anterior teeth. The shell of *Palaeonucula*? sp., also described here, has a different shape, without dorso-anterior angulation, more-prominent umbones, and a coarser ornamentation of commarginal rugae.

Palaeonucula sp.
Figures 4.5–4.8, 7.2

Occurrence.—Aguada Loca, Tehuelches Department, Chubut Province (sample levels AL35/36, AL37, AL39, AL40; Fig. 2.2).

Description.—Small subtrigonal shell, slightly to moderately inequilateral, valves inflated, young shells nearly as high as long (L/H = 1.1), shell longer than high in adults (L/H ~1.5). Umbos very prominent and wide, opisthogyrate, strongly incurved, placed centrally or somewhat posteriorly. Antero-dorsal margin straight or dorsally convex, postero-dorsal margin dorsally concave. Anterior, ventral, and posterior margins rounded. Without lunule or escutcheon.

Hinge gradidentate with convexodont teeth. Anterior part of hinge longer than posterior, with up to ~20 chevron-shaped teeth and sockets, decreasing in size towards umbo. Posterior teeth ~10, larger than anterior ones, also decreasing in size towards umbo.

Posterior adductor muscle scar oval in shape and placed in a very deep depression situated below the posteriormost teeth, and anteriorly limited by a strong ridge or myophoric buttress; anterior adductor muscle scar only slightly impressed. A small punctiform depressed muscle scar (dm in Fig. 4.7) (dorsomedian scar?) occurs in the umbonal region. Between the umbo and the posterior adductor muscle scar, parallel to the dorsal margin, there is a slightly impressed oval muscle scar (pr in Fig. 4.7), probably corresponding to the posterior retractor muscle. Pallial line continuous, parallel to the margin. Internal shell margin appears smooth, although some specimens show very faint crenulations (Fig. 4.5).

External surface with irregularly spaced faint growth lines.

Materials.—The 26 available specimens are preserved as molds, mostly internal, and include a wide size range: (MPEF-PI 2841, 2843, 2863, 2865, 2932, 2934, 2970, 2971, 3157, 3366, 3376, 3889, 5763, 5776 , 6474, 6480, 6482, 6493, 6496, 6498, 6557, 6562, 6563, 6574, 6585, 6592).

Measurements.—See Table 4.

Remarks.—According to its shape, dentition, and details of aductor muscle scars, this species can be referred to *Palaeonucula*. It differs from *Palaeonucula feruglioi* n. sp. described above by a shorter shell, with wider umbones, fewer anterior teeth, presence of conspicuous posterior myophoric buttress, and external shell surface with growth lines only.

Palaeonucula navis (Piette, 1856), from the Hettangian to Pliensbachian of Europe and China, has a similar subtrigonal shell, but its umbones are more posteriorly placed and there is a deep escutcheon (see Terquem and Piette, 1865, pl. 10, figs. 8–10; extensive description and discussion in Hodges, 2000, pl. 1, figs 1–29). The species described here is very similar to a single specimen from the late Pliensbachian of Canada

Table 4. Measurements (in mm) of *Palaeonucula* sp. * = incomplete specimen.

MPEF-PI	L	H	AL	nAT	nPT
2843	15.2*	9.8			8
2863	24.5*	15.4	17.6		10
2865	11.5	8.2	7.5		
2932	21.4	14.6	12	20	
2934	6.7	5.2	3.5		
2970	21.5	14.6	14.8		
2971	26.7	16.2	16.3		
3157	11.3	6.1	8.4		
3366	21.4	11.7	16.2		
3376-1	9.1	7.9	5.3		
6574	8	6.6	4.8	15+	7+
6585*	24.6	12.5	16.5	20	
6592-1	27	15.6	19.2	19	

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

described by Aberhan (2008, pl. 1, fig. 9) as *Palaeonucula* sp. A, and to material from the Chinese Early Jurassic described by Chen (1982, pl. 1, fig. 5–7) as *Palaeonucula* cf. *navis* (Piette).

Palaeonucula triangularis Duff, 1978 (pl. 1, figs. 6–13, 17, 23, text-fig. 6), from the Callovian of England, has a similar trigonal shape, but is more inflated with well-developed escutcheon. Shell shape and strong myophoric buttress are similar to those of *P. acuta* (Borissjak, 1904, pl. 1, fig. 3) from the Middle Jurassic of Russia. The Late Jurassic species *P. putiensis* (Marwick, 1953, p. 87, pl. 10, fig. 4) from New Zealand has a more oval shell outline.

The described specimens cannot be readily referred to any known species. The available material allows characterization the species in detail, but unfortunately poor knowledge of most Early Jurassic *Palaeonucula* species, and the large number of available specific names, prompted the use of open nomenclature for this taxon.

Palaeonucula? sp.
Figure 4.9–4.19, 7.3

Occurrence.—This species is widely distributed in Chubut, at Aguada Loca, Tehuelches Department (AL35-36, AL37, AL39), Betancourt, Tehuelches Department (Bet-33), and Pampa de Agnia, Paso de Indios Department (PA-01), Chubut Province.

Description.—Medium- to large-sized, inflated shell; oval in outline, with very wide opisthogyrate umbos. Anterior and posterior dorsal margin continuous and dorsally convex. Shell much longer than high, L/H ratio 1.5–2. Anterior and posterior margins convex, anterior one wider; the maximum shell height is anterior to the umbones in most specimens. Deeply impressed short escutcheon (Fig. 4.16), no lunule (Fig. 4.19).

Hinge very slightly gradidentate, with convexodont teeth. Both anterior and posterior series of teeth placed in a continuous convex line. Posterior teeth are differentiated in four to five strong, distal chevron-like concavoconvexodont teeth and five narrow, blade-like teeth near the umbo (Fig. 4.17, 4.18). Teeth of anterior series (25–30 in number) are chevron-like concavo-convexodont and decrease gradually in size towards the umbo (Fig. 4.10, 4.11). Small and narrow triangular resilifer placed under umbo below the smallest anterior teeth and directed anteriorly (Fig. 4.11, 4.17, 4.18).

Posterior adductor muscle scar subcircular, placed in a shallow depression, anteriorly limited by a wide and low swelling (Fig. 4.12). Anterior adductor oval in outline, but not so well marked as posterior, placed just below the first teeth (Fig. 4.11). Pallial line very faintly impressed, seemingly truncated.

Shell exterior with irregular commarginal lines, some of them thickened, forming well-developed folds and becoming lamellar-like towards the margin in large shells (Fig. 4.13, 4.14). Inner shell margin smooth.

Materials.—Forty specimens, preserved as internal or external molds, five of them with both valves, one of them open in butterfly position: MPEF-PI 2892, 2920, 2935, 2978, 3144, 3359, 3364, 3369, 3371, 3372, 5765, 5766, 5767, 5770, 5773, 5774, 5775, 5777, 5778, 6479, 6485, 6486, 6489, 6492, 6497, 6500, 6550, 6556, 6564, 6565, 6566, 6567, 6569, 6570, 6575, 6580, 6581, 6583, 6584, 6591.

Measurements.—See Table 5.

Remarks.—This species differs from *Palaeonucula feruglioi* n. sp. and *P.* sp. described above by the presence of a conspicuous escutcheon, rounder and higher anterior shell margin, hinge with more numerous anterior teeth, and smaller resilifer, and by the prominent external commarginal folds in adults. From *Palaeoneilo*? *patagonidica* (Leanza, 1942) this species is distinguished by its ornamentation, and by its shorter and more inflated shell, which is higher anteriorly, stronger teeth, and by the presence of resilifer and escutcheon.

The type species of *Prosoleptus*, *P. lineatus* (Goldfuss, 1837, p. 153, pl. 124, fig. 17; Carter, 1990, fig. 13), from Carnian beds of the Alps, has a similar shell shape with escutcheon and the same number of anterior and posterior teeth, but the shell is shorter, more protruded anteroventrally, and apparently lacks a resilifer.

The oval, rather compressed shell shape and type of commarginal ornamentation precludes reference of this species to *Palaeonucula*, but the anteriorly elongated shell, presence of resilifer, hinge features, and thick shell indicate nuculidae affinities. It cannot be referred with certainty to any Mesozoic nuculid genus, and thus it is here left in open nomenclature until better preserved material allows a proper identification of its generic affinities.

On the other hand, shell shape and hinge of the material from Chubut are closely comparable to shells of some older genera, especially to the Triassic genus *Prosoleptus* Beushausen (1895, p. 95), which, however, has a characteristic antero-ventral protrusion. Also similar is the Carboniferous genus *Spathelopsis* of Hoare et al. (1989), although it has a subrostrate posterior margin and posteriorly gaping valves. Due to the imperfect knowledge of internal details, the systematic affinities of these genera are still uncertain and open to discussion (see Peck et al., 2009, p. 957), but it is worth trying to elucidate their possible relationships with the species here described and other Jurassic species.

Table 5. Measurements (in mm) of *Palaeonucula*? sp.

MPEF-PI	L	H	AL	nAT	nPT
2978-1	19.5	10.6	13.5	19+	9
3144	27.3	13.2	20.9	27	9
3369	28.9	16.5	23.0		9
3371	26.6	12.9	19.4		
3372	25.0	16.7	18.0	22	
5765	18.1	8.3	12.6	25	8
5775	19.3	12.6	11.5		
6479	24.0	12.4	19.0		
6489	25.0	14.0	7.0		
6497	20.8	11.3	14.0	15+	6
6550	19.0	9.5	13.5		
6564	24.0	16.6	16.1		
6565	27.4	16.0	17.1	19+	9
6583	15.0	8.6	9.7		10+
6584-2	26.7	14.5	20.5		
6591-1	33.8	20.2	24.6	20	8+

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

The material here described has some of the diagnostic characters of the genus *Rollieria* Cossmann (1920, p. 82), such as an ovate shell without lunule, with resilifer and hinge rows continuous or forming a very obtuse angle. Nevertheless, the specimens from Chubut are anteriorly elongated, have an escutcheon, and the shell appears to be thicker and more inflated that in other species referred to *Rollieria*. *Rollieria* was regarded as a subgenus of *Nuculana* in Cox et al. (1969, p. N237), and later referred to the Yoldiidae by Hodges (2000, p. 35) on account of its posteriorly elongated shell, with a shallow pallial sinus, and low prosogyrous umbones.

Order Nuculanida Carter, Campbell, and Campbell, 2000
Superfamily Nuculanoidea Adams and Adams, 1858 (1854)

Remarks.—This superfamily includes protobranchs with posterior rudimentary mantle fusion and siphons. Nuculanoid bivalves are diverse and relatively abundant in Chubut, but in the Neuquén Basin they are rare and only diverse in its southern region (Piedra Pintada; see Damborenea, 1987a). In some localities from Chubut, several species can be found together in the same beds (see Table 2). The material from Chubut is generally preserved as high quality molds in very fine-grained siltstones, allowing a precise description of internal characters, such as hinge and muscular impressions.

Family Nuculanidae Adams and Adams, 1858 (1854)
Genus *Praesaccella* Cox, 1940

Type species.—*Nuculana* (*Praesaccella*) *juriana* Cox, 1940, from the Oxfordian of Kutch, India.

Praesaccella ovum (J. de C. Sowerby, 1824)
Figures 6.1–6.6, 7.5

1824 *Nucula ovum* Sowerby, p. 118, pl. 476, fig. 1.
1978 *Nuculana* sp.; Damborenea in Volkheimer et al., tab. 2.
1987a *Nuculana* cf. *ovum* (J. de C. Sowerby); Damborenea, p. 59, pl. 1, figs. 7–9, text-fig. 9.
1992 *Nuculana* cf. *ovum* (J. de C. Sowerby); Damborenea, pl. 115, fig. 15.
1994 *Nuculana* (*Praesaccella*) *ovum* (J. de C. Sowerby); Aberhan, p. 10, pl. 1, figs. 5–12, text-fig. 3.

Occurrence.—Aguada Loca, Tehuelches Department (sample levels AL35, AL37, AL40), Pampa de Agnia, Paso de Indios Department (sample levels PA02), Chubut Province (Fig. 2). This species is also known from several localities in the Neuquén Basin (Damborenea, 1987a, p. 59), and the Pliensbachian to Toarcian of northern Chile (Aberhan, 1994); the material described here extends its geographical range to central Chubut.

Description.—Small nuculaniform shell, inflated, slightly longer than high, with a short posterior rostrum. Outline subtriangular, inequilateral. Umbones strongly opistogyrate, located anteriorly to mid-length. Anterior and ventral margins of shell evenly convex, posterior dorsal margin concave. Posterior end of rostrum convex, located at about mid-height. A low, wide, indistinct ridge extends from the umbones to the end of rostrum, delimiting a postero-dorsal concave shell surface. Inner shell margin smooth. Anterior adductor muscle scar oval in shape and strongly impressed on inner shell surface, below the first hinge teeth (Fig. 6.6). Posterior adductor muscle scar of equal size, rounder and deeply impressed (Fig. 6.2, 6.3), pallian line continuous and clearly marked (Fig. 6.2). Hinge plate strong, anterior portion slightly dorsally convex and posterior part dorsally concave, separated by small, narrow but deep, triangular resilifer (Fig. 6.3). Teeth V-shaped and strong, 10–12 on the anterior series, about the same number on the posterior one. Exterior of shell ornamented by faint but regular commarginal lines over the whole surface (Fig. 6.5).

Materials.—Five right valves and five left valves, preserved as internal or external molds: MPEF-PI 6481, 6483, 6484, 6561, 6568, 6571, 6577, 6578, 6586, 6589.

Measurements.—See Table 6.

Remarks.—As already pointed out by Aberhan (1994), this species can be referred to *Praesaccella* Cox (1940, p, 32), originally described as a subgenus of *Nuculana* Link. For comparisons see Damborenea (1987a, p. 60).

Family Polidevciidae Kumpera, Prantl, and Růžička, 1960

Remarks.—The Ordovician to Late Jurassic family Polidevciidae was recently characterized by Carter et al. (2015, p. 3) by having a "strongly mineralized, prominent external ligament; a small to moderately well-developed resilium, shallow to deep submarginal; paleotaxodont hinge; nacreous shells, not porcelaneous; and shells posteriorly extended without permanent dorsoposterior shell gape."

Genus *Ryderia* Wilton, 1830

Type species.—*Leda renevieri* Oppel, 1856, p. 215, from the Early Jurassic of Great Britain, designated by Cox, 1936, p. 467.

Remarks.—See updated diagnosis of the genus and synonyms in Hodges (2000, p. 40).

There is a group of Late Triassic and Early Jurassic nuculanoid species characterized by a very long, narrow rostrum and

Table 6. Measurements (in mm) of *Praesaccella ovum* (J. de C. Sowerby).

MPEF-PI	L	H	AL	nAT	nPT
6483	14.0	10.6	6.0	9	12
6484	10.9	8.2	3.0		
6568	13.0	9.2	6.1		
6571	11.0	7.7	4.8	8	11
6577-1	13.2	8.0	3.6	11	10
6578	13.1	10.8	5.0		
6586*	11.7	9.3	4.5	8	
6589-1	10.2	7.4	4.2	8	7

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

externally ornamented with radial, oblique (in the sense of Checa, 2002), or divaricate patterns. They were early included in the genus *Ryderia*, but this was incorrectly diagnosed in Cox et al. (1969) as having a pallial sinus, which is absent in all shells examined (also by Hodges, 2000).

A complex pattern of ornamentation is common in many rostrate nuculanoid genera and species from the late Paleozoic to the present, and is most probably a variable character that is highly influenced by function in these active shallow burrowers, and thus of limited phylogenetic value. Furthermore, the intraspecific variability of ornamentation is thought to be high in the few species in which it was analyzed (Jaitly et al., 1995; Hodges, 2000; Yin and McRoberts, 2006; Ayoub-Hannaa et al., 2017). Nevertheless, Chen et al. (1983) regarded ornamentation of nuculanoids as an important feature, and erected the subfamily Veteranellinae to include nuculanids with strong ornamentation. Chen et al. (1983) did not mention *Ryderia* in their analysis, and they referred Late Triassic–Early Jurassic material to *Teinonuculana* Zhang (in Zhang et al., 1977), now regarded as a junior synonym of *Ryderia* (see Yin and McRoberts, 2006, p. 106). The type species of *Teinonuculana* Zhang (in Zhang et al., 1977) has similar features, including ornamentation pattern, to those of the type species of *Ryderia* and to the material from Chubut. Recent revision of the genus *Ryderia* (Hodges, 2000) has shown that it also includes species that may be externally ornamented by commarginal or radial striae, and that the presence of these characters seems to depend largely on preservation. With these arguments in mind, Yin and McRoberts (2006) referred the type species of *Teinonuculana* to *Ryderia*, but Hautmann et al. (2008) doubtfully assigned it to *Phestia*.

According to Hodges (2000), *Ryderia* stratigraphic range extends from the Carboniferous to the late Pliensbachian, but the oldest well-documented records are from Rhaetian beds (Ivimey-Cook et al., 1999; Yin and McRoberts, 2006; Mander et al., 2008; Ros et al., 2014), and it extends into the early Toarcian (Cox, 1965; Liu, 1995; Fürsich et al., 2001). Records of *Ryderia* from the Middle Jurassic are also doubtful; for instance, at least Bathonian specimens from Sinai referred to *Ryderia decorata* (Douvillé, 1916) by Abdelhady and Fürsich (2014, fig. 3.E, 3.F; see also Ayoub-Hanna et al., 2017, fig. 7) could belong to *Nuculana*. On the other hand, the genus *Costinuculana*, recently described from those Bathonian Sinai beds (Ayoub-Hannaa et al., 2017), is certainly closely related to *Ryderia*. According to these authours, *Ryderia* differs from *Costinuculana* "in having a narrower and much more elongated rostrum, a narrow and smooth escutcheon, fine and closely spaced commarginal ribs, in lacking posterior oblique ribs, and in being much more compressed" (Ayoub-Hannaa et al., 2017, p. 436). Nevertheless, some *Ryderia* species, among them the new species described here, do have oblique ribs on the rostrum, although less developed than in *Costinuculana*.

The Permian–Triassic genus *Veteranella* Patte, 1926 is also very closely related, it has similar shell shape and internal characters, and a very variable ornamentation pattern, which may include divaricate, commarginal, and/or radial ribs (see Fang et al., 2009). *Glyptoleda* Fletcher (1945), from the Permian of Australia, has comparable ornamentation, but its rostrum is much shorter than in *Ryderia*.

This is the first description of a *Ryderia* species from the Early Jurassic of Argentina and South America. The late Triassic species described by Jaworski (1922) from Peru as *Leda oxyrhyncha* could belong to *Ryderia*, and the genus was also recorded from Norian beds in southern Chile (Pérez-Barría, 2004, 2005).

Ryderia tehuelchana new species
Figures 5.1–5.18, 7.4

Holotype.—MPEF-PI 2976 (Fig. 5.1, 5.2), specimen with both valves closed, but slightly displaced, preserved as an external mold of the right valve showing ornamentation, and part of the internal mold of the left valve showing hinge details.

Diagnosis.—*Ryderia* with fine divaricate striae on the anterior portion of the shell and undulose, oblique, mostly vertical, ribs on the posterior part of the shell and rostrum, with ~17 anterior and 20 posterior teeth. Rostrum long with central rostral groove.

Occurrence.—Aguada Loca, Tehuelches Department (AL 35, 35 + 36, 37, 39, 40), Pampa de Agnia, Paso de Indios Department (sample level PA02), Chubut Province (Fig. 2).

Description.—Shell very inequilateral, about three times longer than high, with a very long posterior rostrum. Small opisthogyrate umbos anteriorly placed, at about ¼ of total shell length. Valves only moderately inflated (Fig. 5.7, 5.9). Anterior and antero-ventral margins rounded, postero-ventral margin almost straight and convergent with dorsal margin, end of rostrum straight and narrow, posterior dorsal margin widely concave. Escutcheon wide and long, limited by a faint ridge, with a smooth surface (Fig. 5.6, 5.18).

Hinge slightly gradidentate with convexodont teeth (Fig. 5.16). Anterior part of hinge slightly dorsally convex, with ~17 chevron-like teeth and sockets, pointing and decreasing in size towards the umbo. Posterior part of hinge dorsally concave, with laminated triangular teeth and sockets, ~20 in number and slightly larger than those on the anterior part. Hinge teeth series interrupted below umbos with a small triangular ligamental pit, anteriorly directed (Fig. 5.16).

Anterior adductor scar kidney-shaped, placed just in front of distal end of hinge in a relatively deep depression, posteriorly limited by a low ridge (Fig. 5.14, 5.15). Posterior adductor scar elongated and placed in a shallow depression just below and posterior to the hinge end (Fig. 5.13–5.15). At about half length between the anterior adductor and the umbo, and below the hinge platform, there is a deep punctiform scar that continues anteriorly into a neat sulcus parallel to the hinge platform, up to just to the back of the anterior adductor muscle scar, possibly corresponding to the pedal retractor muscle (Fig. 5.15). Visceral muscle scars are also evident, and the main cavity of the shell is divided into two areas, anterior and posterior to a low and wide median ridge extending from the umbo to about half shell height. A small rounded umbonal scar with a smaller punctiform anterior impression appears in the umbonal region anterior to the ridge, and there is another small muscle scar in the umbonal region posterior to the

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

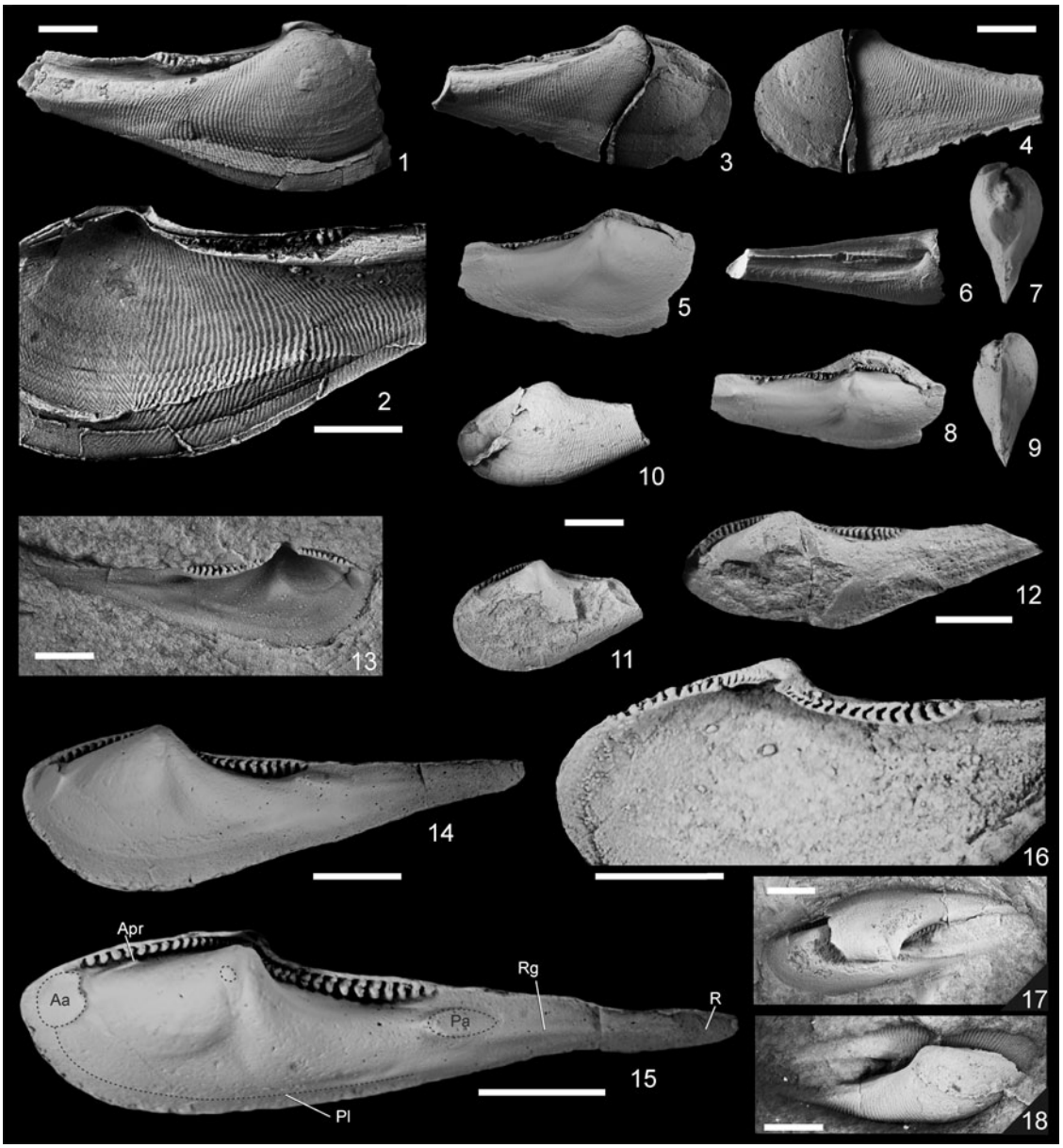


Figure 5. *Ryderia tehuelchana* new species. (**1, 2**) MPEF-PI 2976, holotype, right valve, (**1**) latex cast and (**2**) external mold showing ornamentation; (**3–9**) MPEF-PI 2862, almost complete specimen preserved as external and internal molds of both valves; (**3, 4, 6, 7, 9**) right, left, posterior dorsal, posterior, and anterior views of latex casts of external molds; (**5, 8**) right lateral view and dorsally tilted view of internal mold; (**10, 11**) MPEF-PI 3358, left valve, latex cast of external mold and internal mold; (**12**), MPEF-PI 3363, left valve internal mold; (**13–15**) MPEF-PI 3001, paratype, complete internal mold of left valve, (**13**) latex cast, (**14**) internal mold, (**15**) slightly tilted to show rostrum (R) with rostral groove (Rg), and muscle scars: Aa = anterior adductor; Apr = pedal retractor, Pa = posterior adductor; Pl = pallial line; (**16**) MPEF-PI 6572, latex cast of internal mold of right valve showing hinge; (**17**) MPEF-PI 3890, internal mold of both valves open and slightly displaced; (**18**) MPEF-PI 3902, latex cast of external mold of both valves open and slightly displaced. Scale bars = 5 mm.

ridge (Fig. 5.15). The pallial line is slightly impressed and appears to be continuous. A shallow internal rostral groove (siphonal groove?) extends from the posterior adductor to the end of the rostrum (Fig. 5.15).

Ornament of undulose oblique ribs covering shell posteriorly from umbonal region to the end of rostrum. Anterior region of the shell covered by very fine, chevron- and V-shaped, divaricate striae (Fig. 5.1–5.4). Escutcheon smooth with growth lines only. Inner shell margin smooth.

Etymology.—The specific name refers to a group of native people from southern Patagonia.

Materials.—Four specimens with both valves, in three of them the valves are preserved slightly displaced; 22 isolated right and left valves, preserved as internal or external molds, MPEF-PI 2852, 2862, 2976 (holotype), 2983, 3001 (paratype), 3145, 3151, 3358, 3363, 3888, 3890, 3891, 3892, 3902, 5769, 6459, 6472, 6473, 6475, 6494, 6552, 6572, 6573, 6582, 6588, 6590.

Measurements.—See Table 7.

Remarks.—The oblique and divaricate ribs that characterize this species are special features found in many nuculoid and nuculanoid shells, which often show a high intraspecific

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

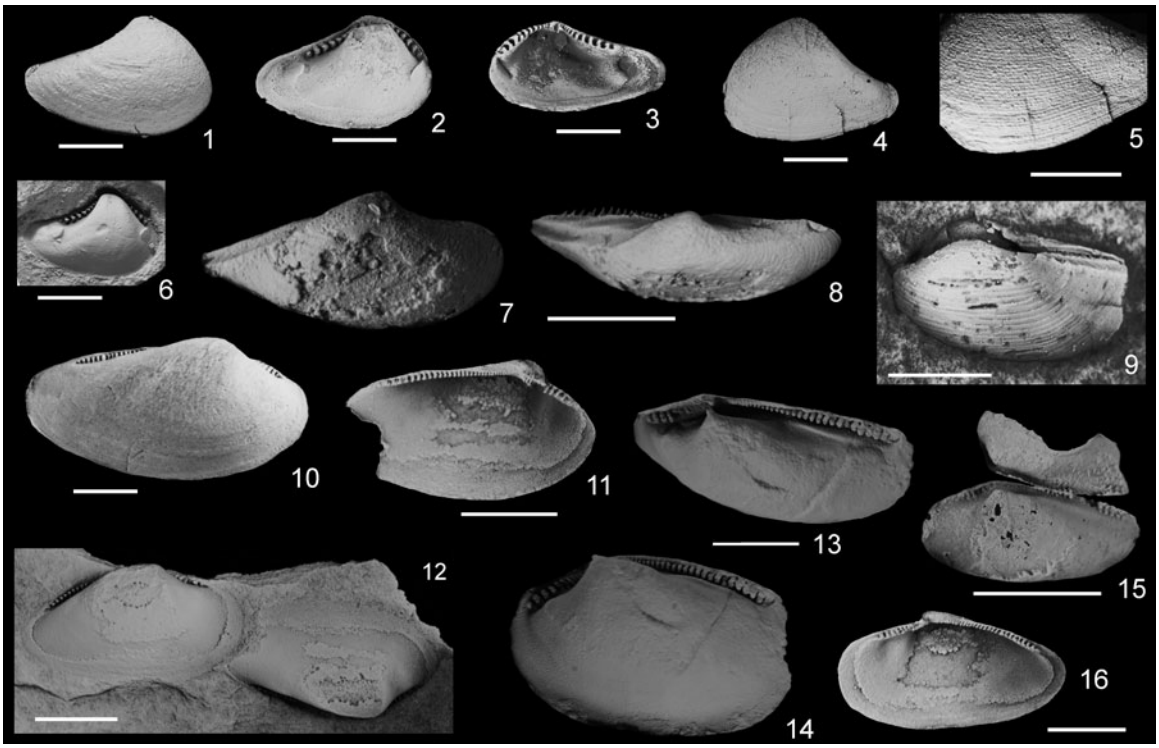


Figure 6. (**1–6**) *Praesaccella ovum* (J. de C. Soweby), (**1–3**) MPEF-PI 6577-1, right valve, (**1**) latex cast of lateral external view, (**2, 3**) internal mold and its latex cast (slightly tilted to show resilifer), (**4, 5**) MPEF-PI 6578, lateral view and detail of ornamentation of latex cast of left valve; (**6**) MPEF-PI 6571, right valve internal mold. (**7–9**) *Phaenodesmia*? *piatnitzkyi* new species, (**7, 8**) MPEF-PI 3004, right valve latex cast in lateral and dorsal views, (**9**) MPEF-PI 6488, incomplete specimen with valves closed, showing carina and ornamentation. (**10–16**) *Palaeoneilo*? *patagonidica* (Leanza), (**10**) lectotype, MLP 6251a, internal mold of right valve, from Piedra Pintada, Neuquén, (**11, 12, 16**) MPEF-PI 3357, latex casts (**11, 16**) and internal mold (**12**) of left and right valves from probably the same individual; (**13, 14**) MPEF-PI 2939, right valve internal mold, (**13**) dorsal views to show muscle scars, and (**14**) lateral view; (**15**) MPEF-PI 2845, internal mold of juvenile specimen with valves open in butterfly position. Scale bars = 5 mm.

variability regarding this character (Seilacher, 1972). Nevertheless, species of *Ryderia* with an ornamentation pattern similar to the material from Chubut are few.

The most similar species is *Ryderia texturata* (Terquem and Piette, 1865), from Rhaetian to Toarcian beds of England, Ireland, Germany, and France, and probably also Caucasus and Japan (Terquem and Piette, 1865, pl. 11, figs. 5–7; Tate, 1870a, pl. 26, pl. 12; 1870b, pl. 1, fig. 5; Tate and Blake, 1876, pl. 12, fig. 8, pl. 13, fig. 4; ?Pcelincev, 1937, pl. 3, fig. 8; ?Hayami, 1961, pl. 16, fig. 1; Hodges, 2000, pl. 3, figs. 5, 8–11, 13–17, text-figs. 46, 47; Aberhan et al., 2011, pl. 1, fig.7). This species has undulose vertical ornament on the rostrum, but only commarginal striae on the anterior part of the shell. *Ryderia doris* (d´Orbigny, 1849), often occurring at the same localities and levels, has a similarly long-rostrate shape, but is ornamented by fine commarginal striae only (Goldfuss, 1837, pl. 125, fig. 11, as *Nucula complanata*; d´Orbigny, 1849, p. 253; Chen, 1982, pl. 1, figs. 8, 9; Pedersen, 1986, pl. 6, fig. A; Hollingworth et al., 1990; Hodges, 2000, pl. 3, figs. 1–4, 6, 7 and references therein; Aberhan et al., 2011, pl. 1, figs. 5, 6).

Another very closely related taxon is *R. vexillata* (Marwick, 1953, p. 88, pl. 10, fig. 7; see also Trechmann, 1923, pl. 15, fig. 5), from the Aratauran (Early Jurassic) of New Zealand. This species differs from *R. tehuelchana* n. sp. by having a posterior ridge extending from the umbo to the ventral end of the rostrum, and by details of the ornamentation pattern, especially on the rostrum, which is smooth.

The only previous certain record of the genus from South America corresponds to a specimen identified as *Ryderia* sp. nov.? from the early Norian of the Biobío region, Chile (Pérez-Barría, 2004, 2005), which is an internal mold of a left valve with a shape similar to the species here described, but without any trace of ornamentation. Although the description of the Chilean material remains unpublished, the material was examined in Concepción University, Chile.

The Triassic Peruvian *Ryderia*? *oxyrhyncha* (Jaworski, 1922, p. 114, pl. 4, fig. 7) has a shorter rostrum and a different ornamentation pattern. *Nuculana divaricata* Zapfe, 1967 (pl. 2, fig. 1) from the Late Triassic of Austria, has a similar ornament pattern to *R. tehuelchana* n. sp., but the shell has a much shorter rostrum, and probably does not belong to *Ryderia*. On the other hand, *Nuculana curvirostris* Alencaster, 1961 (p. 11, pl. 1, figs. 5, 6) from the Carnian of Sonora, Mexico, has a similarly long-rostrate shape and size, but it is ornamented only by regular commarginal lines.

Ryderia sp. A (Aberhan, 1998, pl. 1, fig. 8), from the Late Pliensbachian of the Stikinia Terrane, western Canada, has a much shorter rostrum and its external shell surface is unknown. The shell ornamentation and shape of the rostrum are also very poorly known in *Ryderia kenyana* Cox (1965, pl. 1, fig. 6) from the Toarcian of Kenya.

Costinuculana magharensis Ayoub-Hanna et al., 2017 (figs. 4.1–4.9, 5.1–5.21; see also Abdelhady and Fürsich, 2014, fig. 6A, 6B), from the Bathonian of Sinai (Egypt), has

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Table 7. Measurements (in mm) of *Ryderia tehuelchana* new species. * = incomplete specimen, Im: internal mold.

MPEF-PI	L	H	AL	nAT	nPT	W
2852	16.6*	8.1	7.0			
2862	18.6 (Im)	10.0	7.1 (Im)	13	20	4.6
2976	30.5*	13.6				
2983	13.5*	6.8	5.0			
3001	28.6	9.1	8.1	12*		
3145	24.6	8.0				
3358		9.5	8.1	17		
3363	23.3	8.2	8.2			
3887	25.6*	9.5	6.9			
3890	29.9*	9.0*		13		
6494	27.0	11.3	8.3			
6552-1	21.0	10.3	7.5			
6572*	27.5	11.0	8.4	14+	15+	
6573	21.8*	9.4	7.1		14+	
6590	13.6	8.6	5.7	12	13	

thicker and more globose shells, shorter than those of *R. tehuelchana* n. sp., and differs by its strong oblique posterior ribs, which are asymmetrical in cross-section and may bifurcate ventrally.

Ryderia guangdongensis (Zhang in Zhang et al., 1977), the type species of *Teinonuculana*, from the latest Triassic to Early Jurassic of China (see Zhang et al., 1977, pl. 1, figs. 13–15; Chen et al., 1983, pl. 2, figs. 1–2; Chen, 1987, pl. 1, figs. 2, 8, 9 under several specific names; Yin and McRoberts, 2006, figs. 3.1–3.7, 3.8a), has a narrower rostrum and a posterior carina.

Several living species referred to *Nuculana* have a long rostrum and live as shallow burrowers, such as *Nuculana extenuata* (Dall, 1897); see Coan et al. (2000, pl. 6).

Ryderia tehuelchana n. sp. was most probably a fast shallow burrower, as proposed for *R. texturata* and *R. doris* from Europe by Hodges (2000, p. 45), who suggested that in life the tip of the rostrum most probably was just below the sediment surface. Divaricate ornamentation is present on the anterior part of the shell of several bivalves, many of which are very active burrowers, such as some nuculoids and tellinoids. This feature was given a high systematic significance by some authors (Chen et al., 1983; Hautmann et al., 2011), but others regarded this as a very variable character (e.g., Seilacher, 1972; Squires and Saul, 2006). *Ryderia texturata* (which has oblique ribs in part of the shell) is frequently found in association with similarly shaped specimens only ornamented by fine commarginal striae (usually referred to *R. doris*, see for instance Hodges, 2000; Aberhan et al., 2011), and internal molds cannot be undoubtedly referred to one of them. For this reason, Hodges (2000, p. 46) argued that perhaps this difference reflects intraspecific variation instead.

Family Malletiidae Adams and Adams, 1858

Remarks.—Malletiidae have an external ligament, resilium absent or small, submarginal; hinge teeth paleotaxodont; shells porcelaneous, not nacreous; shells generally posteriorly extended; no permanent dorsoposterior shell gape (Carter et al., 2015); sculpture absent. *Phaenodesmia* and the problematic genus *Palaeoneilo* are placed within this group by most authors.

Genus *Phaenodesmia*? Bittner, 1894

Type species.—*Phaenodesmia klipsteiniana* Bittner, 1894, p. 188 (see also Bittner, 1895, p. 145), from the Carnian of the Alps, by subsequent designation by Diener, 1923, p. 156.

Remarks.—The species here described extends the previously known stratigraphic range of the genus (Anisian to Rhaetian, see discussion in Ros et al., 2014) well into the Early Jurassic. Most of the Jurassic species referred to *Phaenodesmia* by Borissjak (1904) are nuculanid taxa. *Phaenodesmia* was originally diagnosed by Bittner as a nuculid with external ligament having medially placed prosogyrous umbones. During the Middle and Late Triassic the genus had a relatively wide geographic distribution in the Tethys and circum-Pacific areas, including South America (Jaworski, 1922 ; Körner, 1937; Nielsen, 2005).

Rostrate Jurassic species have usually opisthogyrous umbos and are referred to *Nuculana* Link, distinguished from *Dacryomya* Agassiz by its longer rostrum and presence of ridges bordering the escutcheon (Hodges, 2000, p. 21). Nevertheless, some species are imperfectly known and particularly difficult to identify, and could belong to *Phaenodesmia* instead.

Phaenodesmia? *piatnitzkyi* new species
Figures 6.7–6.9, 7.7, 7.8

Holotype.—MPEF-PI 3004, external/internal mold of an almost complete isolated right valve.

Diagnosis.—Nuculanoid shell with wide prosogyrate subcentral umbo and clearly limited escutcheon; rostrum limited by sharp posterior carina and sulcus, ornamented by commarginal, closely spaced regular threads.

Occurrence.—Aguada Loca, Tehuelches Department (sample levels AL39, AL40), Pampa de Agnia, Paso de Indios Department (sample levels PA06, PA07), Chubut Province (Fig. 2).

Description.—Shell small (~1 cm long), inequilateral, tear-shaped in lateral view, rostrate, with wide but low prosogyrate umbo and clearly delimited long and narrow escutcheon. Shell longer than high. Posterior end ventral of mid-height. Shell moderately inflated, with maximum width near mid-length. Umbo placed slightly anterior to mid length. Anterior margin evenly rounded, ventral margin gently convex, postero-dorsal margin nearly straight. Relatively sharp posterior carina from umbo to end of rostrum, accompanied by a sulcus on its dorsal side, which is deeper posteriorly. Rostrum short.

Dentition paleotaxodont, only posterior series of convexodont teeth is partially seen in the specimen, on a long dorsally concave series. There are at least 15 narrow chevron-shaped teeth, which gradually increase in size posteriorly and in dorsal view point to the umbo. Ligamental and muscle characters unknown. Shell thin, ornamented by commarginal, closely spaced, regular threads. The commarginal threads have steep dorsal slopes and gentle ventral slopes, and some of them

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

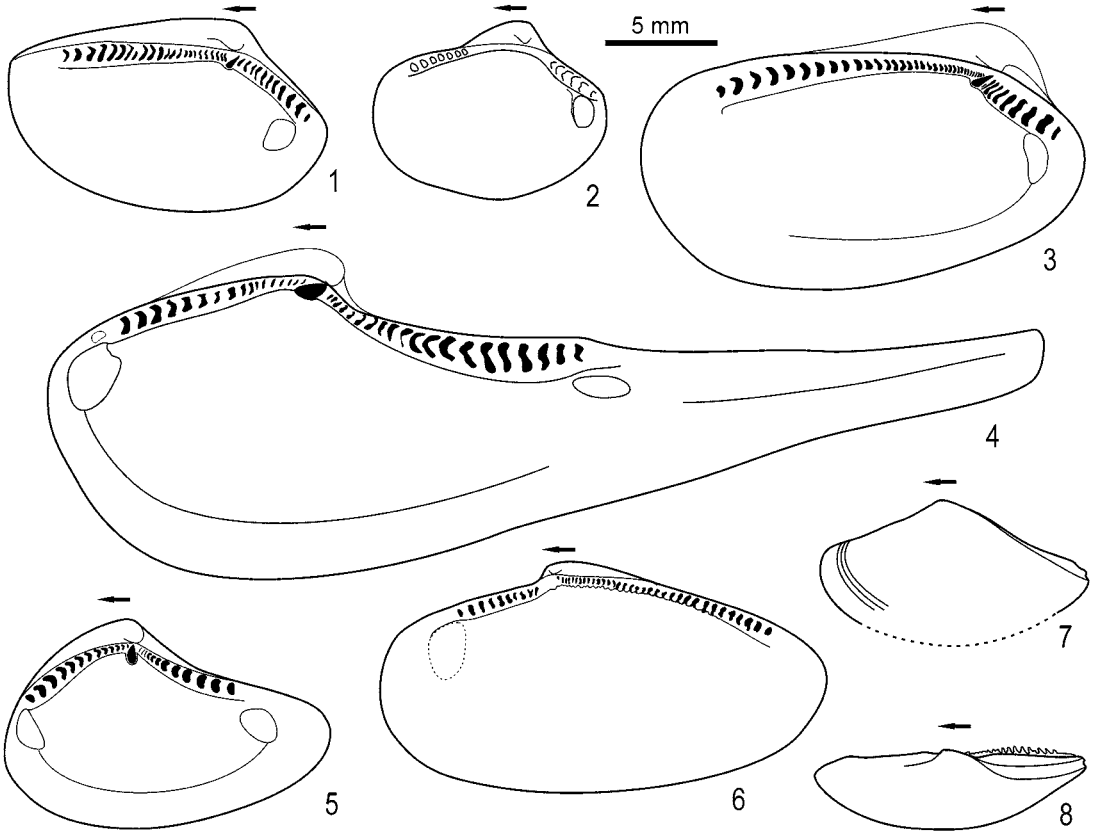


Figure 7. Sketches of right valves showing hinge. (**1**) *Palaeonucula feruglioi* new species, internal view based on specimens MPEF-PI 3897 and 3898; (**2**) *Palaeonucula* sp., internal view based on specimen MPEF-PI 2934; (**3**) *Palaeonucula*? sp., internal view based on specimens MPEF-PI 2978, 6485 and 5765; (**4**) *Ryderia tehuelchana* new species, internal view based on specimens MPEF-PI 3001 and MPEF-PI 2862; (**5**) *Praesaccella ovum* (J. De C. Sowerby), based on specimen MPEF-PI 6577-1; (**6**) *Palaeoneilo*? *patagonidica* (Leanza), internal view based on specimen MPEF-PI 3357; (**7, 8**) *Phaenodesmia*? *piatnitzkyi* new species, dorsal and external view based on specimen MPEF-PI 3004. All to the same scale, scale bar = 5 mm.

become scaly when reaching the carina (Fig. 6.9). Escutcheon smooth, with a shallow and short postumbonal slit, which may correspond to an external ligament.

Etymology.—Dedicated to Alejandro Piatnitzky (1879–1959), who made early comprehensive geological surveys of northern Patagonia for YPF (Yacimientos Petrolíferos Fiscales).

Materials.—Six specimens preserved as internal or external molds, MPEF-PI 3004 (holotype), 6455, 6458, 6464, 6478, 6488.

Measurements.—Holotype: L = 12.2 mm; H = 6.5 mm.

Remarks.—Among Mesozoic protobranchs, the Chinese Norian genus *Eleganuculana* Chen and Yang (1983) has prosogyrous umbones, but it differs from the material here described by its short inflated shells with strong commarginal regular costae, and a wide truncated, non-rostrate, posterior margin limited by a carina and sulcus.

Prosogyrate umbos are very rare in rostrate shells (see Echevarría et al., 2017). This species is referred to *Phaenodesmia*? because it has prosogyrate umbos, which distinguish it from other rostrate Jurassic protobranchs, usually referred to *Nuculana* or *Praesacella*. This species is different from *Dacryomya* species by its prosogyrate umbos and by having a conspicuous posterior carina.

Phaenodesmia peruana Jaworski (1922, p. 116, pl. 5, figs. 1–3), from the Peruvian Triassic, has a similar shape, but the umbones are more anteriorly placed than in the species from Chubut; it also has a less sharp carina without sulcus. The other Peruvian material referred to *Phaenodesmia*, described by Körner (1937, p. 176, pl. 11, fig. 10) as *P.* sp., is less rostrate and lacks a carina.

Phaenodesmia? *piatnitzkyi* n. sp. can be compared with the type species, *P. klipsteiniana* Bittner (1895, pl.18, fig. 12) and with *Phaenodesmia laubeana* Bittner (1895, pl. 18, fig. 15; Broili, 1904, pl. 24, fig. 15), from the European Late Triassic, but these two species have more anterior umbones and a less-developed posterior sulcus.

This species differs from *Ryderia tehuelchana* n. sp., from the same levels and locality, by its prosogyrate umbos, short rostrum, and commarginal ornamentation.

Several living nuculanid species have a posterior carina and sulcus comparable to the species here described, for instance *Nuculana minuta* (Müller, 1776); see Coan et al. (2000, pl. 6); and especially those referred to the subgenus *Costelloleda*, such as *N.* (*C.*) *costellata* (G.B. Sowerby I, 1833; see Coan and Valentich-Scott, 2012, pl. 22), but they have low opisthogyrate umbos and compressed shells with stronger commarginal

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

sculpture. *Saccella* species have a well-defined posterior keel and a shallow posterior sulcus—see for instance *S. impar* (Pilsbry and Lowe, 1932) in Coan and Valentich-Scott (2012, pl. 25)—and they are also comparable with the species here described in inflation and position of posterior end in relation to midline, but they bear an anterior keel or fold which is lacking in our material.

Genus *Palaeoneilo*? Hall and Whitfield, 1869

Type species.—*Nuculites constricta* Conrad, 1842, p. 249, from the Middle Devonian of New York State (see McAlester, 1968; see comments and synonymy in Damborenea, 1987a, p. 53–54; Hodges, 2000, p. 27; and Ros et al., 2014).

Remarks.—There is a long standing and yet unresolved discussion about the generic affiliation of elongate compressed Mesozoic shells with long, apparently uninterrupted series of taxodont teeth, such as the species described below, and most authors (e.g., Damborenea, 1987a; Hodges, 2000; Wasmer et al., 2012) followed Borissjak (1904) and Cox (1937) in referring them to *Palaeoneilo* Hall and Whitfield, 1869, a genus typified by a Devonian species. Nevertheless, recognition of *Palaeoneilo* in Mesozoic beds (Cox, 1937), and its relationships with *Mesosaccella* Chavan, 1946 was never satisfactory, especially since the type species of *Palaeoneilo* (*Nuculites constricta* Conrad, 1842, p. 249, from the Middle Devonian of New York State; see McAlester, 1968) is very poorly known. Wasmer and Hautmann (in Wasmer et al., 2012) pointed out that Triassic species referred to *Palaeoneilo* lack overlap of teeth rows, and also lack a posterior shell constriction, as is characteristic of Paleozoic species. Other authors prefer to refer Mesozoic species to *Mesosaccella* without further discussion, though admitting that this last genus has become a "bucket taxon" (see for instance Duff, 1978; Hryniewicz et al., 2014).

Some of the Triassic malletiids previously referred to *Palaeoneilo* were separated as new genera, and should be discussed in this context. Kurushin (in Dagys and Kurushin, 1985) proposed the new genus *Lapteviella* for small elongated compressed shells previously referred to *Palaeoneilo*, based on material from the Middle Triassic of Siberia. More recently, very large shells with a cuneate outline from the Norian of Yunnan (China), also previously referred to *Palaeoneilo*, were assigned to the new genus *Yongshengia* by Chen and Stiller (2008).

The presence or absence of resilifer is one of the key discussion points, yet in most Mesozoic species this character is imperfectly known. Hinge features were well illustrated by Moberg (1888, pl. 1, fig. 49b) and Troedsson (1951, text-fig. 39) on a right valve of *Palaeoneilo bornholmiensis* (Seebach, 1865) from the Pliensbachian of Sweden; and by Borissjak (1904, text-fig. 1) on a left valve of *Palaeoneilo amygdala* Borissjak, 1904 from the late Jurassic of Russia. These specimens have a continuous series of taxodont teeth, no ligament pit below the umbo, and a shallow furrow along the posterior hinge margin, interpreted as the attachment of an external ligament. Carter (1990) observed that *P. elliptica* (Goldfuss, 1837) has a very small resilifer on right valves only, and this was also reported for adult shells of the Late Triassic genus *Yongshengia* by Chen and Stiller (2008, p. 362).

For the reason stated above, it seems inappropriate to continue using *Palaeoneilo* for Mesozoic species, but the subject cannot be settled without a thorough revision, which is well beyond the possibilities of this paper, thus we prefer to refer the species of this group to *Palaeoneilo*? rather than proposing a new generic taxon for them. The shell features of the species here described do not fit either into the broad diagnosis of *Mesosacella* (Chavan, 1946, p. 197) provided by Duff (1978, p. 27) because they lack the depression or fossette beneath the umbones between anterior and posterior rows of teeths, which are gently concave in our material. This gap separating the taxodont dentition series is also a key character of the genus *Malletia* des Moulins.

Palaeoneilo? *patagonidica* (Leanza, 1942)
Figures 6.10–6.16, 7.6

1942 *Nucula patagonidica* Leanza, p. 151; pl. 1, figs. 1, 2, 4 (non fig. 3).
1966 *Nucula patagonidica* Leanza; Levy, p. 237.
1980 *Nuculoma patagonídica* [sic]; Franchi and Page, p. 217.
1987a *Palaeoneilo patagonidica* (Leanza); Damborenea, p. 54; pl. 1, figs. 1–3; text-fig. 6.
1996 *Palaeoneilo patagonidica* (Leanza); Damborenea, p. 158.
2012 *Palaeoneilo*? sp.; Pagani et al., p. 413, fig. 3.b.

Lectotype.—MLP 6251a, an internal mold of a right valve, designated by Damborenea (1987a, p. 54), from Pliensbachian beds at Subida a Sañicó, Neuquén. This specimen was figured by Leanza (1942, pl. 1, fig. 1) and Damborenea (1987a, pl. 1, fig. 1), and here (Fig. 6.10).

Occurrence.—New collections from Aguada Loca (sample levels AL35-36, AL39), Pampa de Agnia (sample levels PA01, PA06), and Betancourt (sample level Bet 33); also from Lomas de Plate (Piatnitzky collection), and probably Pocitos de Quichaura (collection Franchi and Page).

Description.—Shell ovally elongated in shape, compressed to only moderately inflated, inequilateral, with low umbones. Shell appears to have been thin, and ornamented only by faint commarginal growth lines. The hinge plate is narrow, and the numerous teeth are small. Adductor muscle scars not impressed, pallial line entire.

Materials.—Twenty-three right and left valves preserved as internal or external molds: MPEF-PI 2845, 2851, 2893, 2939, 2982, 2984?, 3008, 3357, 3370, 3896, 5764, 5782, 6468, 6490, 6491, 6551, 6558, 6559, 6576, 6579, 6587; some specimens collected by Piatnitzky (MLP18190, 29246 to 29248). The material listed by Levy (1966, p. 237) and by Franchi and Page (1980, p. 217) from the Pampa de Agnia region, could not be located in the SNGM collections at Buenos Aires.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Measurements.—See Table 8.

Remarks.—This species was already mentioned from Chubut by Levy (1966, p. 237) based on material collected by E. Barreneche, and by Damborenea (1987a, p. 54) on the basis of material collected by Piatnitzky. Specimens from Chubut are usually preserved as internal molds of left and right isolated valves, only a few external molds are available. The reference to *Nuculoma patagonídica* by Franchi and Page (1980, p. 217) from Quichaura (E in Fig. 1) probably belongs here, but the material could not be located at SNGM. The specimens from Chubut show great variability in shell shape, but they agree with the known variability within *Palaeoneilo*? *patagonidica* (Leanza).

Palaeoneilo? *patagonidica* was described in detail by Leanza (1942, p. 151–152; pl. 1, figs. 1, 2, 4) and Damborenea (1987a, p. 54–56, pl. 1, figs. 1–3; text-fig. 6), where comparisons with similar species were made. This species was regarded as a junior synonym of *Palaeoneilo*? *elliptica* (Goldfuss, 1837) by Hodges (2000, p. 28), but is here maintained as a different taxon. According to Hodges (2000), the widespread Carnian to Pliensbachian species *Palaeoneilo*? *elliptica* (Goldfuss) had a very variable shell shape with anteriorly placed umbos, but is characterized by a set of 10 anterior teeth and 22 posterior teeth, and a shallow pallial sinus. Well preserved specimens from Chubut have up to 13 anterior teeth but always more than 25 posterior teeth, and the pallial line is not visible.

The species here described has a shell form and hinge comparable to *Malletia pseudopraecursor* Kurushin (in Dagys and Kurushin, 1985, pl. 5, figs. 5–8), from the Siberian Triassic, but it differs for having a dorsally convex hinge line and narrower umbones.

The type species of *Lapteviella*, *L. prontchistshevi* Kurushin (in Dagys and Kurushin, 1985, pl. 6, fig. 9, pl. 7, figs. 1–6), from the Siberian Anisian, has a narrower posterior region of the shell and a straight posterior hinge line. On the other hand, Late Triassic shells from Chile and Argentina referred to *P. elliptica* (Cecioni and Westermann, 1968) by Damborenea in Damborenea and Manceñido (2012) have a more rounded posterior margin than the material here described.

The species *Yongshengia cuneata* (Chen in Ma et al., 1976), from the Late Triassic of Yunnan (China) has a superficial similarity of shell shape with the Argentine species, but it reaches a much larger size, has far more numerous teeth, and its shell is very thick, with two orders of commarginal and faint radial ornamentation (Chen and Stiller, 2008, figs. 3–5).

Table 8. Measurements (in mm) of *Palaeoneilo*? *patagonidica* (Leanza). * = incomplete specimen.

MPEF-PI	L	H	AL	nAT	nPT
2845	8.5		6.0	24+	
2851	17.2	8.1	5.9		
2939-1	16.3	9.8	11.2	23+	11
2982-1	14.9	7.4	6.4		
3008	15.1	6.3*	5.0		
3357	14.1	8.3	4.7	13	33
6468	10.3	5.8	3.6		
6576*	11.1	7	3.4		20+
6579	12.3	8.4	5		
6587	14.3	9.1	4.4	8+	15+

Paleoecology

Protobranch bivalves are restricted to normal marine environments, and due to their detritivorous feeding habits they only live in organic-rich bottoms as very active shallow burrowers. Living protobranchs are diverse in a variety of marine settings, but especially in high latitude regions and deep waters (Allen, 1978; Whittle et al., 2012). In littoral environments, the preferred type of substrate is variable depending on species (Allen, 1954).

A similar habit was inferred for extinct species, supported by taphonomic evidence. The protobranch diversity at some of the Chubut localities is equivalent to that recorded by Pedersen (1986) in Early Jurassic mudstones from Denmark, and includes both very active burrowers that fed from the sediment while moving (e.g., *Palaeonucula*, *Palaeoneilo*?) and very shallow burrowers that remain stationary once in place (e.g., *Praesaccella*, *Ryderia*, *Phaenodesmia*?).

According to Hodges (2000) the species of *Ryderia*, for instance, were fast burrowers, living stationary with the tip of the long rostrum just below the sediment surface, and most probably fed from the sediment surface. In Chubut, Early Jurassic protobranch records are concentrated in localities along the southern part of the basin, especially Aguada Loca and Betancourt (Fig. 1; Table 2). Some levels (AL35 + 36 and AL39) are particularly rich both with regard to abundance and diversity, suggesting optimum conditions of bottom grain-size and organic contents.

It is interesting to note that in Chubut the beds with protobranch bivalves also contain a low diversity invertebrate fauna, including other bivalves, ammonoids, gastropods, and serpulids (Table 2). Conspicuous bivalves of this recurrent association are (apart from the protobranchs): *Kolymonectes weaveri* Damborenea, 1998, *Parainoceramya apolo* (Leanza, 1942), *Agerchlamys wunschae*? (Marwick, 1953), and *Grammatodon costulatus* (Leanza, 1942), with occasional *Pseudolimea* sp., *Praechlamys* sp., trigoniids, astartids and lucinids. The most abundant elements are either free epifaunal or shallow infaunal, and the proportion of detritivorous vs. suspensivorous bivalves is high. This association can be closely compared with Biofacies B, recognized for the Early Jurassic beds in Piedra Pintada (Damborenea et al., 1975), which is the only region of the Neuquen Basin s.s. where protobranch bivalves are common, although less diverse than in Chubut.

Paleobiogeography

Most of the species described belong to cosmopolitan or nearly cosmopolitan genera and can be compared to species from other regions. Of special interest is the new species referred to *Ryderia*, a genus that was only known from South America for the Late Triassic, from a doubtfully referred species from Peru (Jaworski, 1922) and an unpublished record from southern Chile (Pérez-Barría, 2004, 2005). We also include in this genus a species from New Zealand previously referred to *Nuculana*, *R. vexillata* (Marwick), which, together with the Chilean record just mentioned and the species from Chubut here described, point to high paleolatitude abundance and diversity between Rhaetian and Toarcian times on both hemispheres for this widely distributed genus, which was rare in the Tethys s.s.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

From the paleobiogeographical point of view, this revision of Protobranchia confirms that these bivalves were relatively more diverse in Chubut than in Neuquén during late Pliensbachian–early Toarcian times (Table 1). Only two species were described from northern Chile (Aberhan, 1994), four species are known from the southern areas of the Neuquén Basin, and seven species are here described from Chubut, belonging to the families Nuculidae, Nuculanidae, Polidevciidae, and Malletiidae. At the species level, this is a significant trend for the SE Paleo-Pacific (Damborenea and Echevarría, 2015, fig. 6E), opposed to the general latitudinal gradient of decreasing diversity towards higher latitudes shown by most other bivalve groups. It is interesting to note that this trend is known at a global level for living Nuculanoidea (Crame, 2000; Roy et al., 2000) and for Late Jurassic protobranchs (Crame, 2002), and thus our data suggest a sustained biogeographic pattern of very old origin.

Acknowledgments

The Museo Paleontológico Egidio Feruglio (MEF) technical staff, L. Reiner, P. Puerta, L. Canessa and E. Ruigomez, efficiently aided during field-work, specimen preparation and rubber casts. The thorough revisions by K Hryniewicz, P. Hodges and S. Schneider are greatly acknowledged. This research was financed by several grants from CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina), grants PIP 112-200801-01567 and 112-201101-01088; and ANPCyT (Agencia Nacional de Promoción Científica y Tecnológica, Argentina), projects PICT 33080 and PICT 2011-1589. We also thank MEF for field financial support and logistic facilities.

References

Abdelhady, A.A., and Fürsich, F.T., 2014, Macroinvertebrate palaeocommunities from the Jurassic succession of Gebel Maghara (Sinai, Egypt): Journal of African Earth Sciences, v. 97, p. 173–193.

Aberhan, M., 1994, Early Jurassic Bivalvia of northern Chile. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia: Beringeria, v. 13, p. 1–115.

Aberhan, M., 1998, Early Jurassic Bivalvia of western Canada. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia: Beringeria, v. 21, p. 57–150.

Aberhan, M., 2004, Early Jurassic Bivalvia of northern Chile. Part II. Subclass Anomalodesmata: Beringeria, v. 34, p. 117–154.

Aberhan, M., Scholz, A., and Schubert, S., 2011, Das Ober-Pliensbachium (Domerium) der Herforder Liasmuldo—Teil 3. Taxonomie und Paläoökologie der Bivalvia aus der Amaltheenton-Formation (Unterjura) der Herforder Liasmulde: Geologie und Paläontologie in Westfalen, v. 80, p. 61–109.

Adams, H., and Adams, A., 1858, The Genera of Recent Mollusca, arranged according to their organization: London, Van Voorst, v. 1, 484 p.; vol. 2, 661 p.; vol. 3, 136 p.

Alencaster de Cserna, G., 1961, Paleontología del Triásico superior de Sonora. Parte III. Fauna fósil de la Formación Santa Clara (Cárnico) del Estado de Sonora: Paleontologia Mexicana, v. 11, p. 1–44.

Allen, J.A., 1954, A comparative study of the British species of *Nucula* and *Nuculana*: Journal of Marine Biological Association of the United Kingdom, v. 33, p. 457–472.

Allen, J.A., 1978, Evolution of the deep sea protobranch bivalves: Philosophical Transactions of the Royal Society of London B, v. 284, p. 387–401.

Ayoub-Hannaa, W.S., Abdelhady, A.A., and Fürsich, F.T., 2017, *Costinuculana magharensis* n. gen. n. sp. (Bivalvia, Nuculanidae) from the Middle Jurassic of Gebel Maghara, North Sinai, Egypt: Journal of Paleontology, v. 91, p. 434–443.

Beushausen, H.E.L., 1895, Die Lamellibranchiaten des rheinischen Devon mit Ausschluss der Aviculiden: Abhandlungen der Königlich Preussischen Geologischen Landesanstalt (neue Folge), v. 17, p. 1–514.

Bittner, A., 1894, Zur Kenntnis der Nuculiden und Arciden der Fauna von Sct. Cassian: Verhandlungen der Kaiserlich-Königlichen Geologischen Reichhsanstalt, v. 8, p. 186–191.

Bittner, A., 1895, Lamellibranchiaten der Alpinen Trias. I. Theil: Revision der Lamellibranchiaten von Sct. Cassian: Abhandlungen der Kaiserlich-Königlichen Geologischen Reichhsanstalt, v. 18, p. 1–236.

Blasco, G., Levy, R., and Nullo, F., 1979, Los ammonites de la Formación Osta Arena (Liásico) y su posición estratigráfica, Pampa de Agnia, Prov. del Chubut: 7° Congreso Geológico Argentino, Actas 2, p. 407–429.

Blasco, G., Levy, R., and Ploszkiewicz, V., 1980, Las calizas toarcianas de Loncopán, Departamento Tethuelches, Provincia del Chubur, República Argentina: 2° Congreso Argentino de Paleontología y Bioestratigrafía y 1° Congreso Latinoamericano de Paleontología (Buenos Aires, 1978), Actas 1, p. 191–200.

Borissjak, A., 1904, Die Pelecypoden der Jura-Ablagerungen im Europaeischen Russland. I. Nuculidae: Mémoirs du Comité Géologique St. Petersbourg, nouvelle série, v. 11, p. 1–49.

Bouchet, P., and Rocroi, J.P., 2010, Nomenclator of bivalve families with a classification of bivalve families by R. Bieler, J.G. Carter, and E.V. Coan: Malacologia, v. 52, p. 1–184.

Bradshaw, J.D., and Bradshaw, M.A., 1971, Functional morphology of some fossil palaeotaxodont bivalve hinges as a guide to orientation: Palaeontology, v. 14, p. 242–249.

Bradshaw, M.A., 1999, Lower Devonian bivalves from the Reefton Group, New Zealand: Memoir of the Association of Australasian Palaeontologists, v. 20, p. 1–171.

Broili, F., 1904, Die Fauna der Pachycardientuffe der Seiser Alp (Mit Ausschluss der Gastropoden und Cephalopoden): Palaeontographica, v. 50, p. 145–227.

Carter, J.G., 1990, Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia: Mollusca), *in* Carter, J.G., ed., Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends: New York, Van Nostrand Reinhold, v. 1, p. 135–296.

Carter, J.G., 2001, Shell and ligament microstructure of selected Silurian and Recent palaeotaxodonts (Mollusca: Bivalvia): American Malacological Bulletin, v. 16, p. 217–238.

Carter, J.G., Campbell, D.C., and Campbell, M.R., 2000, Cladistic perspectives on early bivalve evolution, *in* Harper, E.M., Taylor, J.D., and Crame, J.A., eds., The evolutionary biology of the Bivalvia: Geological Society Special Publication 177, p. 47–79.

Carter, J.G., Altaba, C.R., Anderson, L.C., Araujo, R., Biakov, A.S., Bogan, A.E., Campbell, D.C., Campbell, M., Chen, J., Cope, J.C.W., Delvene, G., Dijkstra, H.H., Fang, Z., Gardner, R.N., Gavrilova, V.A., Goncharova, I.A., Harries, P.J., Hartman, J.H., Hautmann, M., Hoeh, W.R., Hylleberg, J., Jiang, B., Johnston, P., Kirkendale, L., Kleemann, K., Koppka, J., Kříž, J., Machado, D., Malchus, N., Márquez-Aliaga, A., Masse, J-P., McRoberts, C.A., Middelfart, P.U., Mitchell, S., Nevesskaja, L.A., Özer, S., Pojeta, J., Jr., Polubotko, I.V., Pons, J.M., Popov, S., Sánchez, T., Sartori, A.F., Scott, R.W., Sey, I.I., Signorelli, J.H., Silantiev, V.V., Skelton, P.W., Steuber, T., Waterhouse, J.B., Wingard, G.L., and Yancey, T., 2011, A Synoptical Classification of the Bivalvia (Mollusca): University of Kansas Paleontological Contributions, v. 4, p. 1–47.

Carter, J.G., Harries, P.J., Malchus, N., Sartori, A.R., Anderson, L.C., Bieler, R., Bogan, A.E., Coan, E.V., Cope, J.C.W., Cragg, S.M., García-March, J.R., Hylleberg, J., Kelley, P., Kleemann, K., Kříž, J., McRoberts, C., Mikkelsen, P.M., Pojeta, J., Jr., Temkin, I., Yancey, T., and Zieritz, A., 2012, Part N, Revised, Volume 1, Chapter 31: Illustrated Glossary of the Bivalvia: Treatise Online (Kansas University Paleontological Institute) v. 48, 209 p.

Carter, J.G., Altaba, C.R., Anderson, L.C., Campbell, D.C., Fang, Z., Harries, P.J., and Skelton, P.W., 2015, The paracladistic approach to phylogenetic taxonomy: University of Kansas Paleontological Contributions, v. 12, p. 1–9.

Cecioni, G., and Westermann, G.E.G., 1968, The Triassic/Jurassic marine transition of coastal Central Chile: Pacific Geology, 1968, v. 1, p. 41–75.

Chavan, A., 1946, L´évolution des faunes marines de Mollusques dans le Nord-Ouest de l´Europe, de la fin du Crétacé a celle de l´Éocene: Bulletin de la Societé Géologique de France, ser. 5, v. 16, p. 193–212.

Checa, A., 2002, Fabricational morphology of oblique ribs in bivalves: Journal of Morphology, v. 254, p. 195–209.

Chen, J.H., 1982, Liassic bivalve fossils from Mount Jinji of Guangdong: Acta Palaeontologica Sinica, v. 21, p. 404–416.

Chen, J.H., 1987, Early Jurassic marine bivalves from Quangdong-Nanling district, southern China: Bulleting of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, v. 12, p. 23–94.

Chen, J., and Stiller, K., 2008, Two new Late Triassic nuculanoidean bivalve genera from north-west Yunnan, China: Neues Jahrbuch für Geologie und Paläontologie, v. 249, p. 357–370.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Chen, J., and Yang, S., 1983, *Eleganuculana*, new genus, and some other bivalves from the upper Triassic of Kangmar in Xizang: Acta Palaeontologica Sinica, v. 22, p. 355–358 (in Chinese with English summary).
Chen, J., Liu, L., and Lan, X., 1983, Veteranellinae, a new subfamily of Nuculanidae (Bivalvia), with the classificatory significance of ornamentations in Palaeotaxodonta: Acta Palaeontologica Sinica, v. 22, p. 616–627.
Coan, E.V., and Valentich Scott, P., 2012, Bivalve Shells of Western North America. Marine Bivalve Mollusks from Baja California to Northern Peru: Santa Barbara Museum of Natural History Monographs 6, 1258 p.
Coan, E.V., Valentich Scott, P., and Bernard, F.R., 2000, Bivalve Shells of Western North America. Marine Bivalve Mollusks from Arctic Alaska to Baja California: Santa Barbara Museum of Natural History Monographs 2, 764 p.
Conrad, T.A., 1842, Observations of the Silurian and Devonian systems of the United States, with descriptions of new species of organic remains: Journal of the Academy of Natural Sciences of Philadelphia, v. 8, p. 228–280.
Cortiñas, J.S., 1984, Estratigrafía y facies del Jurásico entre Nueva Lubecka, Ferrarotti y Cerro Colorado. Su relación con los depósitos coetáneos del Chubut central: Noveno Congreso Geológico Argentino, Actas 2, p. 283–299.
Cossmann, A.È.M., 1920, Rectifications de nomenclature: Revue Critique de Paléozoologie v. 24, p. 81–83.
Cox, L.R., 1936, The Gastropoda and Lamellibranchia of the Green Ammonite Beds of Dorset: Quarterly Journal of the Geological Society of London, v. 94, p. 456–471.
Cox, L.R., 1937, Notes on Jurassic Lamellibranchia. I. On the occurrence of the genus *Palaeoneilo* in the Jurassic of Great Britain: Proceedings of the Malacological Society of London, v. 22, p. 190–193.
Cox, L.R., 1940, The Jurassic Lamellibranch Fauna of Kuchh (Cutch): Memoirs, Geological Survey of India, Paleontologia Indica, ser. 9, v. 3, p. 1–157.
Cox, L.R., 1965, Jurassic Bivalvia and Gastropoda from Tanganiyka and Kenya: Bulletin of the British Museum of Natural History (Geology), Supplement 1, 213 p.
Cox, L.R., Newell, N.D., Branson, C.C., Casey, R., Chavan, A., Coogan, A.H., Dechaseaux, C., Fleming, C.A., Haas, F., Hertlein, L.G., Keen, A.M., LaRocque, A., McAlester, A.L., Perkins, B.F., Puri, H.S., Smith, L.A., Soot-Ryen, T., Stenzel, H.B., Turner, R.D., and Weir, J., 1969, Mollusca 6. Bivalvia, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology. Part N: Lawrence, Kansas, University of Kansas Press and Geological Society of America, v. 1, p. 1–489; v. 2, p. 490–952.
Crame, J.A., 2000, Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of Recent bivalve faunas: Paleobiology, v. 26, p. 188–214.
Crame, J.A., 2002, Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas: Paleobiology, v. 28, p. 184–207.
Dagys, A.S., and Kurushin, N.I., 1985, The Triassic Brachiopods and Bivalves in the North of the Central Siberia: Academy of Sciences of the USSR, Siberian Branch, Transactions, v. 633, 160 p. [in Russian]
Dall, W.H., 1889, On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group: American Journal of Science, ser. 3, v. 38, p. 445–462.
Dall, W.H., 1897, Notice of some new or interesting species of shells from British Columbia and the adjacent region: Bulletin of the Natural History Society of British Columbia, v. 2, p. 1–18.
Damborenea, S.E., 1987a, Early Jurassic Bivalvia of Argentina. Part I: Stratigraphical Introduction and Superfamilies Nuculanacea, Arcacea, Mytilacea and Pinnacea: Palaeontographica A, v. 99, p. 23–111.
Damborenea, S.E., 1987b, Early Jurassic Bivalvia of Argentina. Part II: Superfamilies Pteriacea, Buchiacea and part of Pectinacea: Palaeontographica A, v. 99, p. 113–216.
Damborenea, S.E., 1992, South American Jurassic bivalves, *in* Westermann, G.E.G., ed., The Jurassic of the Circum-Pacific: Cambridge, Cambridge University Press, p. 610–619.
Damborenea, S.E., 1993, Early Jurassic South American pectinaceans and circum-Pacific palaeobiogeography: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 100, p. 109–123.
Damborenea, S.E., 1994, Circum-Pacific correlation of Argentine Early and Middle Jurassic bivalve zones: Geobios, v. 27, Supplement 2, p. 141–147.
Damborenea, S.E., 1996, Palaeobiogeography of Early Jurassic bivalves along the southeastern Pacific margin: 13° Congreso Geológico Argentino y 3° Congreso de Exploración de Hidrocarburos (Buenos Aires) Actas 5, p. 151–167.
Damborenea, S.E., 1998, The Bipolar Bivalve *Kolymonectes* in South America and the Diversity of Propeamussiidae in Mesozoic Times, *in* Johnston, P.A., and Haggart, J.W., eds., Bivalves: An Eon of Evolution. Paleobiological Studies Honoring Norman D. Newell: Calgary, University of Calgary Press, p. 143–155.
Damborenea, S., 2002, Early Jurassic bivalves from Argentina. Part 3: Superfamilies Monotoidea, Pectinoidea, Plicatuloidea and Dimyoidea: Palaeontographica A, v. 265, p. 1–119.
Damborenea, S.E., and Echevarría, J., 2015, Palaeolatitudinal gradients along the southeastern Palaeopacific margin and the distribution of Early Jurassic bivalves: Volumina Jurassica, v. 13, p. 3–16.
Damborenea, S.E., and Manceñido, M.O., 2012, Late Triassic bivalves and brachiopods from southern Mendoza, Argentina: Revue de Paléobiologie, Spec. v. 11, p. 317–344.
Damborenea, S.E., Manceñido, M.O., and Riccardi, A.C., 1975, Biofacies y estratigrafía del Liásico de Piedra Pintada, Neuquén, Argentina: 1° Congreso Argentino de Paleontología y Bioestratigrafía (Tucumán), Actas 2, p. 173–228.
Damborenea, S.E., Echevarría, J., and Ros-Franch, S., 2013, Southern Hemisphere Palaeobiogeography of Triassic–Jurassic Marine Bivalves: Springer Briefs in Earth System Sciences, Dordrecht, Springer, 141 p.
Defrance, M.J.L., 1825, Nucule (Fossiles), *in* Dictionnaire des Sciences Naturelles: Strasbourg and Paris, F. G. Levrault, v. 35, p. 216–219.
Diener, C., 1923, Fossilium Catalogus I: Animalia. Pars 19: Lamellibranchiata triadica: Berlin, W. Junk, 257 p.
Douvillé, H., 1916, Les terrains secondaires dans le Massif de Moghara à l'Est de l'Isthme de Suez: Mémoire de l'Académie des Sciences, Paris, v. 54, p. 1–184.
Driscoll, E.G., 1964, Accessory muscle scars, an aid to protobranch orientation: Journal of Paleontology, v. 38, p. 61–66.
Duff, K.L., 1978, Bivalvia from the English Lower Oxford Clay (Middle Jurassic): The Palaeontographical Society (London), Monographs, v. 132, 137 p.
Echevarría, J., Damborenea, S.E., and Manceñido, M.O., 2017, Constructional morphology of the shell/ligament system in opisthogyrate rostrate bivalves: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 106, p. 221–227.
Fang, Z., Chen, J., Chen, C., Sha, J.Lan, X., and Wen, S., 2009, Supraspecific taxa of the Bivalvia first named, described, and published in China (1927–2007): The University of Kansas Paleontological Contributions (new series), v. 17, 157 p.
Fernández Garrasino, C., 1977, Contribución al conocimiento geológico de la zona comprendida entre Estancia Ferrarotti, Cerro Colorado y Cerrito Negro, Departamento Tehuelches, Provincia del Chubut: Revista de la Asociación Geológica Argentina, v. 32, p. 130–144.
Ferrari, S.M., 2013, New Early Jurassic gastropods from west-central Patagonia, Argentina: Acta Palaeontologica Polonica, v. 58, p. 579–593.
Ferrari, S.M., and Bessone, S., 2015, A new Early Jurassic marine locality from southwestern Chubut Basin, Argentina: Andean Geology, v. 42, p. 349–363.
Feruglio, E., 1934, Fossili Liassici della Valle del Rio Genua (Patagonia): Giornale di Geologia, Annali Reale Museo Geologiche di Bologna, ser. 2, v. 9, 64 p.
Feruglio, E., 1949, Descripción Geológica de la Patagonia: Buenos Aires, Dirección Geológica YPF, v. 1, 334 p.
Fletcher, H.O., 1945, A new genus *Glyptoleda* and a revision of the genus *Nuculana* from the Permian of Australia: Records of the Australian Museum, v. 21, p. 293–312.
Franchi, M.R., and Page, R., 1980, Los basaltos cretácicos y la evolución magmática del Chubut occidental: Revista de la Asociación Geológica Argentina, v. 35, p. 208–229.
Fürsich, F.T., and Werner, W., 1988, The Upper Jurassic Bivalvia of Portugal. Part I. Palaeotaxodonta and Pteriomorphia (Arcoida and Mytiloida): Comunicacoes dos Servicos Geológicos de Portugal, v. 73, p. 103–144.
Fürsich, F.T., Berndt, R., Scheuer, T., and Gahr, M., 2001, Comparative ecological analysis of Toarcian (Lower Jurassic) benthic faunas from southern France and east-central Spain: Lethaia, v. 34, p. 169–199.
Goldfuss, G.A., 1826–1844, Petrefacta Germaniae tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae Rhenanae Servantur quam alia Quaecunquae in Museis Hoenighusiano Muensteriano Aliisque Extant, Iconibus et Descriptionibus Illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der Angrenzender Länder unter Mitwirkung des Herrn Grafen Georg zu Münster: Düsseldorf, Arnz & Co., v. 1, 252 p. (1826–1833); v. 2, 312 p. (1833–1841); v. 3, 128 p. (1841–1844).
Gray, J.E., 1824, A supplement to the appendix of Captain Perry´s voyage for the discovery of a north west passage in the years 1819–1820, containing an account of the subjects of natural history. Appendix 10. Natural history shells: London, J. Murray, p. 211–246.
Hall, J., and Whitfield, R.P., 1869, Preliminary notice of the lamellibranchiata shells of the upper Helderberg, Hamilton and Chemung Groups with others from the Waverly sandstones, part 2: Albany, New York State Museum, 96 p.
Hautmann, M., Stiller, F., Cai, H., and Sha, J., 2008, Extinction-recovery pattern of level-bottom faunas across the Triassic-Jurassic boundary in Tibet: implications for potential killing mechanisms: Palaios, v. 23, p. 711–718.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Hautmann, M., Aghababalou, B., and Krystyn, L., 2011, An unusual Late Triassic nuculid bivalve with divaricate shell ornamentation, and the evolutionary history of oblique ribs in Triassic bivalves: Journal of Paleontology, v. 85, p. 22–28.
Hayami, I., 1961, On the Jurassic Pelecypod faunas in Japan: Journal of the Faculty of Sciences, University of Tokyo Sec. II, Geology, Mineralogy, Geogrphy, Geophysics, v. 13, p. 243–343.
Hayami, I., 1972, Lower Jurassic Bivalvia from the Environs of Saigon, *in* Kobayashi, T. and Toriyama, R., eds., Geology and Palaeontology of Southeast Asia 10: Tokyo, University of Tokyo Press, p. 179–230.
Herbst, R., 1966, La flora liásica del Grupo Pampa de Agnia, Chubut, Patagonia: Ameghiniana, v. 4, p. 337–349.
Hoare, R.D., Heaney, M.J., and Mapes, R.H., 1989, Bivalves (Mollusca) from the Imo Formation (Mississippian, Chesterian) of north-central Arkansas: Journal of Paleontology, v. 63, p. 582–603.
Hodges, P., 2000, The Early Jurassic Bivalvia from the Hettangian and Lower Sinemurian of south-west Britain: The Palaeontographical Society (London), Monographs, v. 614, 64 p.
Hollingworth, N.T.J., Ward, D.J., Simms, M.J., and Clothier, P., 1990, A temporary exposure of Lower Lias (Late Sinemurian) at Dimmer Camp, Castle Cary, Somerset, south-west England: Mesozoic Research, v. 2, p. 163–180.
Hryniewicz, K., Little, C.T.S. and Nakrem, H.A., 2014, Bivalves from the latest Jurassic-earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard: Zootaxa, v. 3859, p. 1–66.
Ivimey-Cook, H.C., Hodges, P., Swift, A., and Radley, J.D., 1999, Bivalves, *in* Swift, A. and Martill, D.M., eds., Fossils of the Rhaetian Penarth Group: London, The Palaeontological Association Field Guides to Fossils, v. 9, p. 83–127.
Jaitly, A.K., Fürsich, F.T., and Heinze, M., 1995, Contributions of the Jurassic of Kachchh, western India. IV. The bivalve fauna. Part 1. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia: Beringeria, v. 16, p. 147–257.
Jaworski, E., 1922, Die marine Trias in Südamerika: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band, 47, p. 93–200.
Keidel, J., 1917, Über das patagonische Tafelland, das patagonische Geröll und ihre Beziehungen zu den geologischen Erscheinungen im argentinischen Andengebiet und Litoral: Zeitschrift des Deutschen Wissenschanftlichen Vereins zur Kultur und Landeskunde Argentiniens, v. 5, p. 219–248; v. 6, p. 311–333.
Körner, K., 1937, Marine (Cassianer-Raibler) Trias am Nevado de Acrotambo (Nord-Peru): Palaeontographica A, v. 86, p. 145–237.
Korobkov, I.A., 1954, Spravochnik i metodicheskoe rukovodstovo po tretichnym molliuskam. Plastinchatozhabernye [Handbook and systematic guide to the Tertiary Mollusca. Lamellibranchia]: Leningrad, Gostoptekhizdat, 444 p. [in Russian]
Kuhn, O., 1935, Revision der Opalinuston (Dogger Alpha)-Fauna in Franken, mit Ausschluss der Cephalopoden: Palaeontologische Zeitschrift, v. 17, p. 109–158.
Kumpera, O., Prantl, F., and Růžička, B., 1960, Revision of the Nuculanidae from the Ostrava-Karviná District (Pelecypoda): Acta Musei Nationalis Pragae (serie B) Historia Naturalis, v. 16, p. 17–80.
Leanza, A.F., 1942, Los pelecípodos del Lías de Piedra Pintada, en el Neuquén: Revista del Museo de La Plata (n.s.) Paleontología, v. 2, p. 143–206.
Levy, R., 1966, Revisión de las trigonias de Argentina. I. Una nueva especie de *Myophorella* del Lías de Pampa de Agnia (Chubut), con consideraciones acerca de la presencia de Myophorellinae en Argentina: Ameghiniana, v. 4, p. 237–241.
Levy de Caminos, R., 1978, Descripción de material paleontológico procedente de la Hoja 45b, Sierra de Tepuel: Unpublished report, Servicio Geológico Nacional, 6 p. (Argentina).
Liu, C.-L., 1995, Jurassic bivalve palaeobiogeography of the Proto-Atlantic and the application of multivariate analysis methods to palaeobiogeography: Beringeria, v. 16, p. 3–123.
Ma, Q., Chen, J., Lan, X., Gu, Z., Chen, C., and Lin, M., 1976, Mesozoic lamellibranchs from Yunnan, *in* Nanjing Institute of Geology and Palaeontology, Academia Sinica, ed., Mesozoic Fossils from Yunnan: Beijing, Science Press, v. 1, p. 161–386. [In Chinese]
Mander, L., Twitchett, R., and Benton, M.J., 2008, Palaeoecology of the Upper Triassic extinction event in the southwestern UK: Journal of the Geological Society of London, v. 165, p. 319–332.
Marwick, J., 1953, Divisions and Faunas of the Hokonui System (Triassic and Jurassic): Palaeontological Bulletin, New Zealand Geological Survey, v. 21, 142 p.
Massaferro, G.I., 2001, El Jurásico temprano del cerro Cuche (Cordillera Patagónica del Chubut): estratigrafía y fósiles: Revista de la Asociación Geológica Argentina, v. 56, p. 244–248.
McAlester, A.L., 1968, Type species of Paleozoic Nuculoid Bivalve Genera: Geological Society of America, Memoir 105, 143 p.
Moberg, J.C., 1888, Om Lias i sydöstra Skåne: Sveriges Geologiska Undersökning Serie C, v. 99, p. 1–86.
Moore, D.R., 1977, Small species of Nuculidae (Bivalvia) from the tropical Western Atlantic: The Nautilus, v. 91, p. 119–128.
Müller, O.F., 1776, Zoologiae Danicae prodromus: seu Animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium: Hafniae, Typiis Hallageriis, 274 p.
Musacchio, E.A., 1975, Sobre algunas consideraciones estratigráficas acerca del Jurásico de Pampa de Agnia, Chubut: Revista de la Asociación Geológica Argentina, v. 30, p. 115.
Musacchio, E.A., 1981, Estratigrafía de la Sierra Pampa de Agnia, en la región extraandina de la Provincia del Chubut, Argentina: 8° Congreso Geológico Argentino (Buenos Aires) Actas 3, p. 343–357.
Musacchio, E.A., and Riccardi, A.C., 1971, Estratigrafía principalmente del Jurásico, en la Sierra de Agnia, Chubut, República Argentina: Revista de la Asociación Geológica Argentina. v. 26, p. 272–273.
Nielsen, S.N., 2005, The Triassic Santa Juana Formation at the lower Biobío River, south central Chile: Journal of South American Earth Sciences, v. 19, p. 547–562.
Nullo, F.E., 1983, Descripción Geológica de la Hoja 45c, Pampa de Agnia, Provincia de Chubut: Servicio Geológico Nacional (Argentina), Boletín 199, 94 p.
Oppel, A., 1856–1858, Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands: Jahrbuch Verein für Vaterländische Naturkunde Württemberg, v. 12 (1856), p. 121–556; v. 13 (1857), p. 141–396; v. 14 (1858), p. 129–291.
d´ Orbigny, A., 1849–1852, Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés: faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique, 1st ed.: Paris, Masson, v. 1, 394 p.; v. 2, 428 p.; v. 3, 387 p.
Pagani, A., Damborenea, S.E., Manceñido., M.O., and Ferrari, S.M., 2011, New Early Jurassic decapod crustacean from Patagonia (Chubut Province), Argentina: Paläontologische Zeitschrift, v. 85, p. 143–154.
Pagani, M.A., Manceñido, M.O., Damborenea, S.E. and Ferrari, S.M., 2012, The ichnogenus *Lapispira* from the Early Jurassic of Chubut, Patagonia, Argentina: Revue de Paléobiologie, Special Volume, v. 11, p. 409–416.
Patte, E., 1926, Études paléontologiques relatives a la géologie de l´est du Tonkin (Paléozoïque et Trias): Bulletin du Service Géologique de l´Indochine 15, p. 1–231.
Pcelincev, V., 1937, [The Jurassic Gastropoda and Pelecypoda of the USSR. 1. The Gastropoda and Pelecypoda from the Liassic and lower Dogger of the Tethys in the limits of the USSR (The Crimea and Caucasus)]: Paleontology of USSR Monographs, v. 48, 85 p. [in Russian]
Peck, R.L., Bailey, J.B., Heck, R.J., and Scaiff, N.T., 2009, X-ray CT scan as an aid to identification and description of a new bivalve species (Mollusca) from the Mississippian Bluefield Formation, southeastern West Virginia: Journal of Paleontology, v. 83, p. 954–961.
Pedersen, G.K., 1986, Changes in the bivalve assemblage of an early Jurassic mudstone sequence (the Fjerritslev formation in the Gassum 1 well, Denmark): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 53, p. 139–168.
Pelseneer, P., 1889, Sur la classification phylogénétique des Pélécypodes: Bulletin Scientifique de la France et de la Belgique, v. 20, p. 27–52.
Pérez, E., Aberhan, M., Reyes, R., and Hillebrandt, A. von, 2008, Early Jurassioc Bivalvia of northern Chile. Part III. Order Trigonioida: Beringeria, v. 39, p. 51–102.
Pérez-Barría, L.P., 2004, Estudio taxonómico de la fauna de invertebrados del Triásico del Biobío (VIII Región, Chile): una aproximación preliminar: Ameghiniana Suplemento Resúmenes, v. 41, p. 18R.
Pérez-Barría, L.P., 2005, Revisión taxonómica de la fauna de moluscos del Triásico del Biobío (VIII Región, Chile). Nuevas evidencias sobre las relaciones paleobiogeográficas entre Chile y Nueva Zelanda: 19° Congresso Brasileiro de Paleontologia e 6° Congresso Latino-Americano de Paleontología, CD-ROM/Resumos/Taxonomia e Sistematica/pdf, Aracaju, Sergipe, Brasil.
Perrot, C.J., 1961, Estudio geológico de las inmediaciones del paraje "El Molle" Departamento Tehuelches, Prov, de Chubut: Revista de la Asociación Geológica Argentina, v. 15, p. 53–79.
Piatnitzky, A., 1936, Estudio geológico de la región del rio Chubut y del rio Genua: Boletín de Informaciones Petroleras 13, no. 137, p. 83–118.
Piette, E., 1856, Notice sur les Grès d´Aiglemont et de Rimogne: Bulletin de la Societé Géologique de France, ser. 2, v. 13, p. 188–207.
Pilsbry, H.A., and Lowe, H.N., 1932, West Mexican and Central American mollusks collected by H. N. Lowe, 1929–31: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 84, p. 33–144.
Quenstedt, F.A., 1851–1852, Handbuch der Petrefaktenkunde, 1st Edition: Tübingen, Laupp & Siebeck, p. 1–528 (1851); p. 529–792 (1852).
Quenstedt, F.A., 1856–1857, Der Jura: Tübingen, Laupp & Siebeck, p. 1–368 (1856); p. 369–842 (1857).
Quenstedt, W., 1930, Die Anpassung an die grabende Lebensweise in der Geschichte der Solenomyiden, und Nuculaceen: Geologische und Paleontologische Abhandlungen (neue Folge), v. 18, p. 5–119.

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press

Riccardi, A.C., 2008a, The marine Jurassic of Argentina: a biostratigraphic framework: Episodes, v. 31, p. 326–335.
Riccardi, A.C., 2008b, El Jurásico de Argentina y sus amonites: Revista de la Asociación Geológica Argentina, v. 63, p. 625–643.
Riccardi, A.C., Damborenea, S.E., and Manceñido, M.O., 1990, Lower Jurassic of South America and Antarctic Peninsula, *in* Westermann, G.E.G., and Riccardi, A.C., eds., Jurassic taxa ranges and correlation charts for the Circum-Pacific. 3. South America and Antarctic Peninsula: Newsletters on Stratigraphy, v. 21, p. 75–103.
Riccardi, A.C., Damborenea, S.E., Manceñido, M.O. and Ballent, S.C., 2000 [1999], El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. 3. Bioestratigrafía, *in* Caminos, R., ed., Geología Argentina: Instituto de Geología y Recursos Minerales, Anales 29, p. 419–432.
Robbiano, J.A., 1971, Contribución al conocimiento estratigráfico de la sierra del Cerro Negro, Pampa de Agnia, Provincia de Chubut, República Argentina: Revista de la Asociación Geológica Argentina, v. 26, p. 41–56.
Roemer, F.A., 1835–1839, Die Versteinerungen des norddeutschen Oolithen-Gebirges: Hannover, Han'schen Hofbuchhandlung, p. 1–74 (1835); p. 75–218 (1836); Nachtrag, p. 1–59 (1839).
Ros, S., Márquez-Aliaga, A., and Damborenea, S., 2014, Comprehensive database on Induan (Early Triassic) to Sinemurian (Early Jurassic) marine bivalve genera and their paleobiogeographic record: University of Kansas Paleontological Contributions 8, 219 p.
Roth, S., 1908, Beitrag zur Gliederung der Sedimentablagerungen in Patagonien und Pampas region: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band, v. 26, p. 92–150.
Roy, K., Jablonski, D., and Martien, K.K., 2000, Invariant size-frequency distributions along a latitudinal gradient in marine bivalves: Proceedings of the National Academy of Sciences USA, v. 97, p. 13150–13155.
Schenck, H.G., 1934, Classification of nuculid pelecypods: Bulletin du Musée Royal d´Histoire naturelle de Belgique, v. 10, p. 1–78.
Schenck, H.G., 1939, Revised nomenclature for some nuculid pelecypods: Journal of Paleontology, v. 13, p. 21–41.
Seebach, K. von, 1865, Beiträge zur geologie der Insel Bornholm: Zeitschrift der deutschen geologischen Gessellschaft, v. 17, p. 338–347.
Seilacher, A., 1972, Divaricate patterns in pelecypod shells: Lethaia, v. 5, p. 325–343.
Sha, J., Fürsich F. T. Smith P. L., and Wang, L., 1998, Palaeotaxodonta, Pteriomorphia, and Isofilibranchia (Bivalvia) from the Jurassic of the main ridge of the Tanggula Mountains, Qinghai-Xizang Plateau, China: Beringeria, v. 21, p. 3–55.
Sharma, P.P., Zardus, J.D., Boyle, E.E., González, V.L., Jennings, R.M., McIntyre, E., Wheeler, W.C., Etter, R.J., and Giribet, G., 2013, Into the deep: a phylogenetic approach to the bivalve subclass Protobranchia: Molecular Phylogenetics and Evolution, v. 69, p. 188–204.
Sowerby, G.B. I, 1821–1834, The Genera of Recent and Fossil Shells: London, v. 1, pls. 1–126 + text (not numbered) [1821–1825]; v. 2, pls. 127–162 + text (not numbered) [1825–1834].
Sowerby, J. de C., 1823–1825, The Mineral Conchology of Great Britain; or Coloured Figures and Description of those Remains of Testaceous Animals or Shells Which Have Been Preserved at Various Times and Depths in the Earth: London, B. Meredith, v. 5, 168 p.
Squires, R.L., and Saul, L.R., 2006, Cretaceous *Acila* (*Truncacila*) (Bivalvia: Nuculidae) from the Pacific Slope of North America: The Veliger, v. 48, p. 83–104.
Tate, R., 1870a, On the palaeontology of the Junction Beds of the Lower and Middle Lias in Gloucestershire: Quarterly Journal of the Geological Society of London, v. 26, p. 394–408.
Tate, R., 1870b, Appendix 1. A list of the Irish Liassic fossils with notes on the new critical species: Report of the Belfast Naturalists´ Field Club, p. 3–24.
Tate, R., and Blake, J., 1876, The Yorkshire Lias: London, J. Van Voorst, p. 357–412.
Terquem, O., and Piette., E., 1865, Le Lias inférieur de l'Est de la France comprénant la Meurthe, la Moselle, le rand-Duché de Luxembourg, la Belgique et la Meuse: Mémoires de la Societé Géologique de France, ser. 2, v. 8, 175 p.
Trechmann, C.T., 1923, The Jurassic rocks of New Zealand: Quarterly Journal of the Geological Society of London, v. 79, p. 246–286, 309–312.
Troedsson, G., 1951, On the Höganäs Series of Sweden (Rhaeto-Lias): Lunds Universitets Arsskrift, N.F. Avd 2, v. 47, p. 1–268.
Turner, J.C.M., 1982, Descripción geológica de la Hoja 44c, Tecka, Provincia del Chubut: Servicio Geológico Nacional (Argentina), Boletín 180, 92 p.
Ugarte, F., 1966, La Cuenca Compuesta Carbonífero-Jurásica: Anales de la Universidad de la Patagonia San Juan Bosco, v. 1, p. 37–68.
Vicente, J.C., 2005, Dynamic paleogeography of the Jurassic Andean Basin: pattern of transgression and localisation of main straits through the magmatic arc: Revista de la Asociación Geológica Argentina, v. 60, p. 221–250.
Vizán, H., 1989, Estudios paleontológicos y paleomagnéticos preliminares de la Formación Lepá (río Gualjaina-Chubut): Revista de la Asociación Geológica Argentina, v. 43, p. 327–337.
Volkheimer, W., Manceñido, M.O., and Damborenea, S.E., 1978, Zur Biostratigraphie des Lias in der Hochkordillere von San Juan, Argentinien: Münstersche Forschungen zur Geologie und Paläontologie, v. 44/45, p. 205–235.
Wahnish, E., 1942, Observaciones geológicas en el Oeste del Chubut. Estratigrafía y fauna del Liásico en los alrededores del rio Genua: Servicio Geológico Nacional (Argentina), Boletín 51, 73 p.
Waller, T.R., 1990, The evolution of ligament systems in the Bivalvia, *in* Morton, B., ed., The Bivalvia, Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986: Asian Marine Biology, v. 7, p. 47–91.
Wasmer, M., Hautmann, M., Hermann, E., Ware, D., Roohi, G., Ur-Rehman, K., Yaseen, A., and Bucher, H., 2012, Olenekian (Early Triassic) bivalves from the Salt Range and Sutghar Range, Pakistan: Palaeontology, v. 55, p. 1043–1073.
Weaver, C., 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina: University of Washington Memoir 1, 469 p.
Whittle, R.J., Quaglio, F., Crame, J.A., and Linse, K., 2012, Nuculidae (Bivalvia) in the Cape Melville Formation, King George Island, Antarctica, with an overview of the bivalve fauna: Antarctic Science, v. 24, p. 625–633.
Wilton, C.P.N., 1830, Memoir on the geology of the shore of the Severn, in the parish of Awre, Gloucestershire: Quarterly Journal of Science, Literature and Arts, Jan-June, p. 64–73.
Yin, J., and McRoberts, C.A., 2006, Latest Triassic–earliest Jurassic bivalves of the Germig Formation from Lanongla (Tibet, China): Journal of Paleontology, v. 80, p. 104–120.
Yonge, C.M., 1939, The Protobranchiate mollusca; a functional interpretation of their structure and evolution: Philosophical Transactions of the Royal Society of London, ser. B, v. 230, p. 79–147.
Yonge, C.M., 1959, The status of the Protobranchia in the bivalve mollusca: Proceedings of the Malacological Society of London, v. 33, p. 210–214.
Zapfe, H., 1967, Beiträge zur Paläontologie der nordalpinen Riffe. Die Fauna der Zlambach-Mergel der Fischerwiese bei Aussee, Steiermark (excl. Coelenterata und Mikrofossilien): Annalen des Naturhistorischen Museums in Wien, v. 71, p. 413–480.
Zhang, R., Wang, D., and Zhou, Z., 1977, Mesozoic and Cenozoic bivalves, *in* Hubei Institute of Geological Sciences, ed., Palaeontological Atlas of Central South China: Nanjing, Geological Publishing House, v. 3, p. 4–65 (in Chinese).

Accepted: 5 February 2019

https://doi.org/10.1017/jpa.2019.12 Published online by Cambridge University Press