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Early Jurassic marine gastropods from Argentina: a palaeobiogeographical analysis based on Vetigastropoda

S. M. Ferrari[a,b]*

[a]*Museo Paleontológico Egidio Feruglio, CONICET, Av. Fontana, 140. U9100GYO, Trelew-Chubut, Argentina;* [b]*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina*

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Gastropods are represented in the Early Jurassic of Argentina by Vetigastropoda, Caenogastropoda and Opisthobranchia. The present paper describes nine new vetigastropod species from the Early Jurassic marine deposits of the Neuquén Basin: *Proconulus*? *argentinus* sp. nov., *Chartronella atuelensis* sp. nov., *Striatoconulus? axialis* sp. nov., *Guidonia disciformis* sp. nov., *Ambercyclus andinus* sp. nov., *Ambercyclus chilcaensis* sp. nov., *Discohelix sanicoensis* sp. nov., *Cryptaenia sudamericana* sp. nov. and *Cryptaenia globosa* sp. nov. Another three vetigastropods are reported for the first time in this region – *Chartronella gradata* Ferrari, *Ataphrus mulanguiniensis* Ferrari and *Colpomphalus*? aff. *musacchioi* Ferrari – extending their palaeobiogeographical distributions in the Andean region of Argentina. *Lithotrochus humboldtii* (von Buch), *Lithotrochus rothi* Damborenea & Ferrari, and an undetermined ataphrid species were also retrieved from marine beds of the Neuquén Basin. A quantitative palaeobiogeographical analysis was performed integrating available data on the entire marine vetigastropod species thus far recorded from Argentina. The primary results of the analysis show two clearly discernible palaeobiogeographical units in the Andean region of Argentina. The local vetigastropod species from the Neuquén and Chubut basins may be interpreted considering palaeogeographical control as a determinant in the distribution of these taxa, including the separate evolution of the Neuquén basin until the late Pliensbachian. However, a shallow marine connection between the Neuquén and Chubut basins along the Palaeo-Pacific seaway during the late Pliensbachian–early Toarcian may explain faunal exchange between both basins at that time.

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Keywords: Vetigastropoda; systematics; palaeobiogeography; Early Jurassic; Argentina

Introduction

Knowledge of Argentinian Early Jurassic marine gastropods from the Chubut Basin has been reviewed recently by Ferrari (2009, 2011, 2012, 2013, 2014) and Ferrari *et al*. (2014). Those contributions provide an updated systematic database to interpret the gastropod faunas in this region, recording at least 13 gastropod families from the Early Jurassic (late Pliensbachian–early Toarcian) marine deposits of the Mulanguiñeu and Osta Arena formations in Chubut Province, which are represented by 20 genera, two subgenera and 33 species. Most of these genera represent first records for the Argentinian Jurassic. Early Jurassic gastropods from the Neuquén Basin are still poorly known, despite being widely distributed and locally diverse (for syntheses, see Ferrari 2009; Riccardi *et al*. 2011). Their potential use in palaeobiogeography awaits systematic revisions. Only the most abundant or most conspicuous species have been described thus far, but the existing fauna is far more diverse. For instance, Damborenea *et al*. (1975) and Volkheimer *et al*. (1978) gave preliminary reports of gastropod species in late Pliensbachian deposits at Piedra Pintada in southern San Juan Province. Ferrari *et al*. (in press) recently reported members of Trochotomidae Cox, for the first time in the Neuquén Basin during the Early Jurassic, outlining palaeobiogeographical implications of these records for the southern hemisphere at that time.

The summarized information obtained from these recent studies indicates that gastropod species are represented in the Early Jurassic of Argentina by three major taxa: Vetigastropoda, Caenogastropoda and Opisthobranchia. The present paper is focused on the vetigastropod faunas, pending further research on the caenogastropods and opisthobranchs. Its aim is to improve and update systematic knowledge of Argentinian Jurassic marine vetigastropods from the Neuquén Basin, and to reassess the Jurassic gastropod collections currently existing in Argentina, supplying new evidence on Early Jurassic marine gastropods in South America. Fifteen vetigastropod

*Email: mferrari@mef.org.ar

species are described here from the Neuquén Basin, among which nine are new to science. A quantitative palaeobiogeographical analysis using PAST statistical software (Hammer *et al*. 2001) is performed integrating the available systematic data of the entire fauna of marine vetigastropod species known from the Early Jurassic of Argentina. This approach provides a first quantitative palaeobiogeographical scheme for the southern hemisphere based on Mesozoic vetigastropod faunas.

Geological setting

The Neuquén Basin (Fig. 1), which extends between 34° S and 41° S, is a Mesozoic back-arc basin on the western convergent margin of the South American plate (Legarreta & Gulisano 1989), generated by extension linked to the fragmentation of Gondwanaland and the opening of the South Atlantic Ocean (Uliana & Biddle 1988). Between 34° S and 37° S, it was restricted to a narrow north–south strip, but it broadened eastwards south of 37° S to form the wide Neuquén embayment. The basin became filled with more than 6000 m of marine and continental sedimentary and extrusive rocks of Late Triassic to Eocene age (Legarreta & Gulisano 1989; Gulisano & Gutiérrez Pleimling 1995). It originated from a series of unconnected, asymmetrical, north–south-oriented half grabens (Tankard *et al*. 1995), which controlled the subsidence and sedimentation during a first rifting phase in the Middle Triassic–Sinemurian (Ramos 1992), when non-marine and mainly non-fossiliferous siliciclastic deposits and volcanic rocks filled the half grabens at the basin margins (Legarreta & Gulisano 1989). From Rhaetian times the basin centre became rapidly filled by nearshore sandstones and offshore shales, partly due to a Sinemurian–Toarcian regional sag phase (Vergani *et al*. 1995) which caused the half grabens to coalesce in the Pliensbachian (Legarreta & Gulisano 1989) when transgression increased. Features, areal distribution, and age of the basal sag deposits depended on basement topography, controlled by the main faults and horsts, which also locally conditioned the beginning of the transgression and the partial synchronism between terrestrial and marine units of Late Triassic–Early Jurassic age (Gulisano 1981; Gulisano & Gutiérrez Pleimling 1995).

Many localities in the Neuquén Basin contain Early Jurassic gastropods, including those discussed below. In southern San Juan Province, Pliensbachian–Toarcian sediments, originally described by Volkheimer *et al.* (1978) as the Los Patos Formation (see Damborenea 1987), yield vetigastropod species at the Río de Los Patos Sur locality (Fig. 1, locality A). In Mendoza Province, Hettangian–Toarcian sediments, referable to the Puesto Araya Formation, of the Atuel–western Malargüe depocentre contain vetigastropods at Arroyo Las Chilcas (Fig. 1, locality B), Arroyo Malo (Fig. 1, locality C), Quebrada de los Caballos (Fig. 1, locality D), Arroyo La Bajada (Fig. 1, locality E), Cerro Puchenque (Fig. 1, locality F), and Cerro Tricolor (Fig. 1, locality G). Vetigastropods were found in Pliensbachian–Toarcian deposits in the Cuyo Group beds of the Piedra Pintada Formation, within the Neuquén embayment in southern Neuquén Province, at Arroyo Lonqueo (Fig. 1, locality H), Estancia Santa Isabel (Fig. 1, locality I), Carrán Curá (Fig. 1, locality J), Cerro Roth (Fig. 1, locality K) and Sañicó (Fig. 1, locality L).

Early Jurassic sediments in Chubut Province are distributed along a NW–SE belt of outcrops between 42°30′ S and 44°30′ S, and 69°30′ W and 71° W (Riccardi 1983; Giacosa & Márquez 2000). In the south-western region of Chubut Province, Early Jurassic marine deposits crop out in the Ferraroti and Nueva Lubecka areas where they are known as the Mulanguiñeu Formation (Fernández Garrasino 1977). The most extensive deposits of this unit outcrop on the western slope of Salar de Ferraroti and Lomas Occidentales near the Rio Genoa valley. The single vetigastropod species described here from Chubut Province comes from Lomas Occidentales (Fig. 1, locality M) east and west of the old telegraph station of Nueva Lubecka.

Material and methods

The vetigastropod material here described was collected by S. Damborenea, M. Manceñido, Javier Echevarría (Museo de Ciencias Naturales de La Plata), S. Lanés (Universidad de Buenos Aires) and by M. Ferrari (Museo Paleontológico Egidio Feruglio) during several fieldtrips in the Neuquén Basin. Stratigraphical sections for localities yielding gastropods in the Neuquén Basin were described by Damborenea (1987), and in the Chubut Basin by Ferrari (2013). All of the specimens were found in the Early Jurassic (Hettangian/*Kamerkarites bayoensis* faunule to early Toarcian/*Peronoceras pacificum* Zone beds) according to the current ammonite biozonation (Riccardi 2008a, b; Riccardi *et al*. 2011).

The Argentinian vetigastropod material is stored in the Museo de Ciencias Naturales de La Plata (MLP) collection and in the Museo Paleontológico Carmen Funes, Plaza Huincul (MCF-PIPH). The specimens were prepared by technical staff (Santiago Bessone, Leandro Canessa and Norberto Pfeiffer) at MEF laboratory, and latex casts were obtained from specimens preserved as external moulds. The material was coated with ammonium chloride to enhance sculpture details for photography. Photographs were taken using a digital camera with a binocular lens at MPEF, and using scanning electronic microscopy (SEM) at ALUAR (Pto. Madryn). Quantitative palaeobiogeographical analysis was performed using a statistical software (PAST; Hammer *et al*. 2001).

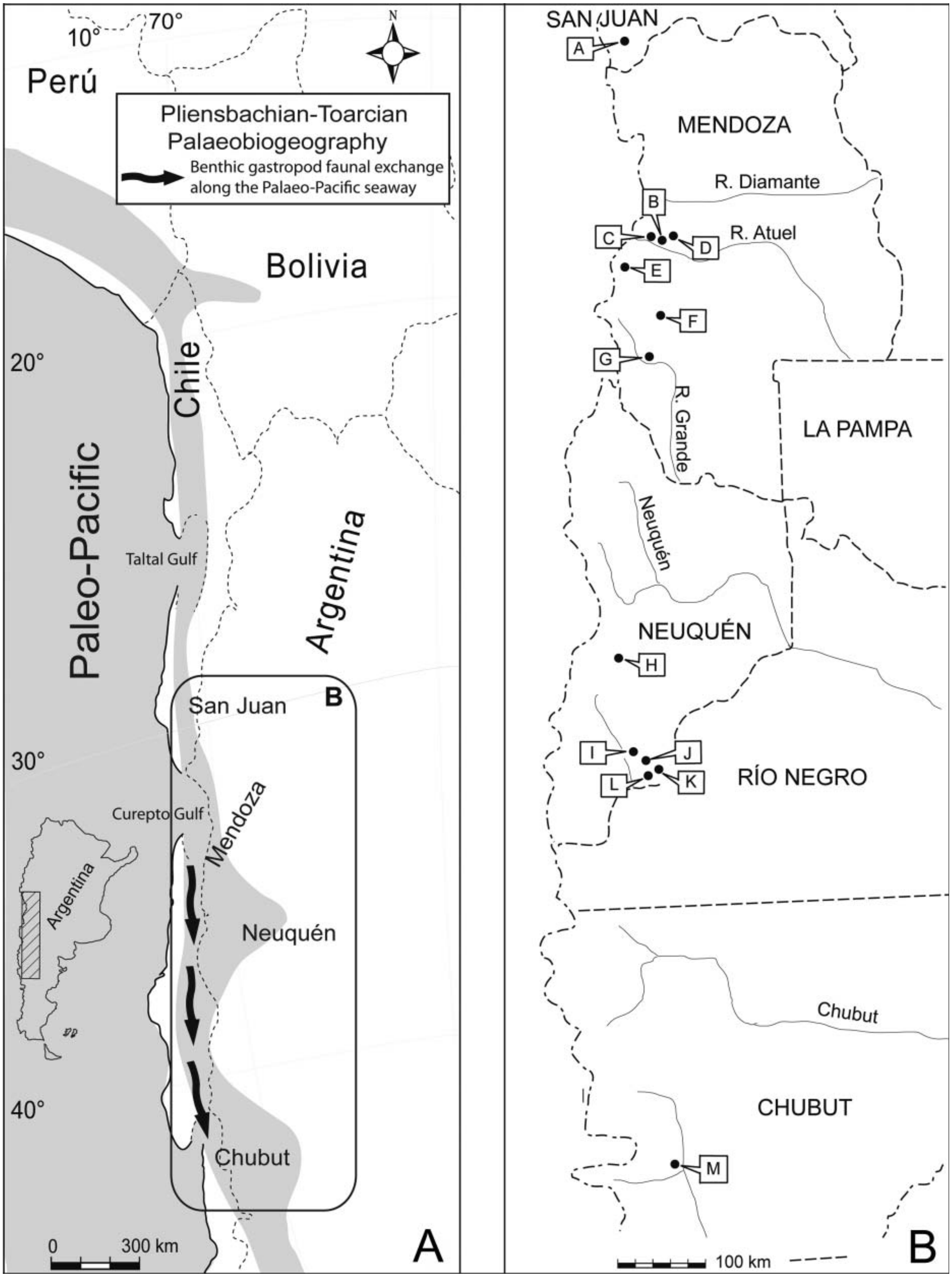

Figure 1. **A,** map of the Andean region of South America showing the palaeobiogeographical distribution of vetigastropod species during the Early Jurassic. **B,** location map of the main localities with vetigastropod species described in the text. Abbreviations: A, Río de los Patos Sur; B, Arroyo Las Chilcas; C, Arroyo Malo; D, Quebrada de los Caballos; E, Arroyo La Bajada; F, Cerro Puchenque; G, Cerro Tricolor; H, Arroyo Lonqueo; I, Estancia Santa Isabel; J, Carrán Curá; K, Cerro Roth; L, Sañicó; M, Lomas Occidentales.

Institutional abbreviations

MLP: Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina; **MPEF**: Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; **MCF-PIPH**: Museo Paleontológico Carmen Funes, Plaza Huincul, Neuquén, Argentina; **MB.Ga**: Museum für Naturkunde Humboldt-Universität zu Berlin; **ALUAR**: Aluminio Argentino. Pto. Madryn, Chubut, Argentina.

Systematic palaeontology

Order **Vetigastropoda** Salvini-Pläwen, 1980
Superfamily **Trochoidea** Rafinesque, 1815
Family **Trochidae** Rafinesque, 1815
Genus ***Lithotrochus*** Conrad, 1855

Type species. *Turritella andii* d'Orbigny, 1842 (= *Pleurotomaria humboldtii* von Buch, 1839).

Occurrence. Early Jurassic (early Sinemurian–late Pliensbachian); Peru, Chile and Argentina.

Remarks. The genus *Lithotrochus* is endemic to South America and has been recently recorded in the Argentinian Jurassic by Damborenea & Ferrari (2008) and Ferrari (2013). The *Lithotrochus* material reported here provides new evidence of the genus in the Early Jurassic of the Neuquén Basin.

Lithotrochus humboldtii (von Buch, 1839)
(Fig. 2A–W)

1839 *Pleurotomaria humboldtii* von Buch: 9, pl. 2, fig. 26.
non 1942 *Lithotrochus humboldti* (von Buch); Wahnish: 60, pl. 2, fig. 4.
2008 *Lithotrochus humboldtii* (von Buch); Damborenea & Ferrari: 202, fig. 4.1–4.21, 7.1 [with complete synonymy].
2013 *Lithotrochus humboldtii* (Von Buch); Ferrari: 581, fig. 2A.

Material. MCF-PIPH 549–51, 562, 616–8, 683, 685, 686, 689, 691, 695–7, 699–701. MLP 3898, 3900, 3901, 9539, 12156, 12158, 18207, 18494, 18495–501, 18502–5, 20922, 27868, 27911. Well-preserved and replaced teleoconchs; two internal moulds.

Occurrence. El Pedrero and Arroyo Las Chilcas, Sinemurian, Puesto Araya Formation, Mendoza Province. Cerro Roth and Cerro del Vasco, Pliensbachian, Piedra Pintada Formation, Neuquén Province. Arroyo Pescado and Lomas Occidentale, Pliensbachian, Lepá and Mulanguñeu formations, Chubut Province, Argentina.

Description. Dextral, anomphalous, high conical shell, with trochiform shape on juvenile whorls to cyrtoconoid shape on mature whorls. The teleoconch comprises up to 6 whorls, with a mean height of 34 mm and a mean width of 36.5 mm. Adult specimens have an apical angle of 85–95°, whereas in juvenile specimens the apex is of 109–115°. A peripheral carina and imbricate whorls are developed on adult growth stages. The shell surface is ornamented by regularly spaced spiral cords intercepted by fine prosocline growth lines. The base is slightly convex with well-developed spiral ribs and weak prosocline growth lines. The aperture is quadrangular and holostomatous, with the peristome discontinuous and not thickened. A smooth and more or less thin callus covers the columellar lip.

Dimensions. See Table 1.

Remarks. According to the emended diagnosis proposed by Damborenea & Ferrari (2008, p. 201), the material here described certainly belongs to *Lithotrochus humboldtii* (von Buch). This is the first record of the species in the Early Jurassic marine sequences of Neuquén Province. Most specimens were found in very well-preserved condition, enabling morphological characterization of the species to be improved. For comparisons with other similar species, see Damborenea & Ferrari (2008, p. 204).

Table 1. Dimensions (mm) of *Lithotrochus humboldtii* (von Buch).

Specimen	Height	Width	Apical angle
MCF-PIPH 701	16.2	18.4	*
MCF-PIPH 700	33.2	35.2	*
MCF-PIPH 699	37.6	43.6	*
MCF-PIPH 697	31.9	36.4	*
MCF-PIPH 696/b	40.5	40.2	109° j
MCF-PIPH 696/a	29.2	33.9	86°
MCF-PIPH 695	46.8	43.3	87°
MCF-PIPH 691	17.2	24	*
MCF-PIPH 689	44.9	42	95°
MCF-PIPH 686	38	49.4	*
MCF-PIPH 685	53.4	55.4	*
MCF-PIPH 683	30.2	37.6	*
MCF-PIPH 618	21.7	30.4	115° j
MCF-PIPH 617	40.98	41.2	*
MCF-PIPH 616	35.3	37	*
MCF-PIPH 562	47.7	43	*
MCF-PIPH 551/b	22.7	24.5	*
MCF-PIPH 551/a	20.2	24.8	*
MCF-PIPH 550	43.6	39	85°
MCF-PIPH 549/b	22.8	26	*
MCF-PIPH 549/a	34.9	40	*

*Missing data. Abbreviation: j, juvenile.

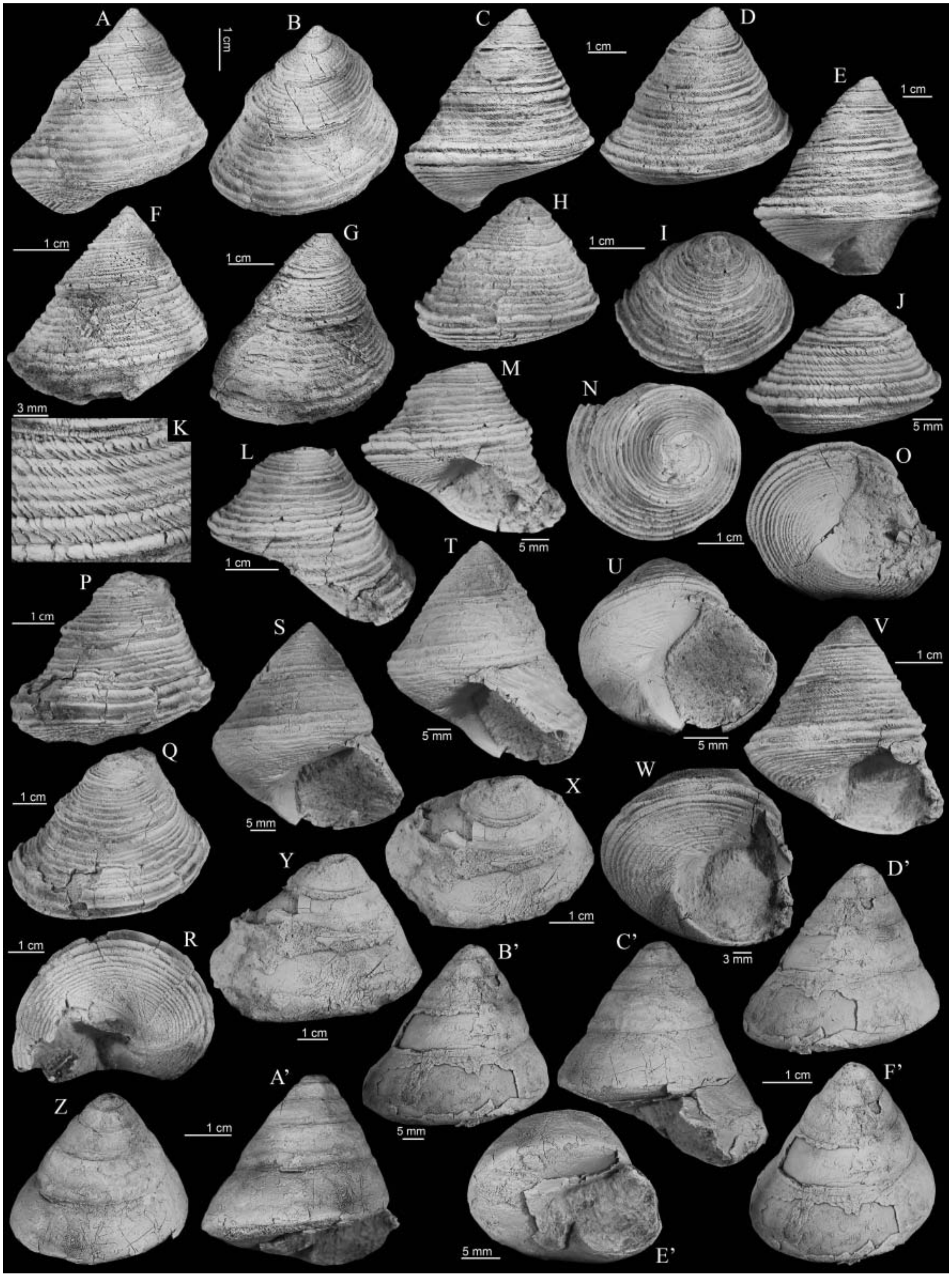

Figure 2. **A−W,** *Lithotrochus humboldtii* (von Buch, 1839); **A, B,** MCF-PIPH 550; **A,** lateral view; **B,** lateral and apical views; **C−E, V, W,** MCF-PIPH 695; **C, D,** lateral views; **E, V,** lateral and apertural views; **W,** basal and apertural views; **F, G,** MCF-PIPH 696a, lateral views; **H−K,** MCF-PIPH 618; **H, J,** lateral views; **I,** apical view; **K,** ornament detail; **L−O,** MCF-PIPH 683; **L, M,** lateral and apertural views; **N,** apical view; **O,** basal and apertural views; **P−R,** MCF-PIPH 686; **P, Q,** lateral and apical views; **R,** basal and apertural views; **S−U,** MCF-PIPH 689; **S, T,** lateral and apertural views; **U,** basal and apertural views. **X, Y,** *Lithotrochus rothi* Damborenea & Ferrari, 2008, MCF-PIPH 706; **X,** apical view; **Y,** lateral view. **Z−F′,** *Proconulus*? *argentinus* sp. nov., MCF-PIPH 694, holotype; **Z,** apical view; **A′−D′, F′,** lateral and apical views; **E′,** basal and apertural views.

Lithotrochus rothi Damborenea & Ferrari, 2008
(Fig. 2X, Y)

?2001 *Lithotrochus andinus* (Möricke); Gründel: 48, pl. 2, figs 4, 5.
2008 *Lithotrochus rothi* Damborenea & Ferrari: 206, fig. 6.1−6.4, 7.2.
?2013 *Lithotrochus* cf. *rothi* Damborenea & Ferrari; Ferrari: 581, fig. 2B.

Material. MCF-PIPH 706, 5 fragmentary and replaced teleoconchs (additional material to that previously described by Damborenea & Ferrari 2008).

Occurrence. Cerro Roth, Pliensbachian, Piedra Pintada Formation, Neuquén Province, Argentina.

Description. Dextral, anomphalous shell, trochiform in juvenile stages to slightly cytoconoid in mature whorls. The protoconch is not preserved. The teleoconch consists of 3−4 fragmentary whorls with a mean height of 23 mm and a mean width of 26.7 mm; the apex forms an angle of 104°. The shell lack spiral cords on the whorl surface and only bears fine prosocline growth lines. Weak spiral riblets are present on the base.

Dimensions. MCF-PIPH 706/a: height = 42.4 mm; width = 43 mm; apical angle = 104°. MCF-PIPH 706/b: height = 20.2 mm; width = 21.6 mm. MCF-PIPH 706/c: height = 13.9 mm; width = 20 mm. MCF-PIPH 706/d: height = 15.4 mm; width = 22.5 mm.

Remarks. Damborenea & Ferrari (2008) pointed out that *Lithotrochus rothi* differs from *L. humboldtii* in lacking spiral ornament on the outer whorl surface and in having fine prosocline growth lines; however, the two species are very similar in general shell morphology and apertural details (see species diagnosis in Damborenea & Ferrari 2008, p. 206).

Family **Proconulidae** Cox, 1960a
Subfamily **Proconulinae** Cox, 1960a
Genus ***Proconulus*** Cossmann, 1918

Type species. *Trochus guillieni* Cossmann, 1885, Middle Jurassic (Bathonian) of France.

Occurrence. Early Jurassic−Late Cretaceous; cosmopolitan.

Remarks. Gründel (2000) proposed a new diagnosis for *Proconulus* and the family Proconulidae based on the conical shell shape, mostly with straight or concave flanks, weakly convex to flat base, teleoconch whorls with spiral and axial ribs, and columella with a broad callus and a half-moon-shaped deepening on it. Monari *et al*. (1996) revised the systematic position of the genus and considered that species of *Proconulus* share a conical shell shape, with a high spire and convex base, and a columellar structure with a groove bordered by a sharp outer ridge.

Monari *et al*. (1996) and Damborenea & Ferrari (2008) suggested that these features relate *Proconulus* with the extant Calliostomatidae. Here, I adopt the classification of Gründel (2000) and Monari *et al*. (1996) but propose using open nomenclature for the questionably assigned Argentinian species as it shows a simple callus and a smooth columellar lip.

Proconulus*? *argentinus sp. nov.
(Fig. 2Z−F′)

Diagnosis. Conical, trochiform, anomphalous shell; externally smooth or with fine spiral lines on the outer face; apical angle of 94°; periphery angular and convex; sutures fine and impressed; aperture quadrangular; columellar lip forming a simple callus.

Derivation of name. Refers to the first, uncertain occurrence of the genus in the Jurassic of Argentina.

Material. Holotype, MCF-PIPH 694, a well-preserved, replaced teleoconch.

Occurrence. Cerro Roth, Pliensbachian, Piedra Pintada Formation, Neuquén Province, Argentina.

Description. Dextral, conical, trochiform, medium sized and high-spired shell. The protoconch is not preserved. The teleoconch comprises 6 slightly convex to flattened whorls, with a height of 41 mm and a width of 38.8 mm. The apex forms an angle of 94°. Sutures are clearly delimited, fine and impressed. The shell is smooth, although very weak and fine spiral lines appear on the spire. The periphery of the shell is angular and convex. The base is flattened without an open umbilicus. The aperture is subquadrangular with the columellar lip thickened as a simple callus.

Remarks. The analysed material shows some typical characters of *Proconulus*, but it also resembles *Anticonulus* Cossmann, 1918 in general shell morphology and ornament pattern. *Anticonulus* differs from *Proconulus* in having an open umbilicus and a simple inner lip. The reason for keeping the single specimen here described within the genus *Proconulus* is based on the absence of umbilicus, with the columellar lip thickened as a callus. However, it is placed doubtfully in *Proconulus* due to the lacking of a columellar structure with a groove bordered by a sharp outer ridge, which is a diagnostic feature of *Proconulus*. Most probably the single specimen here analysed belongs to a new trochid genus but the material is too sparse to propose a new genus.

Proconulus? *argentinus* sp. nov. is the first (albeit uncertain) record of the genus in the Early Jurassic of Argentina, extending its palaeobiogeographical distribution into the marine Jurassic of South America.

Proconulus? *epuloides* Szabó, 2009 (p. 70, fig. 67A–D) (Szabó 1981, p. 56, pl. 1, figs 2, 3), ascribed by Monari *et al*. (2008) to the subgenus *Muricotrochus* (*Laeviconulus*), from the Early Jurassic (late Sinemurian) of Hungary differs from *P*.? *argentinus* sp. nov. in being higher and with a slightly cyrtoconoid spire, and in having prosocline growth lines on the shell surface and opisthocyrt growth lines on the base. In the Argentinian species the growth lines are not visible. *Proconulus*? *scherinus* (Gemmellaro, 1874) (see Szabó 2009, p. 69, fig. 67E–H; 1981, p. 56, pl. 1, figs, 4, 5), from the Early Jurassic (Sinemurian–Pliensbachian) of Hungary, differs from *P*.? *argentinus* sp. nov. in having a more acute apex, and a better developed collabral ornament with visible prosocline growth lines on the shell surface and opisthocyrt growth lines on base.

The type species of *Proconulus*, *Trochus guillieni* Cossmann, 1885 (see Cossmann 1918, p. 276, pl. 9, fig. 30) from the Middle Jurassic (Bathonian) of France, differs from *Proconulus*? *argentinus* sp. nov. in having a narrower apical angle of 40–60° and spiral ornament on the shell surface. *Proconulus rimosus* Szabó, 1981 (p. 57, pl. 1, figs 9–13), from the Middle Jurassic (Bajocian) of Hungary, differs from the species described here in having a slightly developed, narrow step-like sutural ramp on the juvenile whorls, a strong spiral keel above the suture, longitudinal cords on the adult shell surface and a more convex base. *Proconulus epuliformis* Szabó, 1981 (p. 56, pl. 1, figs 6–8), from the Middle Jurassic (Bajocian) of Hungary, has a greater number of teleoconch whorls and stronger spiral and collabral elements. *Proconulus convexoconcavus* Gründel, 2000 (p. 220, pl. 4, figs 11–14), from the Middle Jurassic of Germany, differs from *P*.? *argentinus* sp. nov. in having the flanks of the teleoconch whorls in the apical part convex and in the abapical part concave, 12 spiral cords on mature whorls, and many axial ribs in the apical part of whorls. *Proconulus coelotropis* (Schmidt, 1905) and *Proconulus viadrinus* (Schmidt, 1905) (see Gründel & Kaim 2006, pp. 128, 129, figs 6, 7), both from the Late Jurassic (Oxfordian) of Poland, differs from *P*.? *argentinus* sp. nov. in having more developed spiral cords on the shell surface.

Family **Ataphridae** Cossmann, 1915
Subfamily **Ataphrinae** Cossmann, 1915
Tribe **Costataphrini** Gründel, 2008
Genus ***Chartronella*** Cossmann, 1902

Type species. *Chartronella digoniata* Cossmann in Chartron & Cossmann, 1902, Early Jurassic (Hettangian) of France.

Occurrence. Triassic–Jurassic; Europe, Africa, Peru and Argentina.

Remarks. Argentinian *Chartronella* were included by Ferrari (2011) in the tribe Colloniini Cossmann, considering that they are very similar to the extant *Cantrainea* (see also Kaim *et al*. 2009). However, the genus is here transferred to the tribe Costataphrini following the classification of Gründel (2008). The single report of *Chartronella* in the marine Jurassic of Argentina was supplied by Ferrari (2011, 2014), from late Pliensbachian–early Toarcian deposits of Chubut Province. The occurrence of the genus in coeval marine sediments of the Piedra Pintada Formation extends the palaeogeographical distribution of *Chartronella*, and also of the family Ataphridae, in Argentina.

Chartronella gradata Ferrari, 2014
(Fig. 3A–T)

p. 1975 *Bathrotomaria* sp. Damborenea *et al*.: Cuadro I, 51.
2014 *Chartronella gradata* Ferrari: 6, fig. 3i–s.

Emended diagnosis. Dextral, definitely gradate shell; cyrtoconoidal juvenile shell combined with slightly coeloconoidal later whorls; spire angle of 67–93°; first teleoconch whorl planispiral, convex and smooth; adult teleoconch with 5–6 angular whorls; outer face flat to concave with prosocline growth lines and edged by two strong spiral keels, the adapical one peripheral and corresponding to the angulation of the whorl, and the abapical one bordering the base; fine prosocline growth lines also on the ramp of whorls; base holostomatous and circular; aperture with a crescent-shaped columellar lip.

Material. MLP 12176a/b, 12177, 12179, 12180, 34559, 34460a/b, 34561; MCF-PIPH 545, 548, 552, 558, 560, 565, 682, 687, 690, 704. Well-preserved and replaced teleoconchs.

Occurrence. Cerro Roth and Carrán Curá, Pliensbachian, Piedra Pintada Formation, Neuquén Province; Lomas Occidentales, late Pliensbachain–early Toarcian, Mulanguiñeu Formation, Chubut Province, Argentina.

Description. Dextral, anomphalous, gradate, conical and moderately high-spired, cyrtoconoidal juvenile shell with slightly coeloconoidal later whorls. The spire forms an angle of about 68–93°. First teleoconch whorl is fragmentary, consisting of one planispiral convex whorl. Adult teleoconch comprises 5–6 angular whorls with a mean height of 29.3 mm and mean width of 28.3 mm; the upper portion of the whorls forms a ramp which gives the periphery of the shell an angular outline. The periphery bears a strong keel. The outer face is flat to slightly concave and bordered by two spiral keels; the uppermost is peripheral and coincides with the angulation, and the abapical one is weaker and borders the suture. Fine and

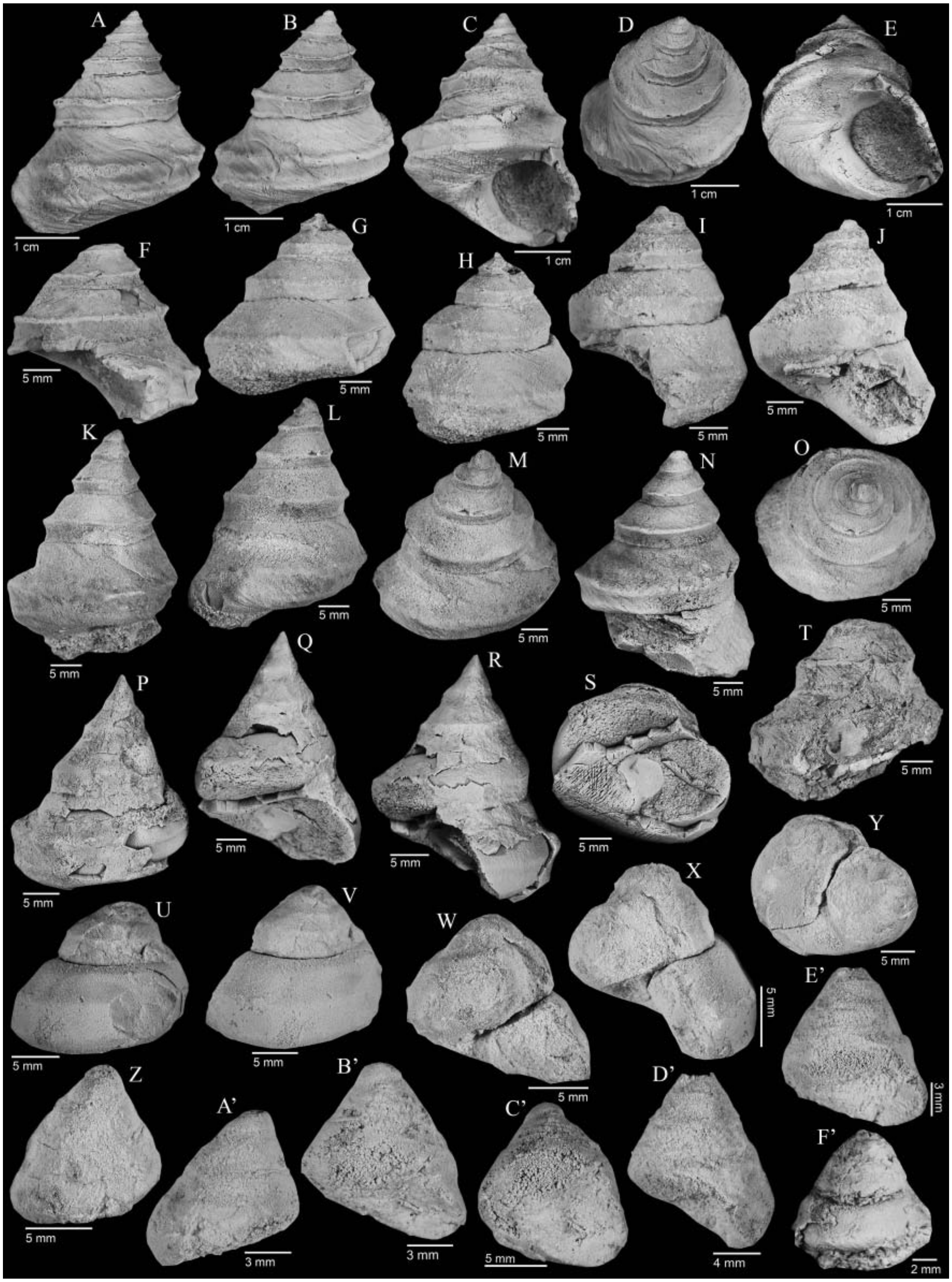

Figure 3. **A−T,** *Chartronella gradata* Ferrari, 2014; **A−E,** MCF-PIPH 552; **A−C,** lateral and apertural views; **D,** apical view; **E,** basal and apertural views; **F,** MCF-PIPH 690, lateral view; **G−J,** MLP 12179; **G−I,** lateral views; **J,** apertural views; **K−O,** MLP 12176a; **K, L, N,** lateral views; **M, O,** apical views; **P−S,** MLP 12176b; **P−R,** lateral and apertural views; **S,** basal and apertural views; **T,** MLP 12177, lateral view. **U−Y,** *Chartronella atuelensis* sp. nov., MLP 34562, holotype; **U, V,** lateral views; **W, X,** lateral and apertural views; **Y,** basal and apertural views. **Z−E′,** *Ataphrus mulanguiniensis* Ferrari, 2011, MLP 34564a/b; **Z−C′,** MLP 34564/a; **Z, A′,** apical and lateral views; **B′,** lateral and apertural view; **C′,** basal and apertural view; **D′,E′,** MLP 34564/b, lateral and apertural views. **F′,** Ataphridae? indet., MLP 15832, lateral view.

Table 2. Dimensions (mm) of *Chartronella gradata* Ferrari, 2014.

Specimen	Height	Width	Apical angle
MLP 12179	28.7	25.8	93°
MLP 12176/b	28.2	23.5	*
MLP 12176/a	37.8	31.2	68°
MLP 34561	16	16.9	*
MLP 34460/a	33.5	32.6	*
MLP 34559	23.6	27.2	*
MCF-PIPH 690/b	23.9	28	*
MCF-PIPH 690/a	28.9	28	*
MCF-PIPH 687/c	27.2	27.4	*
MCF-PIPH 687/b	31.1	30.1	*
MCF-PIPH 687/a	28.5	27.9	*
MCF-PIPH 565	31.9	31	*
MCF-PIPH 560	*	*	*
MCF-PIPH 558/a	23.2	29	*
MCF-PIPH 552	39.7	32.9	78°
MCF-PIPH 548/b	34.5	34.7	*
MCF-PIPH 548/a	40	33.6	*
MCF-PIPH 545/b	22.2	27.4	*
MCF-PIPH 545/a	27.4	21.9	*

*Missing data.

prosocline growth lines are weakly developed on the ramp and clearly developed on the outer face. The base is flat to slightly convex, ornamented by marked prosocline growth lines. The aperture is holostomatous and circular, with the peristome discontinuous and indented by the peripheral spiral keel; columellar lip thickened forming a crescent-shaped callus.

Dimensions. See Table 2.

Remarks. The material shows the typical characters of the genus *Chartronella*, including a strongly gradate shell outline, two spiral keels, and a crescent-shaped columellar lip (see diagnosis in Gründel 2008). Moreover, identification as *Chartronella gradata* is suggested by the following features: cyrtoconoidal juvenile shell combined with coeloconoidal later whorls; teleoconch with about five whorls; prosocline growth lines developed on the shell surface; flat to slightly convex base; and circular and holostomatous aperture with the outer lip forming an obtuse angle with the columellar lip.

Chartronella gradata was recently reported from Early Jurassic marine beds (late Pliensbachian–early Toarcian) of the Mulanguiñeu Formation in Chubut Province (Ferrari 2014). The record of this species in coeval marine sediments of the Piedra Pintada Formation of Neuquén Province extends the palaeogeographical distribution of the genus (and family). The well-preserved specimens also allow emendment of the species diagnosis. For comparisons of *Chartronella gradata* with other similar species from Argentina, western Tethys and the Peruvian region, see Ferrari (2014, p. 6).

Chartronella atuelensis sp. nov.
(Fig. 3U–Y)

Diagnosis. Turbiniform, gradate, relatively low-spired shell; sutural band narrow and oblique; ramp wide and strongly oblique; outer face straight and vertical; sutures impressed; last whorl expanded and convex; teleoconch smooth with two peripheral spiral keels; base ornamented by 2–3 regularly spaced spiral cords; aperture subcircular, with strongly crescent-shaped columellar lip.

Derivation of name. In reference to the type locality, Rio Atuel, Mendoza Province.

Material. Holotype, MLP 34562, well-preserved and replaced teleoconch.

Occurrence. Between Arroyo El Alumbre and Arroyo Malo, Río Atuel region, Mendoza Province, Argentina; middle Hettangian/*Kamerkarites bayoensis* zone, Puesto Araya Formation.

Description. Dextral, holostomatous, anomphalous, slightly cyrtoconoidal, gradate, small to medium sized and relatively low-spired shell. The protoconch is not preserved. The teleoconch consists of 3 angulated whorls, with a height of 15 mm and a width of 18 mm. The spire is fragmentary. Sutures are impressed in a spiral furrow. A narrow, slightly oblique sutural band is present. The ramp of the whorls is wide and strongly oblique; on mature whorls it is weakly convex, and becomes slightly concave abapically. The outer face is straight and vertical, bordered by a peripheral spiral keel which coincides with the angulation of whorls. The last teleoconch whorl is more expanded and convex than the spire whorls, and two peripheral spiral keels border its outer face. The abapical spiral keel is completely visible on the last whorl but covered by subsequent whorls on the spire. Apart from the spiral keels, the shell is smooth. The base is slightly convex and bordered by a peripheral abapical spiral keel. Two (or probably three) additional regularly spaced spiral cords appear on the base. The aperture is holostomatous and subcircular; the columellar lip is concave and strongly crescent-shaped.

Remarks. On the basis of the diagnosis of the genus provided by Gründel (2008; see also Ferrari 2011), the single specimen described here suggests inclusion in the genus *Chartronella*. *Chartronella atuelensis* sp. nov. provides new evidence for the occurrence of the genus in Argentina, extending its palaeogeographical distribution to the Río Atuel region of Mendoza Province. Moreover, it provides a new record in the marine Hettangian, extending also its chronostratigraphical distribution in Argentina.

Chartronella atuelensis sp. nov. is very similar to *Chartronella gradata* Ferrari, 2014 (p. 6. fig. 3i–k), recently reported from the Early Jurassic (Pliensbachian–Toarcian) of Chubut Province. The new species, however, has a lower-spired shell, more convex whorls, 2–3 regularly spaced spiral keels on the base, and a more concave crescent-shaped columellar lip. *Chartronella paganieae* Ferrari, 2011 (p. 69, fig. 7.1–7.10), from the late Pliensbachian–early Toarcian of Chubut Province, differs from the new species in being smaller and in having a lower spire. *Chartronella spiralis* Ferrari, 2011 (p. 71, fig. 9.1–9.6), from the Early Jurassic (late Pliensbachian-early Toarcian) of Chubut Province, has five regularly spaced spiral keels crossed by prosocline collabral lines on the shell surface, and the last teleoconch whorl is considerably more expanded than the earliest whorls; these characters are absent in *C. atuelensis* sp. nov. The type species, *Chartronella digoniata* Cossmann, 1902 (see Gründel 2008, p. 186, fig. 2.10–2.11) from the Early Jurassic (Hettangian) of France, differs from the new species in having a more gradate shell outline, a more concave ramp on the mature whorls, a strong peripheral keel, and better developed spiral cords on the shell surface.

Chartronella pacifica (Jaworski, 1923) (see Haas 1953, p. 81, pl. 5, figs 31–41, 45–47, 54), from the Late Triassic of Peru, is higher and has a more conical shell shape, strongly developed spiral and collabral elements, and strong nodes on the adult whorls. *Chartronella wortheniaeformis* Cox, 1949 (p. 36, pl. 2, figs 13–15) (Haas 1953, p. 83, pl. 5, figs 42–44, 48, 55), also from the Late Triassic of Peru, differs from the Argentinian form in having less convex whorls and in having weak spiral threads on the shell surface.

Genus ***Ataphrus*** Gabb, 1869

Type species. *Ataphrus crassus* Gabb, 1869 by original designation; Late Cretaceous, Martinez, California, USA.

Occurrence. Early Jurassic–Late Cretaceous; Europe, Asia, Africa and America.

Ataphrus mulanguiniensis Ferrari, 2011
(Fig. 3Z–E′)

2011 *Ataphrus mulanguiniensis* Ferrari: 65, figs 3.1–3.11 and 4.1–4.6.

Material. MLP 34563a/b, MLP 34564a/b, moderately well-preserved and replaced teleoconchs.

Occurrence. Estancia Santa Isabel, Neuquén Province, Argentina; Pliensbachian, Piedra Pintada Formation.

Description. The specimens show a dextral, conical, turbiniform, small and relatively low-spired shell. The protoconch is not preserved. The teleoconch consists of 4–5 flat to slightly convex whorls, with a mean height of 12.6 mm and a mean width of 12.4 mm. The apex forms an apical angle of about 80° in the best-preserved specimens. The last teleoconch whorl is more expanded than earlier whorls. The suture is weakly impressed in a spiral furrow. The shell is smooth apart from weak abapical spiral threads bordering the suture. Growth lines are not visible. The base is slightly convex to flat; the aperture is circular and the columellar lip forms a crescent-shaped callus.

Dimensions. MLP 34563/a: height = 11.2 mm; width = 10.8 mm. MLP 34563/b: height = 13.5 mm; width = 15.8 mm. MLP 34564/a: height = 12.5 mm; width = 11.4 mm; apical angle = 80°. MLP 34564/b: height = 13.4 mm; width = 11.6 mm.

Remarks. According to the diagnosis proposed by Ferrari (2011, p. 65), the material here described certainly belongs to *Ataphrus mulanguiniensis*, a species previously reported in Early Jurassic marine deposits of Chubut Province. The new record of *A. mulanguiniensis* in the Early Jurassic of Neuquén Province extends its palaeobiogeographical distribution. For comparisons of *Ataphrus mulanguiniensis* with other similar and coeval species, see Ferrari (2011, p. 66).

Ataphridae? indet.
(Fig. 3F′)

Material. MLP 15832, fragmentary and replaced teleoconch.

Occurrence. Cerro Puchenque, Mendoza Province, Argentina; late early Toarcian (*Peronoceras pacificum* Zone), Puchenque Formation.

Description. Fragmentary, turbiniform, small sized and low-spired shell, with a height of 9 mm and a width of 8.6 mm. The protoconch is not preserved. The teleoconch comprises 3 slightly convex whorls. The suture is impressed in a spiral furrow. The shell is smooth. The base is flat, and the aperture and the columellar callus are not observed.

Remarks. Regarding general shell morphology, the single specimen seems similar to *Ataphrus mulanguiniensis*. However, some diagnostic features of the genus and family, such as the crescent-shaped columellar lip, are not visible and thus the specimen is left in open nomenclature.

Tribe **Homalopomatini** Keen, 1960
Genus ***Striatoconulus*** Gründel, 2000

Type species. *Striatoconulus latus* Gründel, 2000; Middle Jurassic (Callovian) of Poland.

Occurrence. Early Jurassic (Toarcian) to Middle Jurassic (Callovian); Poland and Argentina.

Remarks. Representatives of the genus *Striatoconulus* Gründel, 2000 are characterized by the presence of a shell with convex flanks, distinct sutures, smooth first teleoconch whorls, mature whorls and base covered by spiral cords and a lack of axial ribs on the shell surface, small umbilicus, and an aperture with a columellar callus and a half-moon-shaped deepening (Gründel 2000; Kaim 2004).

Species of *Striatoconulus* were previously reported in Early Jurassic (early Toarcian) marine deposits of Chubut Province by Ferrari (2009). The new species here described shows the occurrence of the species in the Neuquén Basin, and extends its chronostratigraphical range into the Pliensbachian.

Striatoconulus*? *axialis sp. nov.
(Fig. 4A, B)

Diagnosis. Dextral, discoidal, small to medium sized and low-spired shell; teleoconch with 4 slightly convex whorls; earliest whorls smooth; last whorl greatly expanded with a flattened sutural band; sutures impressed in a spiral furrow; ornamentation spiral predominantly; earliest whorls with prosocline axial riblets and nodular elements at the crossing points of spiral cords.

Derivation of name. Referring to the presence of axial riblets on the earliest teleoconch whorls.

Material. Holotype, MLP 12162, fragmentary teleoconch preserved as external mould.

Occurrence. Sañicó, Neuquén Province, Argentina; Pliensbachian, Piedra Pintada Formation.

Description. Dextral, discoidal, small sized and low-spired shell, with a height of 7.8 mm and a width of 12.7 mm. The protoconch is not preserved; the teleoconch comprises 4 convex whorls; earliest teleoconch whorls are smooth. Last teleoconch whorls are more expanded than the spire. Spire whorls are strongly convex; the last teleoconch whorl has a flattened sutural band and becomes slightly convex toward the periphery. The suture is clearly visible in a spiral furrow. The selenizone is not clearly visible. The ornament is predominantly spiral, consisting of regularly spaced cords separated by weak spiral furrows. On juvenile whorls, strong, regularly spaced and prosocline axial riblets run from suture to suture and intersect the spiral elements. Weak nodes appear at intersection points of spiral and axial elements. The axial riblets tend to disappear towards mature whorls. Basal, apertural and umbilical characters are missing.

Remarks. The single specimen shows the diagnostic features of the genus *Striatoconulus*, including a low-spired shell, convex teleoconch whorls, earliest whorls smooth and mature whorls with predominantly spiral furrows; however, the presence of axial riblets on the earliest whorls separates the new species from other representatives of the genus. The single specimen described is retained doubtfully in *Striatoconulus*, considering that the basal and umbilical features are not preserved.

Striatoconulus? *axialis* sp. nov. shows close resemblance to *Striatoconulus* sp. Ferrari, 2009 (p. 451, fig. 2C), from the Early Jurassic (early Toarcian) of Chubut Province, although the latter species lacks axial elements on the earliest whorls. The type species, *Striatoconulus latus* Gründel, 2000 (p. 228, pl. 6, figs 11–15) (Kaim 2004, p. 29, fig. 15), from the Middle Jurassic (Bathonian) of Poland, is very similar to *Striatoconulus*? *axialis* sp. nov. but has more convex whorls, with more rounded edges on the flanks, and lacks axial riblets on the earliest whorls.

Family **Nododelphinulidae** Cox, 1960b
Genus ***Guidonia*** De Stefani, 1880

Type species. *Trochus rotulus* Stoliczka, 1861, subsequent designation by Haas (1953, p. 56); Hierlatz Alpe (Northern Calcareous Alps, Austria), Early Jurassic (Late Sinemurian).

Occurrence. Late Triassic (Norian) to Early Jurassic (Sinemurian–Pliensbachian); Europe, New Zealand and South America.

Remarks. Haas (1953) described many species of *Guidonia* De Stefani, 1880 from the Late Triassic of Peru and chose *Trochus rotulus* Stolitzka, 1861 as its type species, including it in the family Trochonematidae Zittel. Gründel (2004) assigned *Guidonia* to the family Liotiidae Adams & Adams, whereas Szabó (2009), on the basis of the presence of bicarinate whorls and the gradate shell outline, included the genus in the family Nododelphinulidae Cox, also pointing out that the shell shape of *Guidonia* resembles that of *Chartronella*, which could suggest accommodation in another family. Similarities between *Guidonia* and *Chartronella* were noted by Ferrari (2011). The classification of *Guidonia* in Nododelphinulidae was subsequently followed by Gatto & Monari (2010). Here I adopt the classification of Szabó (2009) and Gatto & Monari (2010).

Guidonia disciformis sp. nov.
(Fig. 4C–H)

Diagnosis. Gradate, very small, low-spired, discoidal shell; teleoconch with 3 whorls; wide, flattened ramp; outer face narrow and vertical, edged by two acute spiral cords; last teleoconch whorl expanded; collabral riblets on the ramp of last whorl; base flat with 3–4 acute spiral keels; umbilical area wide; aperture quadrangular.

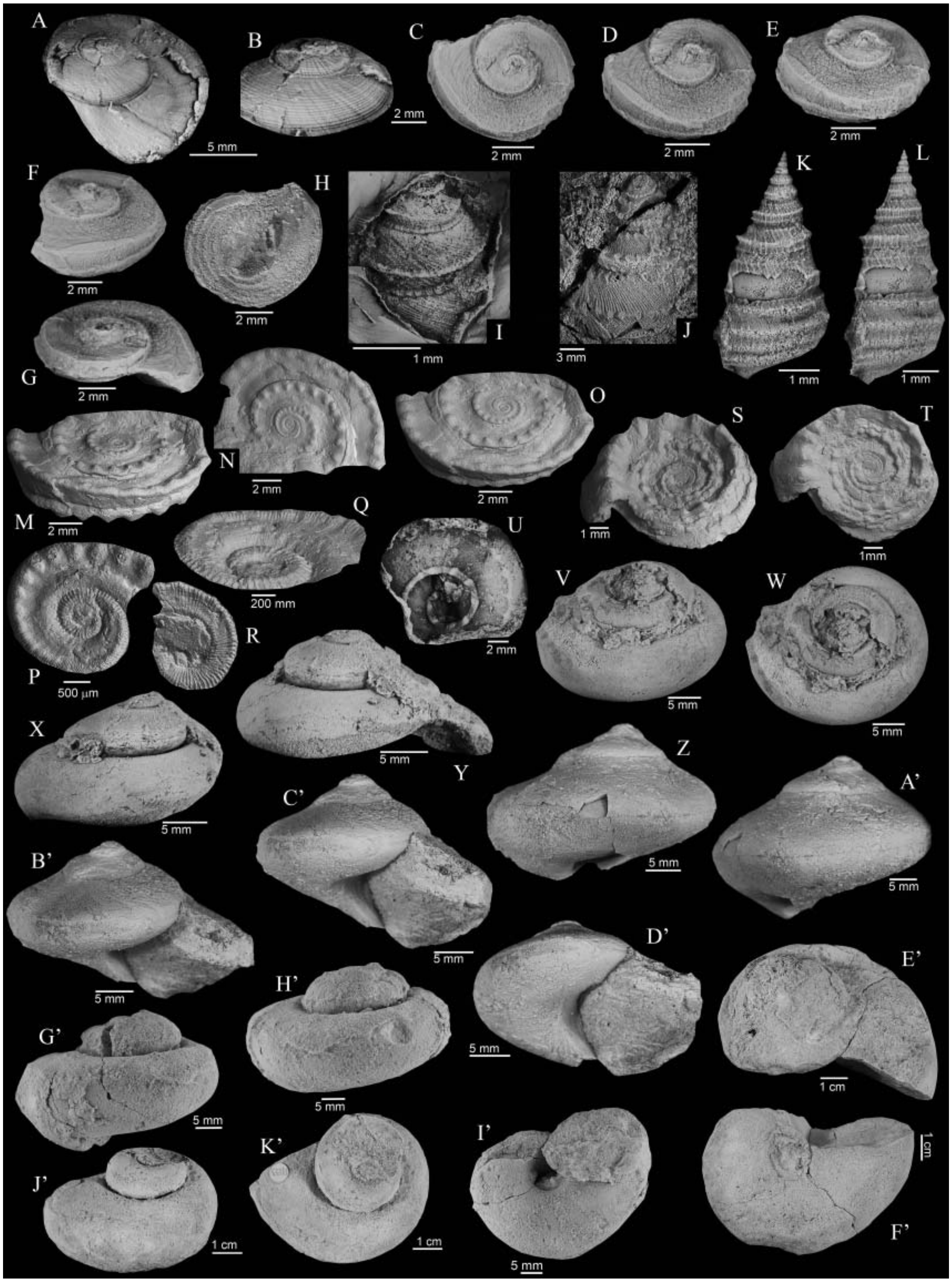

Figure 4. **A, B,** *Striatoconulus*? *axialis* sp. nov., MLP 12162, holotype; **A′,** apical view; **B′,** ornament detail. **C−H,** *Guidonia disciformis* sp. nov., MCF-PIPH 703, holotype; **C, D,** apical views; **E−G,** apical and lateral views; **H,** basal view. **I, J,** *Ambercyclus andinus* sp. nov.; **I,** MCF-PIPH 544, holotype, lateral and apical views; **J,** MB. Ga. 767, lateral and apical views. **K, L,** *Ambercyclus chilcaensis* sp. nov., MLP 34557, holotype, lateral views. **M−T,** *Discohelix sanicoensis* sp. nov.; **M−R,** MLP 34565, holotype; **M,** lateral and apical views; **N, O,** apical views; **P−R,** juvenile whorls detail; **S−T,** MLP 34566, paratype, apical views. **U,** *Colpomphalus*? aff. *musacchioi* Ferrari, 2014, MCF-PIPH 543, basal and umbilical views. **V−F′,** *Cryptaenia sudamericana* sp. nov.; **V−Y,** MLP 28702, paratype; **V, W,** apical views; **X, Y,** lateral views; **Z−D′,** MCF-PIPH 698, holotype; **Z, A′,** lateral views; **B′, C′,** lateral and apertural views; **D′,** basal and apertural views; **E′, F′,** MLP 34570, paratype; **E′,** apical view; **F′,** basal and umbilical views. **G′−K′,** *Cryptaenia globosa* sp. nov.; **G′−I′,** MLP 34568, holotype; **G′, H′,** lateral views; **I′,** basal and umbilical views; **J′, K′,** MLP 17133; **J′,** lateral view; **K′,** apical view.

Derivation of name. Referring to the strongly discoidal general shell morphology.

Material. Holotype, MCF-PIPH 703, well-preserved and replaced teleoconch.

Occurrence. Cerro Roth, Neuquén Province, Argentina; Pliensbachian, Piedra Pintada Formation.

Description. Dextral, gradate, discoidal, small sized and very low-spired shell, with a height of 3.2 mm and a width of 6.8 mm. The protoconch is not preserved. The teleoconch is fragmentary and consists of 3 whorls; last whorl is much more expanded than the spire. The teleoconch whorls form a wide, flattened and horizontal ramp; the outer face is very narrow, flat and almost vertical. Sutures are delimited in a furrow and run on the outer face of previous whorls. On the ramp of the last whorl, marked and prosocline growth lines form collabral riblets. The spiral ornament consists of two acute, peripheral keels bordering the outer face of the whorls at the angulation and at the outer edge of the base, respectively. Both keels are completely visible on last whorl but the abapical keel is covered by the preceding whorl on the spire. Apart from the spiral keels, the shell is smooth. The base is flat to slightly convex and ornamented by 3−4 acute spiral keels. The umbilical area is wide and the umbilicus not deeply developed. The aperture is fragmentary and quadrangular, with the outer lip thin and indented by the peripheral spiral keels.

Remarks. The material shows the typical characters of *Guidonia*, such as a low or depressed spire, main elements of the ornamentation consisting of two spiral keels which border the lateral whorl face, prosocline collabral riblets on the ramp, and a wide umbilicus.

Guidonia disciformis sp. nov. represents the first occurrence of the genus in the Early Jurassic of Argentina, and indeed South America. The new species resembles *Chartronella paganiae* Ferrari, 2011 (p. 69, fig. 7.1−7.10), from the Early Jurassic of Chubut Province; however, *G. disciformis* is smaller, has a lower spired shell, fine growth lines on the ramp of the last whorl, and a wide umbilical area. *Guidonia riedeli* Bandel *et al*., 2000 (p. 82, pl. 4, figs 1−3, 5), from the Early Jurassic of New Zealand, is also very similar to the Argentinian form. *G. riedeli*, however, has the teleoconch whorls covered by fine spiral lirae, the axial ornament is also present on base, and the outer face of the last whorl is wider and more concave. The type species, *Guidonia pseudorotula* Gatto & Monari, 2010 (p. 786, text-fig. 6H−N) (Szabó 2009, p. 73, fig. 71C, D) from the Early Jurassic (late Sinemurian) of Austria, differs from *G. disciformis* in having a higher and more gradate shell, a sutural ramp that is moderately oblique, a flat and vertical outer face, and in having a wider umbilicus.

Haas (1953) described species of *Guidonia* from the Late Triassic of the Pucara Group that are very similar to *G. disciformis* sp. nov. *Guidonia planetecta* Haas, 1953 (p. 67, pl. 4, figs 19, 21−31, 33−35, 37, 38, 44, 45) is of similar size but has a higher spire and a more gradate shell outline, more acute spiral elements which appear to have small and very weak nodes, more convex base, and a wide, deep and funnel-shaped umbilicus. *Guidonia bifasciata* Haas, 1953 (p. 74, pl. 4, figs 76−78, 81−85, pl. 5, figs 1−3, 7, 8, 14, 15, 21, 22) differs from *G. disciformis* in having a higher spire, more acute spiral ribs crossed by very weak axial ribs which form small nodes at the intersection points, and a circular aperture.

Superfamily **Eucycloidea** Koken, 1897
Family **Eucyclidae** Koken, 1897
Genus ***Ambercyclus*** Ferrari *et al*., 2014

Type species. *Ambercyclus orbignyana* (Hudleston, 1892) (= *Purpurina ornata* d'Orbigny, 1850; preoccupied), Middle Jurassic (Bajocian) of England.

Occurrence. Early Jurassic (Sinemurian) to Middle Jurassic (Bajocian); Europe and South America.

Remarks. The genus *Ambercyclus* was recently proposed by Ferrari *et al*. (2014) to include eucyclid forms having morphological characters intermediate between *Amberleya* and *Eucyclus*. According to these authors, species of *Ambercyclus* have: "trochiform shell, with a distinctly conical to slightly pagodiform and a small umbilicus; juvenile whorls are convex, mature whorls are characterized by a strong peripheral spiral keel with pointed nodes; weaker spiral keel with small nodes is located below the peripheral keel; a third spiral keel appear near the adapical suture; fine prosocline collabral ribs connect nodes of spiral elements. Sutures are incised in a fine spiral furrow. The base is strongly convex with regularly spaced spiral cords, with or without nodes. The aperture is oval, with the inner lip thickened forming a concave callus and the outer lip thin, indented by peripheral spiral cord" (Ferrari *et al*., 2014, p. 1178). The material described here shows the typical characters of *Ambercyclus*.

Ambercyclus andinus sp. nov.
(Fig. 4I, J)

2001 *Amberleya*? sp. Gründel; 50, pl. 3, figs 1, 2.

Diagnosis. Gradate, conical to slightly coeloconoidal shell; teleoconch with 4 whorls; apical angle of 113°; wide ramp; sutures impressed in a deep furrow; peripheral spiral keel with conspicuous nodes; adapical spiral keel weaker; a third very weak spiral keel below the suture; nodes formed at the crossing points of axial and spiral elements; strongly prosocline axial riblets on the shell surface.

Derivation of name. In reference to the Andean region of South America, where the material was found.

Material. Holotype: MCF-PIPH 544, fragmentary replaced teleoconch preserved as an external mould. Paratype: MB.Ga.767 (Gründel 2001), fragmentary teleoconch preserved as negative and external mould.

Occurrence. Cerro Roth, Neuquén Province, Argentina; Pliensbachian, Piedra Pintada Formation. Cerro de Cuevitas, Antofagasta region, Chile; Early Jurassic, early Sinemurian.

Description. Dextral, trochiform, gradate, conical to slightly coeloconoidal, medium sized and high-spired shell. The protoconch is not preserved. The fragmentary available specimens comprise 4 conical to slightly coeloconoidal whorls, with a mean height of 19.5 mm and a mean width of 15.5 mm. The apex forms an angle of 113°. The ramp of whorls is wide; the upper portion of the whorls shows a slightly convex angulation just below the suture. Sutures are clearly impressed in a deep spiral furrow. Ornament consists of axial, spiral and nodular elements. Spiral elements comprise two spiral keels on the outer face of whorls; the adapical is peripheral, strongly developed as a carina, and coincides with the angulations; the abapical is weaker and borders the suture. Another shallower spiral keel seems to be present just below the suture. Nodular elements arise at the crossing points of spiral and axial elements; nodes are stronger on the peripheral carina. Axial ornament consists of strongly prosocline collabral riblets on the ramp and in the outer face. Apertural and basal characters are missing.

Dimensions. MCF-PIPH 544, holotype: height = 21 mm; width = 16 mm; apical angle = 113°. MB.Ga. 767, paratype: height = 17.8 mm; width = 14.8 mm.

Remarks. Gründel (2001, p. 50, pl. 3, figs 1, 2) described *Amberleya*? sp. from the Early Jurassic (Sinemurian) of Chile; his specimen is included here in the synonymy of *A. andinus* sp. nov.

Eucyclus subtiliscostatus Gründel (2001, p. 49, pl. 2, figs 8−10), from the Early Jurassic (Hettangian) of Chile, differs from *A. andinus* sp. nov. in having two equally and more strongly developed spiral keels, both peripheral; crowded, opisthocyrt growth lines on the flanks and orthocline on the outer face. It also lacks conspicuous nodes. *Eucyclus* sp. Gründel (2001, p. 50, pl. 2, figs 11, 12), from the Early Jurassic (Sinemurian) of Chile, is smaller, has a higher spire, more gradate teleoconch whorls, two peripheral keels, and less-developed and more spaced axial riblets. *Eucyclus* (*Eucyclus*) *mitterseensis* Szabó (2009, p. 75, fig. 73), from the Early Jurassic (Sinemurian) of Austria, is similar to *A. andinus* in general shell morphology and ornament pattern, with spiral angulation near the lower suture, but, has a weaker abapical spiral carina covered by the suture on the earliest whorls, and growth lines which are moderately prosocline.

The type species of *Ambercyclus*, *Ambercyclus orbignyana* (Hudleston, 1892, p. 285, pl. 22, figs 7, 8), from the Middle Jurassic (Bajocian) of England, also resembles *A. andinus* sp. nov. However, *A. orbignyana* has 2 equally developed peripheral spiral keels. *Ambercyclus murchisoni* (Münter, 1844), from the Middle Jurassic (Bajocian) of the Central High Atlas (Morocco) (Conti & Monari 2001, p. 195, fig. 6.13−6.17), differs from the Argentinian species in having more conspicuous to spinose nodes at peripheral keels, a more gradate shell, and weaker collabral ribs.

Ambercyclus chilcaensis sp. nov.
(Fig. 4K−L)

Diagnosis. Strongly gradate shell; protoconch with 1.5 convex and smooth whorls; teleoconch with 8 whorls; apical angle of 43°; sutures impressed in a spiral furrow; oblique and narrow subsutural band; outer face concave and narrow; a third weak spiral cord on the outer rim of the subsutural shelf; mature whorls angular with 2 peripheral spiral keels; nodes of adapical and peripheral keels connected by prosocline axial riblets; axial riblets orthocline between the peripheral keels; base strongly convex and bearing spiral cords.

Derivation of name. With reference to the type locality Arroyo Las Chilcas.

Material. Holotype, MLP 34557, well-preserved and replaced teleoconch. Paratype, MLP 34558, fragmentary and replaced teleoconch.

Occurrence. Arroyo Las Chilcas, Río Atuel, Mendoza Province, Argentina; late Sinemurian (*Orthechioceras−Paltechioceras* Faunule), Puesto Araya Formation.

Description. Dextral, gradate, conical, small to medium sized and high-spired shell. The protoconch consists of 1.5 strongly convex and smooth whorls. The two earliest teleoconch whorls are angular with 2 regularly spaced spiral keels both peripheral. The teleoconch consist of 8 strongly gradate whorls, with a mean height of 12 mm and a mean width of 5.8 mm. The apex forms an angle of 43°. Sutures are weakly impressed in a spiral furrow. The whorl outline shows a very narrow, oblique and concave subsutural band, a strongly oblique and concave ramp, and a vertical, concave and narrow outer face. The outer face is bordered by 2 strongly nodular, peripheral, acute and regularly spaced spiral keels; a third weak, nodular, adapical spiral cord borders the outer rim of the subsutural shelf. Nodes of adapical and peripheral keels are connected by prosocline axial riblets. On the outer face, the axial ribs become orthocline. The base is strongly convex and ornamented by 3 acute and nodular spiral keels. Axial riblets are othocline on the base. The aperture is missing.

Dimensions. MLP 34557, holotype: height = 10.7 mm; width = 4.8 mm; apical angle = 43°. MLP 34558, paratype: height = 13.3 mm; width = 6.9 mm.

Remarks. *Ambercyclus chilcaensis* sp. nov. differs from *A. andinus* sp. nov. in being smaller, in having two peripheral spiral keels on the whorls, less conspicuous nodes at the intersection points of spiral and axial elements, and orthocline growth lines and collabral riblets on the outer face.

The occurrence of *A. chilcaensis* and *A. andinus* in the Early Jurassic of Neuquén basin extends the genus range in Argentina.

Ambercyclus espinosus (Ferrari, 2009), from the Early Jurassic of Chubut Province, differs from *A. chilcaensis* sp. nov. in being larger, having a stronger peripheral spiral keel, and more widely spaced and spinose nodes (Ferrari *et al*. 2014). Another Argentinian species similar to the one described here is *A.*? *isabelensis* Ferrari *et al*., 2014, from the Early Jurassic of Mendoza, Neuquén and Chubut provinces. *A.*? *isabelensis*, however, is larger than *A. chilcaensis* sp. nov., has a strongly developed prosocline and opisthocyrt axial ribs, and more spinose nodes on the shell surface and on the base (Ferrari *et al*. 2014).

The type species, *Ambercyclus orbignyana* (Hudleston, 1892) (p. 285, pl. 22, figs 7, 8) from the Middle Jurassic (Bajocian) of England, is also comparable to *A. chilcaensis* sp. nov. but the European form has 5 spiral keels on the base, and lacks prosocline axial riblets on the whorl surface. *Ambercyclus capitaneus* (Münster, 1844) (Hudleston 1892, p. 277, pl. 21, fig. 12), from the Middle Jurassic of Germany and England, is larger than the Argentinian species, has a slightly more convex shell and a spire angle of 55°, and also has more acute nodes on the spiral elements. *Ambercyclus ornatus* (Sowerby, 1819), from the Middle Jurassic of Morocco, also resembles *A. chilcaensis*, but *A. ornatus* is larger, has a more gradate shell and more pointed nodes (Conti & Monari 2001, p. 196, fig. 6.6–6.12).

Superfamily **Cirroidea** Cossmann, 1916
Family **Discohelicidae** Schöder, 1995
Genus ***Discohelix*** Dunker, 1847

Type species. *Discohelix calculiformis* Dunker, 1847, Early Jurassic (early Pliensbachian), Germany.

Occurrence. Early Jurassic (Sinemurian) to Middle Jurassic (Bajocian/Callovian?); cosmopolitan.

Remarks. According to Gründel (2005) and Bandel (2010), *Discohelix* is typically planispiral with a disc-like quadrangular shell, the upper side concave to nearly plane, and the underside concave with a wide umbilicus. The cross section of the whorls is trapezoidal, and the whorl diameter increases slowly. The protoconch is as in Trochidae. The ornament comprises fine spiral and axial lines, and few axial folds present only on the periphery in many species. The early teleoconch is smooth or has fine spiral lines and axial ribs, and a strong peripheral spiral rib may appear later. The lateral side lacks axial ribs. The type species of the genus is known from the Pliensbachian of Germany (according to Gründel 2005). Here, the characterizations of Gründel (2005) and Bandel (2010) are followed to include the Argentinian material in *Discohelix*.

Other members of the family Discohelicidae, such as *Colpomphalus*, were previously reported in the Early Jurassic of Argentina and Chile (see Gründel 2001; Ferrari 2014). The differences between *Colpomphalus* and *Discohelix* were clearly stated by Gründel (2005): *Colpomphalus* has few teleoconch whorls and the lateral side of the shell is high and oblique, with opisthocyrt growth lines. *Discohelix* is more depressed and symmetrical, with the outer face strongly concave to nearly planar, and without growth lines on the lateral side of the shell.

Discohelix sanicoensis sp. nov.
(Fig. 4M–T)

Diagnosis. Small, discoidal, planispiral and biconcave shell; first teleoconch whorl convex with strong axial ribs; earliest whorls with two nodular spiral bumps; mature whorls with strongly nodular peripheral spiral keel; axial riblets absent in mature whorls; side of last whorl oblique, biangular and smooth; base bordered by a strong nodular spiral keel; aperture slightly oblique.

Derivation of name. In reference to Sañicó, the type locality.

Material. Holotype: MLP 34565. Paratypes: MLP 34566, 12 teleoconchs preserved as negative moulds. Additional material: MLP 34567, 1 teleoconch preserved as negative mould.

Occurrence. North of Sañicó and Arroyo Lonqueo, Neuquén Province, Argentina, Pliensbachian, Piedra Pintada Formation and ‘Cuyo’ Group.

Description. Dextral, depressed discoidal, planispiral, biconcave, small sized shell, with a mean height of 2.4 mm and a mean width of 9.3 mm. The first teleoconch whorl is convex and ornamented by strong, crowded and regularly spaced axial riblets. The earliest whorls are concave with two nodular spiral bumps located in adapical and abapical positions. The adapical spiral bump disappears towards the mature whorls, and the abapical spiral bump becomes stronger as a keel, peripheral, acute, with rounded to pointed nodes. Weak and crowded axial ribs appear on the side of juvenile whorls; these axial ribs trend to disappear towards mature growth stages. The surface of mature whorls is strongly concave and smooth, bordered by a prominent peripheral spiral keel with acute and pointed nodes. The side of the last whorl is angular and lacks axial ribs. The base is delimited by a strongly nodular spiral keel. The aperture is fragmentary and slightly oblique.

Dimensions. MLP 34565, holotype: height = 2 mm; width = 11 mm. MLP 34566, paratype: height = 2.7 mm; width = 7.4 mm.

Remarks. Features such as the convex protoconch ornamented with strong axial ribs, the strongly concave surface of the mature whorls, and the presence of an acute peripheral spiral keel with pointed nodes, separate the new species from other representatives of the genus.

Discohelix sanicoensis sp. nov. is the first reported species of the genus in the Early Jurassic of South America. It differs from the type species, *Discohelix calculiformis* Dunke, 1847 (Gründel 2005, p. 734, fig. 3), from the Early Jurassic (early Pliensbachian) of Germany, in having a medium to large sized shell, smaller and more rounded nodes on the peripheral keel, and opisthocyrt growth lines on the side of the last whorl. Szabó (2009) described several discohelicid species similar to *D. sanicoensis* sp. nov. *Discohelix pseudornata* Szabó, 2009 (p. 9, fig. 3A−D, M, N), from the Early Jurassic (Sinemurian) of Austria, differs from *D. sanicoensis* sp. nov. in having delicate growth lines and weak, sub-regularly repeating collabral ridges on the shell surface, as well as carinae with crowded and rounded granules which become sparser and elongated on the last whorl. Another European species similar to *D. sanicoensis* is *D. reticulata* Szabó, 2009 (p. 17, fig. 12), also from the Early Jurassic (Sinemurian) of Austria but this species has marked riblet-like growth lines which run suture to suture, and the last whorl is strongly convex but earlier whorls are flattened. *D. excavata* (Reuss) (Szabó 2009, p. 11, fig. 5; Gatto & Monari 2010, p. 789, text-fig. 7G−J), from the Early Jurassic (late Sinemurian−late Pliensbachian) of Europe, resembles *D. sanicoensis*; however, the European species has a much higher teleoconch, with up to eight whorls, less-pointed nodes, closely and very regularly spaced collabral elements on the last whorl, and strongly excavated apical and umbilical sides of the shell.

Genus ***Colpomphalus*** Cossmann, 1916

Type species. *Straparollus altus* d'Orbigny, 1853, Middle Jurassic (Bathonian), France.

Occurrence. Early−Middle Jurassic; Europe and South America.

Colpomphalus*? aff. *musacchioi Ferrari, 2014
(Fig. 4U)

aff. 2014 *Colpomphalus musacchioi* Ferrari: 11, fig. 5a−j.

Material. MCF-PIPH 543, fragmentary teleoconch preserved as negative and external mould.

Occurrence. Cerro Roth, Neuquén Province, Argentina; Pliensbachian, Piedra Pintada Formation.

Description. Phaneromphalous, discoidal and medium sized shell, with a width of 17 mm. The fragmentary teleoconch consist of 1−1.5 shell whorls in basal view. The base is flat with a sharply angulated outer rim bordering a row of conspicuous nodes. The umbilicus is wide and deep, and is also bordered by a row of conspicuous nodes. Weak growth lines are visible in basal view on the outer face of whorls. Other characters are not preserved.

Remarks. According to the diagnosis proposed by Ferrari (2014), the single specimen here described seems to be conspecific with *Colpomphalus musacchioi* Ferrari, 2014 (p. 11, fig. 5a−j), from the Early Jurassic (early Toarcian) of Chubut Province. However, in the single available specimen, only the basal and umbilical characters are preserved, whereas other diagnostic features of the genus, such as lateral sides high and oblique with opisthocyrt growth lines, and abapical keel with fewer and larger nodes than the adapical keel, are not observable. For this reason, the material is referred doubtfully to *Colpomphalus*.

Superfamily **Ptychomphaloidea** Wenz, 1939
Family **Ptychomphalidae** Wenz, 1938
Genus ***Cryptaenia*** Eudes-Deslongchamps, 1864

Type species. *Pleurotomaria heliciformis* Eudes-Deslongchamps, 1849, Late Pliensbachian, France.

Occurrence. Early Jurassic (Hettangian−Pliensbachian); Europe and South America.

Remarks. The genus *Cryptaenia* was recently revised by Gründel (2011, p. 61) to include taxa with: "shells lens-shaped with a spira from the same height as the convex base. Both are connected by a broad convexity without an edge. Selenizone mostly not very distinct and covered by the following whorl. Shell mostly sculptureless. Growth lines may be strengthened and some weak spiral furrows may be developed. A broad callus covers the centre of the base." *Cryptaenia* is very similar to *Ptychomphalus* Agassiz, 1837 but has a more trochiform shell with a higher spire and a selenizone that is mostly visible on the last whorl (Gründel 2011).

Cryptaenia sudamericana sp. nov.
(Fig. 4V−F′)

p. 1978 *Ptychomphalus* sp. Volkheimer *et al.*: 212, tab. 2.

Diagnosis. Sublenticular shell; peripheral selenizone weak, narrow and concave; ornament absent or comprising two spiral threads; base slightly convex; umbilicus opened or covered by a callus; aperture subquadrangular with the peristome discontinuous.

Derivation of name. Referring to the first occurrence of this genus in the Jurassic of South America.

Material. Holotype: MCF-PIPH 698. Paratypes: MLP 34572, 28702, 34570, 34571.

Occurrence. Cerro Roth, Neuquén Province; Pliensbachian, Piedra Pintada Formation. Quebrada de los Caballos, Mendoza Province; Pliensbachian, Puesto Araya Formation. Cerro Tricolor, Mendoza Province; early Toarcian, Puesto Araya Formation. Río de los Patos Sur, San Juan Province; late Pliensbachian.

Description. Dextral, sublenticular, cryptomphalous to phaneromphalous, medium to large sized and low-spired shell, with a mean height of about 18 mm and a mean width of about 35 mm. The apex forms an angle of 113−127°. The coeloconoidal spire comprises 2−3 whorls; the last teleoconch whorl is greatly expanded. Whorls are slightly convex to flat, becoming strongly convex toward the outer face. Ramps of whorls are widely horizontal. The periphery is angular, and probably with a row of weak nodes. On the periphery, the selenizone is weak, nearly narrow and concave. The selenizone is exposed only on last teleoconch whorls and overlapped by earlier whorls on the spire. Sutures are clearly impressed in a deep spiral furrow. The shell is externally smooth or ornamented by 2 spiral keels; one spiral keel is located in an adapical position bordering the suture; and the second keel, more developed as a carina, is peripheral. The selenizone is located below the peripheral spiral carina and bordered by a weak spiral cord, abapically. The base is slightly convex to flat, and the umbilicus is widely opened or may be covered by an encircled callus. The aperture is subquadrangular and the peristome discontinuous; the columellar lip thickened and extending as a callus into the umbilical area.

Dimensions. MCF-PIPH 698, holotype: height = 21.2 mm; width = 32.4 mm, apical angle = 114°. MLP 28702, paratype: height = 13.7 mm; width = 26 mm; apical angle = 123°. MLP 34572, paratype: height = 7.4 mm; width = 12.2 mm. MLP 34570, paratype: height = 30 mm; width = 71 mm.

Remarks. The present material shows the typical characters of *Cryptaenia*, such as: lens-shaped shell, with low spire and convex base; smooth surface; selenizone not very distinct and covered by the following whorl; and umbilicus covered by a callus.

Cryptaenia sudamericana sp. nov. shows a close resemblance to the type species, *Cryptaenia heliciformis* Eudes-Deslongchamps, 1849 (Fischer & Weber 1997; p. 155, pl. 25, figs 15, 16; Szabó 2009, p. 25, fig. 19 [as *Ptychomphalus heliciformis*]; Gründel 2011, p. 61, pl. 2, figs 8, 9 [as *Pleurotomaria heliciformis*]), from the Early Jurassic (late Sinemurian−late Pliensbachian) of Europe. However, the European species has a strongly rounded periphery, lower spire, more convex whorls and a simple, not discontinuous outer lip. *Cryptaenia rotellaeformis* (Dunker, 1847) (Gründel 2003, p. 3, pl. 1, figs 1−3; Monari *et al*. 2011, p. 368, fig. 12C [as *Ptychomphalus rotellaeformis*]; Gründel 2011, p. 61, pl. 1, figs 8−10), from the Early Jurassic (early/late Hettangian) of Germany, differs from the Argentinian species in being smaller, having fine prosocline growth lines on the shell surface, a wider selenizone, a more convex base and a columellar callus encircling the umbilical area. *Ptychomphalus expansus* (Sowerby, 1821) (Szabó 2009, p. 24, fig. 17), from the Early Jurassic of Europe and northern Africa, resembles *C. sudamericana* sp. nov. but is smaller and has concavities below the subsutural band and above the periphery. *P. keiricserensis* Szabó, 2009 (p. 24, fig. 18), from the Early Jurassic (late Sinemurian−early Pliensbachian) of Hungary, differs from the Argentinian species in being smaller, having prosocline growth lines and colabrally elongated nodes along the suture. Moreover, the base has prosocyrt growth lines and fine spiral lines. *Ptychomphalina*? *discoidea* Haas, 1953 (p. 27, pl. 1, figs 46, 47, 54, 58), from the Late Triassic of Peru, is very similar to the species described here but is much smaller, has a widely opened and funnel-shaped umbilicus, and the aperture is circular rather than subquadrangular.

Part of the material here described was referred to *Ptychomphalus* sp. by Volkheimer *et al*. (1978), but was neither described nor figured.

Cryptaenia globosa sp. nov.
(Fig. 4G′−K′)

v. 1978 Gastropoda sp. indet I Volkheimer *et al*.: 212, tab. 2.

Diagnosis. Dextral, lens- like to strongly globose, low-spired shell; cyrtoconoidal spire; last whorl greatly expanded; subsutural band concave; sutures impressed in a deep spiral furrow; ornamentation lacking; base strongly convex; deep and narrow umbilicus; subcircular aperture.

Derivation of name. Refers to the strongly globose shell shape.

Material. Holotype: MLP 34568; paratypes: MLP 34569, 17133, 17498. Fragmentary and replaced teleoconchs.

Occurrence. Arroyo La Bajada, Mendoza Province, Pliensbachian, Puesto Araya Formation; Río de los Patos Sur, San Juan Province, late Pliensbachian.

Description. Dextral, sublenticular to strongly globose, phaneromphalous, medium to large sized and low-spired shell, with a mean height of 28 mm and a mean width of 49.6 mm. The fragmentary apex forms an angle of about 140°. The cyrtoconoidal spire comprises 2–3 strongly convex whorls; the last teleoconch whorl is greatly expanded and convex. The subsutural band is concave. The selenizone is not clearly visible on the periphery of whorls. Sutures are clearly impressed in a deep spiral furrow. The shell is externally smooth. The base is strongly convex, and the umbilicus deep and narrowly opened. The aperture is subcircular, with the outer and basal lip strongly convex.

Dimensions. MLP 34568, holotype: height = 22 mm; width = 37 mm; apical angle = 140°. MLP 34569, paratype: height = 15.2 mm; width = 33.4 mm. MLP 17133, paratype: height = 34 mm; width = 55 mm; apical angle = 148°. MLP 17498, paratype: height = 41 mm; width = 74 mm.

Remarks. Following the characterization of Gründel (2011), the species here described fits into the genus *Cryptaenia*. *Cryptaenia globosa* sp. nov. differs from *C. sudamericana* sp. nov. in being larger, in having strongly convex whorls and a globular shell, a slightly more concave subsutural band, more convex base, more obtuse apical angle, subcircular aperture and a narrow umbilicus. *C. globosa* resembles the type species of *Cryptaenia*, *C. heliciformis*, but is slightly smaller, has a lower spire and lacks the concave sutural band.

Part of the material described here was referred to Gastropoda sp. indet. I by Volkheimer *et al*. (1978) but was neither described nor figured.

Cryptaenia globosa sp. nov. and *C. sudamericana* sp. nov. are the first species of the genus to be described from the Early Jurassic of South America, extending the palaeobiogeographical distribution of *Cryptaenia* into the southern hemisphere.

Discussion

Palaeobiogeographical implications

Nine new vetigastropod species are described from the Neuquén Basin; *Proconulus*? *argentinus* sp. nov., *Chartronella atuelensis* sp. nov., *Striatoconulus*? *axialis* sp. nov., *Guidonia housciformis* sp. nov., *Ambercyclus andinus* sp. nov., *A. chilcaensis* sp. nov., *Discohelix sanicoensis* sp. nov., *Cryptaenia sudamericana* sp. nov. and *C. globosa* sp. nov. Three other vetigastropods are reported for the first time from this region: *Chartronella gradata* Ferrari, 2014, *Ataphrus mulanguiniensis* Ferrari, 2011 and *Colpomphalus*? aff. *musacchioi* Ferrari, 2014, extending their palaeobiogeographical ranges in the Andean region of Argentina. *Lithotrochus humboldtii* (von Buch, 1839), *Lithotrochus rothi* Damborenea & Ferrari, 2008, and an undetermined ataphrid species are also identified.

As mentioned by Ferrari (2014), marine gastropods have been little used in palaeobiogeographical analyses of Mesozoic invertebrate faunas. Although earlier authors did not try to explain their distributional patterns, data on Early Jurassic marine gastropods from the western Tethys (Szabo 1994) showed that endemism is highly developed, resulting in characteristic and separable palaeobiogeographical units. Ferrari (2009) argued that Early Jurassic marine gastropods from west-central Patagonia are represented by several local species; however, a quantitative palaeobiogeographical analysis based on Argentinian Mesozoic gastropods has not been undertaken as gastropods from the Neuquén Basin were poorly known. This paper describes vetigastropod species from this basin and, together with the recent contributions by Ferrari *et al*. (2014, in press), permits the palaeobiogeographical analysis that follows.

In the present contribution, a clustering analysis was carried out in order to assess the palaeobiogeographical distributional patterns of the Early Jurassic marine vetigastropod faunas recorded in the Chubut and Neuquén basins of Argentina, including a large variety of depositional palaeoenvironments. The analysis has been performed with PAST statistical software (Hammer *et al*. 2001) employing Ward's method of clustering for the samples (Fig. 5). The data considered in the analysis integrates members of 11 vetigastropod families reported from 28 marine localities in the Neuquén and Chubut basins (Fig. 5; Supplemental Material). The gastropod sample includes representatives of the families Eucyclidae, Ataphridae, Pleurotomariidae, Trochidae, Proconulidae, Discohelicidae, Cirridae, Nododelphinulidae, Ptychomphalidae, Trochotomidae, and also an uncertain family, comprising a total of 35 vetigastropod species. The localities in Chubut Province are Aguada Plate, Lomas Occidentales, Cerro La Trampa, La Casilda, Aguada Loca, Lomas de Betancourt, Cañadón Puelman, Puesto Currumil and Puesto Peña (Fig. 5; Supplemental Material). From the Neuquén Basin, the localities sampled are represented in Neuquén, Mendoza and San Juan provinces: Sañicó, Cerro del Vasco, Cerro Roth, Carrán Curá, Estancia Santa Isabel, Arroyo Lonqueo, Catán Lil, Milla Michicó, Estación Rajapalo, Cerro Tricolor, Cerro Puchenque, Arroyo Blanco, Arroyo La Bajada, Portezuelo Ancho, Quebrada de los Caballos, Arroyo Malo, Arroyo Las Chilcas, El Pedrero and Río de los Patos Sur (Fig. 5; Supplemental Material).

The primary results of the analysis display two clearly discernible palaeobiogeographical units for Early Jurassic marine vetigastropod species in Argentina. The late Pliensbachian–early Toarcian of the Chubut Basin is characterized by a local fauna of nine marine gastropod species – *Calliotropis*? sp. (Ferrari 2014), *Leptomaria* sp. (Ferrari

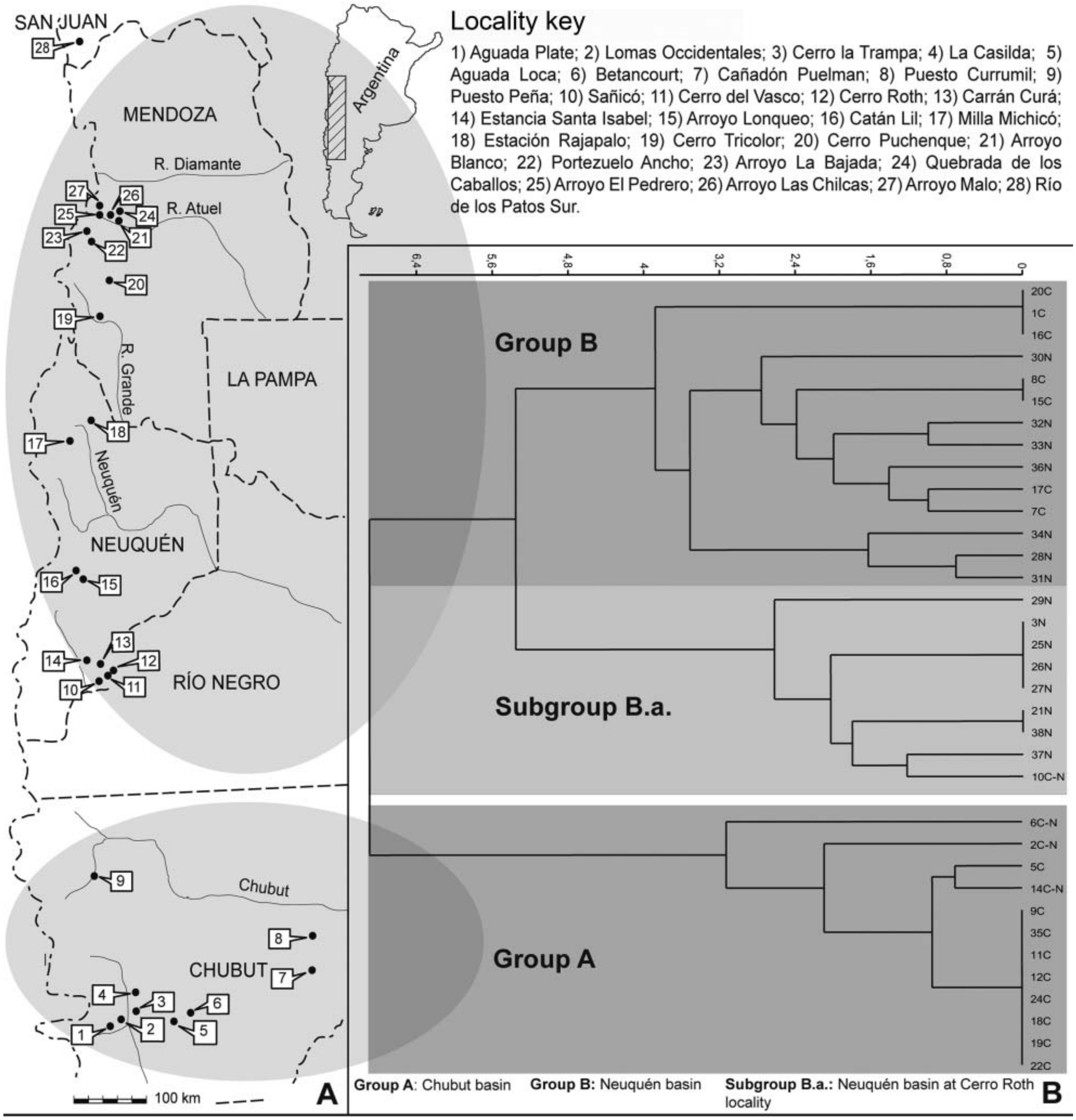

Figure 5. **A,** location map of the main localities with vetigastropod species in the Early Jurassic of Argentina. **B,** cluster analyses using Ward's algorithm; note good clustering of the Chubut vetigastropod species dominated samples next to the Neuquén vetigastropod species dominated samples. Geographical abbreviations: C, Chubut Basin; N, Neuquén Basin; C-N, Chubut and Neuquén basins. Species abbreviations: 1C, *Ambercyclus espinosus* Ferrari, 2009; 2C-N, *Ambercyclus*? *isabelensis* Ferrari *et al*., 2014; 3N, *Ambercyclus andinus* sp. nov.; 4N, *Ambercyclus chilcaensis* sp. nov.*; 5C, *Amberleya* cf. *americana* Möricke, 1894; 6C-N, *Calliotropis* (*Riselloidea*) *keideli* Ferrari *et al*., 2014; 7C, *Calliotropis* (*Riselloidea*) cf. *keideli* Ferrari *et al*., 2014; 8C, *Calliotropis* (*Riselloidea*) sp. Ferrari *et al*., 2014; 9C, *Calliotropis*? sp. (in Ferrari 2014); 10C-N, *Chartronella gradata* Ferrari, 2014; 11C, *Chartronella spiralis* Ferrari, 2011; 12C, *Chartronella paganiae* Ferrari, 2011; 13N, *Chartronella atuelensis* sp. nov.*; 14C-N, *Ataphrus mulanguiniensis* Ferrari, 2011; 15C, *Lewisiella*? sp. (in Ferrari 2011); 16C, *Striatoconulus* sp. (in Ferrari 2009); 17C, *Pleurotomaria* sp. (in Ferrari 2014); 18C, *Leptomaria* sp. (in Ferrari 2014); 19C, *Hamusina*? *wahnishae* Ferrari, 2014; 20C, *Colpomphalus musacchioi* Ferrari, 2014; 21N, *Colpomphalus*? aff. *musacchioi* Ferrari, 2014; 22C, *Jurassiphorus*? cf. *triadicus* Haas, 1953; 23C-N, *Lithotrochus humboldtii* (von Buch)*; 24C, *Lithotrochus* cf. *rothi* Damborenea & Ferrari, 2008; 25N, *Lithotrochus rothi* Damborenea & Ferrari, 2008; 26N, *Proconulus*? *argentinus* sp. nov.; 27N, *Guidonia disciformis* sp. nov.; 28N, *Discohelix sanicoensis* sp. nov.; 29N, *Cryptaenia sudamericana* sp. nov.; 30N, *Cryptaenia globosa* sp. nov.; 31N, *Striatoconulus*? *axialis* sp. nov.; 32N, *Pleurotomaria* cf. *multicincta* (Zietten, 1830); 33N, *Pleurotomaria* sp. (in Weaver 1931); 34N, *Trochus* cf. *perinanus* d'Orbigny, 1850; 35C, *Trochus* sp. (in Wahnish 1942); 36N, *Trochus* sp. (in Behrendsen 1891); 37N, *Trochotoma* (*Trochotoma*) *protonotilis* Ferrari *et al*., in press; 38N, *Trochotoma* (*Placotoma*) *neuquensis* Ferrari *et al*., in press. * = species removed from the analysis.

2014), *Chartronella spiralis* Ferrari, 2011, *Chartronella paganiae* Ferrari, 2011, *Hamusina*? *wahnishae* Ferrari, 2014, *Jurassiphorus*? cf. *triadicus* Haas, 1953, *Lithotrochus* cf. *rothi* Damborenea & Ferrari, 2008, *Trochus* sp. (Wahnish 1942) and *Amberleya* cf. *americana* (Wahnish, 1942) – which are not represented in the Neuquén Basin (Fig. 5, Group A). On the other hand, the Pliensbachian sediments in the Neuquén Basin have 15 local vetigastropod species: *Pleurotomaria* cf. *multicincta* Weaver, 1931, *Trochus* sp. (of Behrendsen 1891), *Pleurotomaria* sp. (of Weaver 1931), *Cryptaenia sudamericana* sp. nov., *Cryptaenia globosa* sp. nov., *Striatoconulus*? *axialis* sp. nov., *Trochus* aff. *perinanus* d'Orbigny, 1842, *Discohelix sanicoensis* sp. nov., *Proconulus*? *argentinus* sp. nov., *Lithotrochus rothi* Damborenea & Ferrari, 2008, *Colpomphalus*? aff. *musacchioi* Ferrari, 2014, *Ambercyclus andinus* sp. nov., *Guidonia disciformis* sp. nov., *Trochotoma* (*Trochotoma*) *protonotialis* Ferrari *et al*., in press, and *Trochotoma* (*Placotoma*) *neuquensis* Ferrari *et al*., in press (Fig. 5, Group B). Note that *Chartronella gradata*, together with *Proconulus*? *argentinus*, *Lithotrochus rothi*, *Colpomphalus*? aff. *musacchioi*, *Ambercyclus andinus*, *Guidonia disciformis*, *Cryptaenia sudamericana*, *Trochotoma* (*Trochotoma*) *protonotialis* and *Trochotoma* (*Placotoma*) *neuquensis* form a subgroup within the Neuquén Basin which occur at the Cerro Roth locality (Fig. 5, Group B.a). Some taxa, such as *Ataphrus mulanguiniensis* Ferrari, 2011, *Ambercyclus*? *isabelensis* Ferrari *et al*., 2014, *Calliotropis* (*Riselloidea*) *kedeli* Ferrari *et al*., 2014, and *Chartronella gradata* Ferrari, 2014, are represented in both palaeogeographical areas, showing a wide distribution along the Andean region of Argentina. *Lithotrochus humboldtii* (von Buch, 1839), *Chartronella atuelensis* sp. nov. and *Ambercyclus chilcaensis* sp. nov. were removed from the analysis as they are represented through a wider span of time within the Early Jurassic, from the middle Hettangian to the Pliensbachian. Moreover, most of the species described in the Neuquén Basin are recorded only from the Pliensbachian, and thus there is no certainty that they are coeval with those from the Chubut Basin. The palaeobiogeographical units are interpreted, at least partially, to reflect different faunal stocks of different ages.

The Neuquén and Chubut basins contain a high number of local or pseudo-endemic gastropod species and are thus interpreted here as separate palaeogeographical units. The presence of these pseudo-endemic marine vetigastropods could indicate that their distribution was mainly controlled palaeogeographically, even though Gatto & Monari (2010) pointed out that environmental control is a determinant in the palaeobiogeographical distribution of some Tethyan marine gastropod species.

The latitudinal distributions of bivalve species within the same basins was analysed by Damborenea (1996) and Damborenea *et al*. (2010, 2012), but although some endemic bivalve species were recognized in these regions for late Pliensbachian/early Toarcian times, they do not show such a clear-cut pattern as the gastropods. Nevertheless, some bivalve superfamilies were significantly more diverse in the Chubut Basin, whereas several others were more diverse in the Neuquén Basin (Damborenea *et al*. 2012, fig. 4.17). The study of Early Jurassic marine bivalves from Chubut Province, including a detailed characterization of most taxa represented and the revision of their systematic position, is still in process.

Vicente (2005) summarized the evolution of the Jurassic Andean retroarc basin at a global scale for the Central Andes, checking the time of the marine transgressions along the Andean region of South America and distinguishing two main gulfs through the arc from which waters flowed simultaneously northwards and southwards in a narrow retroarc furrow. One of these gulfs was located at 25° S and is known as the Taltal Gulf (Fig. 1); the Curepto Pacific Gulf was located further south at 35° S (Fig. 1). Both Pacific gulfs appeared in the Late Triassic and extended during the Hettangian, and their evolution as separate basins ended in the middle Pliensbachian, giving rise to a continuous elongated basin from Chubut Province to northern Peru (Vicente 2005) (Fig. 1). According to Vicente (2005), the Curepto Gulf was established as a Pacific connection with the Neuquén Basin as early as Hettangian times, and at the beginning of the early Pliensbachian the marine transgression began to spread longitudinally through the Andean region of Argentina towards the north and south, reaching the central Chubut Basin in the late Pliensbachian (Fig. 1). A palaeogeographical interpretation of the vetigastropod distributional patterns in the Andean region of Argentina is most probably related to the independent and separate evolution of the Neuquén Basin since the early Hettangian to early Pliensbachian, and the absence of marine deposits in Chubut at that time. However, a shallow marine connection between the Neuquén and Chubut basins during the late Pliensbachian–early Toarcian throughout the Palaeo-Pacific seaway (arrows in Fig. 1) may also explain the common occurrence of some vetigastropod species in both palaeogeographical areas. Thus, the Palaeo-Pacific seaway (as indicated in Fig. 1) could have been a dispersal route enabling benthic vetigastropod marine faunal exchange between the Neuquén and Chubut basins since the late Pliensbachian.

Most of the new vetigastropod species here described characterize a palaeobiogeographical unit for the Neuquén Basin, which is clearly separable from the Chubut fauna. This suggests that new and updated taxonomic data can greatly assist qualitative and quantitative palaeobiogeographical studies, enabling interpretation of the distributional patterns of Mesozoic benthic gastropods along the Andean region of South America, and also in the southern hemisphere.

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Supplemental material

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