

## Systematic revision of Late Triassic marine gastropods from Central Perú: considerations on the Late Triassic/Early Jurassic faunal turnover

S. Mariel Ferrari<sup>1,2</sup>

<sup>1</sup> Museo Paleontológico Egidio Feruglio, Av. Fontana 140, U9100GYO, Trelew, Chubut, Argentina.  
mferrari@mef.org.ar

<sup>2</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Av. Rivadavia 1917, C1033AAJ, Ciudad Autónoma de Buenos Aires Argentina.

---

**ABSTRACT.** The Late Triassic/Early Jurassic boundary is marked by a mass extinction event which had an important effect on the marine benthic communities on a global scale. In the Andean region of South America, however, the impact of this phenomenon on the earliest Mesozoic marine invertebrate associations has not been evaluated thus far. The present contribution is a systematic revision of the Late Triassic marine benthic gastropod faunas from the Pucará Group of Central Perú, giving a detailed characterization of 18 species and an updated systematic assignment of representatives of the genera *Chartroniella*, *Phymatifer*, *Ptychomphalina*, *Paracerithium*, *Rhabdocolpus* and *Omphaloptycha*. This research includes a comparison of the Peruvian fauna with their related counterparts from the Early Jurassic of Argentina and the Early/Middle Jurassic of New Zealand. This approach attempts to interpret the Late Triassic/Early Jurassic faunal turnover after the end Triassic crisis and establishes a palaeobiogeographical scheme for the gastropod faunal exchange in the Southern Hemisphere across the palaeo-Pacific seaway during the Late Triassic/Early Jurassic.

**Keywords:** *Gastropoda*, *Late Triassic/Early Jurassic*, *Diversity*, *Palaeobiogeography*, *South America*.

**RESUMEN.** Revisión sistemática de los gastrópodos marinos del Triásico superior de Perú Central: consideraciones sobre el recambio faunístico en límite Triásico tardío/Jurásico temprano. El límite Triásico tardío/Jurásico temprano está marcado por un evento de extinción en masa que tuvo un efecto importante en las comunidades marinas bentónicas a escala global. Sin embargo, el impacto de dicho fenómeno sobre las asociaciones de invertebrados marinos del Mesozoico temprano en la región andina de América del Sur no ha sido evaluado hasta el momento. La presente contribución es una revisión sistemática de la fauna de gastrópodos marinos bentónicos procedentes del grupo Pucará en Perú Central, en la que se da una caracterización morfológica detallada de 18 especies y una asignación sistemática actualizada de representantes de los géneros *Chartroniella*, *Phymatifer*, *Ptychomphalina*, *Paracerithium*, *Rhabdocolpus* y *Omphaloptycha*. Este trabajo incluye una comparación de las faunas peruanas con faunas similares correspondientes al Jurásico temprano de Argentina y al Jurásico temprano/medio de Nueva Zelanda. Asimismo, el presente enfoque apunta a interpretar, el recambio faunístico que tuvo lugar en el límite Triásico tardío/Jurásico temprano después de la gran crisis de finales del Triásico, y a establecer un esquema paleobiogeográfico para los gastrópodos en el Hemisferio Sur a lo largo del corredor Paleo-Pacífico.

**Palabras clave:** *Gastrópoda*, *Triásico tardío/Jurásico temprano*, *Diversidad*, *Paleobiogeografía*, *América del Sur*.

## 1. Introduction

The Late Triassic marine gastropods from the Pucará Group (Central Perú) were studied by Haas (1953), who described 181 gastropod species which many are represented by only few and/or fragmentary specimens. Most of the species defined by Haas (1953) were subsequently compared with coeval and better preserved gastropod assemblages from the St. Cassian Formation (in northern Italy) (Bandel, 1994). Bandel (1994) related many genera (and families) of five major gastropod taxa (Vetigastropoda, Decoglossa, Neritimorpha, Caenogastropoda and Heterobranchia) from the St. Cassian Formation with those marine gastropods from the Pucará Group and noted several similarities in their taxonomic composition. Later, Bandel *et al.* (2000) compared some gastropod species from the Early/Middle Jurassic of New Zealand with representatives of the Peruvian association and also found resemblance between these associations. However, a detailed comparison of the Late Triassic fauna from Perú with other South American Mesozoic gastropods has not been assessed so far.

Several Argentinean Early Jurassic marine gastropods have been described by Ferrari (2009, 2011, 2012, 2013, 2014a, 2014b) and Ferrari *et al.* (2014) from the Chubut Province. Up to date, 13 gastropod families from the Early Jurassic (late Pliensbachian-early Toarcian) marine deposits of the Mulanguíñeu and Osta Arena formations (Chubut Province), representing 20 genera, 2 subgenera and at least 30 species are reported. However, the study of Early Jurassic gastropods from the Neuquén Basin is still pending. Damborenea *et al.* (1975) preliminarily reported 15 gastropod species from the late Pliensbachian beds at Piedra Pintada (southern Neuquén), and Ferrari *et al.* (in press) contributed to the paleontological knowledge of the family Trochotomidae in the Early Jurassic of the Neuquén basin. Recently, Ferrari (2011, 2012, 2013, 2014a, 2014b.) Ferrari *et al.* (2014) has described in detail and referred many gastropod species from Argentina to the genera *Chartroniella*, *Calliotropis*, *Ambercyclus*, *Colpomphalus*, *Cryptaenia*, *Guidonia*, *Hamusina*, *Jurassiphorus*, *Procerithium*, *Cryptaulax*, *Oonia*, *Striactaeonina*, *Actaeonina*. Most of the species described thus far from Argentina show close taxonomic affinities to the Late Triassic gastropod faunas reported by Haas (1953) from the Pucará Group of Central Perú. For instance, the genera *Chartroniella*, *Eucycloscala*,

*Phymatifer*, *Ptychomphalina*, *Guidonia*, *Hesperocirrus*, *Sororcula*, *Jurassiphorus*, *Paracerithium*, *Rhabdocolpus*, *Cryptaulax* and *Omphaloptycha* are in common with the Early Jurassic fauna from Argentina.

The Late Triassic/Early Jurassic boundary is marked by a mass extinction event which had an important effect on the marine benthic communities at world wide scale. In recent years, several studies greatly improved the knowledge on the systematics and phylogeny of the extant and fossils gastropods, suggesting that generic and higher level assignments of the older literature need systematic revision (Monari *et al.*, 2011). Thus, an updated systematic knowledge of marine benthic faunas would certainly facilitate palaeobiogeographical and diversity comparisons across the Late Triassic/Early Jurassic boundary.

The present paper aims at a systematic revision of the Late Triassic Peruvian gastropods originally described by Haas (1953), including a detailed characterization and an updated systematic assignment of 18 taxa, and the comparison with their related counterparts from the Early Jurassic of Argentina. An updated systematic assignment of the genera *Chartroniella*, *Phymatifer*, *Ptychomphalina*, *Paracerithium*, *Rhabdocolpus* and *Omphaloptycha* is also provided. The selection of the 18 Peruvian gastropod species relies on their striking resemblance and their close systematic affinities with the Early Jurassic fauna from Argentina, and with the Early/Middle Jurassic gastropod association from New Zealand. This approach attempts to interpret the Late Triassic/Early Jurassic faunal turnover after the Late Triassic marine mass extinction in South America, and establishes a palaeobiogeographical scheme for the gastropod faunas across the palaeo-Pacific sea way during the Late Triassic/Early Jurassic boundary. The Peruvian seaway is considered the most plausible mechanism for biotic exchange from Perú to the Andean region of Argentina.

## 2. Material and methods

The Late Triassic marine gastropod species described by Haas (1953) from the Pucará Group are currently stored in the American Museum of Natural History (AMNH) invertebrate collection. The material examined in the AMNH collection includes 18 gastropod species, represented by 5 holotypes, 9 paratypes and 9 syntypes. During the

present research, the specimens were reinvestigated and redescribed, and new photos have been taken by the technical staff of the AMNH and by the author. The quality of the new photos relies on the relatively bad preserved conditions of the specimens. Most of the AMNH gastropod material is coarsely silicified and generally poorly preserved, showing broken, fragmentary and desarticulated early whorls. The AMNH gastropod material was compared with Early Jurassic faunas from Argentina which are currently stored in the MLP, MCF-PIPH and MPEF-PI collections. Comparisons were also made with the New Zealand gastropods described by Bandel *et al.* (2000) and with Antarctic gastropods described by Edwards (1980) and Thompson and Turner (1986). For the updated systematic assignment the recent classifications of Bandel (1993, 2006, 2009, 2010), Bandel *et al.* (2000), Gründel (1999, 2001b, 2005, 2008), Gründel and Nützel (2012), Kaim (2004), Kaim *et al.* (2009), Nützel and Erwin (2004), Szabó (2009), Gatto and Monari (2010), and Ferrari (2014a).

A biodiversity analysis and rarefaction curves have been calculated for each accessible sample of marine gastropod taxa recovered thus far from Perú and Argentina using a statistical software PAST (Hammer *et al.*, 2001). The samples contained a total of 248 species representing 34 families.

**Institutional abbreviations:** AMNH: American Museum of Natural History, New York, USA; 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.

### 3. Systematic palaeontology

#### Order Vetigastropoda Salvini-Pläwen, 1980

##### Family Ataphridae Cossmann, 1915

##### Subfamily Ataphrinae Cossmann, 1915

##### Tribe Colloniini Cossmann, 1916

##### Genus *Chartronella* Cossmann, 1902

**Type species:** *Chartronella digoniata* Cossmann in Chartron and Cossmann, 1902, from the Early Jurassic of France.

**Occurrence:** Triassic-Jurassic; Europe, Asia, Africa, Perú and Argentina.

**Remarks:** Haas (1953) described two species of *Chartroniella* and included representatives of the

genus in the family Paraturbinidae Cossmann. Gründel (2008) proposed an updated diagnosis of *Chartronella* and moved it to the tribe Costataphrini Gründel. Ferrari (2011) however, suggested that representatives of *Chartronella* should be assigned the tribe Collonini Cossmann, based on their resemblance with the extant *Cantrainea* Jeffreys (see Iaso Kaim *et al.*, 2009). In the present study, the proposal on Ferrari (2011) is followed and the genus name *Chartronella* is retained instead of *Chartroniella*.

#### ***Chartronella pacifica* (Jaworski, 1923) comb. nov.**

Fig. 1A-E

1923 *Chartroniella pacifica* (Jaworski); Haas, 1953: p. 81, pl. 5, figs. 31-41, 45-47, 54.

**Material examined:** AMNH No. 35552A, No. 35552B, No. 35552C, No. 35552D, No. 35552E, No. 35553, No. 26530B; 7 teleoconchs, 'well preserved' and replaced.

**Occurrence:** Cerro de Pasco locality, 21 km E, 3.5 km SSE of Huanco Jenks Lot 26, and and 20 km N, 10 km SSE of Goyllarisquisga, Central Perú; Upper Triassic, Pucará Group.

**Description:** Dextral, trochiform, conical to slightly cyrtconical shell, with a weak change in the rate translation toward mature whorls. The protoconch is not clearly visible; the teleoconch consist of about six whorls. The mean height of the shell is 26.94 mm and the mean width is 20.72 mm. The sutural ramp is narrowly horizontal and tends to disappear on last whorl. The flank of whorls is flattened to slightly convex; the outer face becomes straight and vertical. The periphery of the shell coincides with the angulation and is bordered by a strong nodular keel; a weaker abapical spiral keel appears on latest whorls. The peripheral spiral keel bears rounded nodes; nodes are stronger and more acute on last whorl. Crowded prosocline collabral ribs appear and are also present at mature growth stages. The base is flat to slightly convex and expanded, without ornamentation. The aperture is holostomatous and subcircular; the outer lip is thin and indented by the peripheral spiral keel; the columellar lip is crescent-shaped.

**Affinities:** According to the characterization of Gründel (2008), the specimens here analyzed fit in definition of *Chartronella*, with an angular shell, two strong peripheral keels (the abapical keel is covered by subsequent whorls on the spire and is visible only

on mature whorls), and a crescent shaped- columellar lip as the most diagnostic features of the genus (see also Ferrari, 2011)

The specimens assigned to *Chartronella pacifica* (Jaworski, 1923) com. nov. (Haas, 1953, p. 81, pl. 5, figs. 31-41, 45-47, 54) are very similar in general shell morphology and size to *Chartronella gradata* Ferrari (2014a, p. 6, fig. 3i-s) (Fig. 1H-J), from the Early Jurassic (late Pliensbachian-early Toarcian) of Patagonia (Argentina); however, the Peruvian form has more developed and acute nodes on adult whorls. New material tentatively assigned to *Chartronella atuelensis* Ferrari, 2014b (Fig. 1K-L) has been recently reported from the Early Jurassic (Pliensbachian) of the Neuquén Basin (Argentina). The Argentinean form, however, is slightly smaller, has a lower spire and a more convex sutural ramp. *Chartronella paganiae* Ferrari (2011, p. 69, fig. 7.1-10) (Fig. 1M-O) from the Early Jurassic (late Pliensbachian-early Toarcian) of Patagonia, is another species comparable to

*C. pacifica*. *C. paganiae*, however, is much smaller, has a lower spire, and lack strongly prosocline collabral ribs on the shell surface. *Chartronella spiralis* Ferrari (2011, p. 71, fig. 9.1-6) (Fig. 2A-C) from the late Pliensbachian-early Toarcian of Patagonia has strongly developed spiral cords on the outer face of last whorl and on base, lower spire and a less conical shell.

***Chartronella wortheniaeformis* (Cox, 1949) comb. nov.**  
Fig. 1F-G

1949 *Chartroniella wortheniaeformis* Cox: p. 36, pl. 2, figs. 13-15; Haas, 1953: p. 83, pl. 5, figs. 42-44, 48, 55.

**Material examined:** AMNH No. 26531; ‘well preserved’ teleoconch.

**Occurrence:** Cerro de Pasco locality, 21 km E, 3.5 km SSE of Huanco Jenks Lot 26, Central Perú; Late Triassic, Pucará Group.

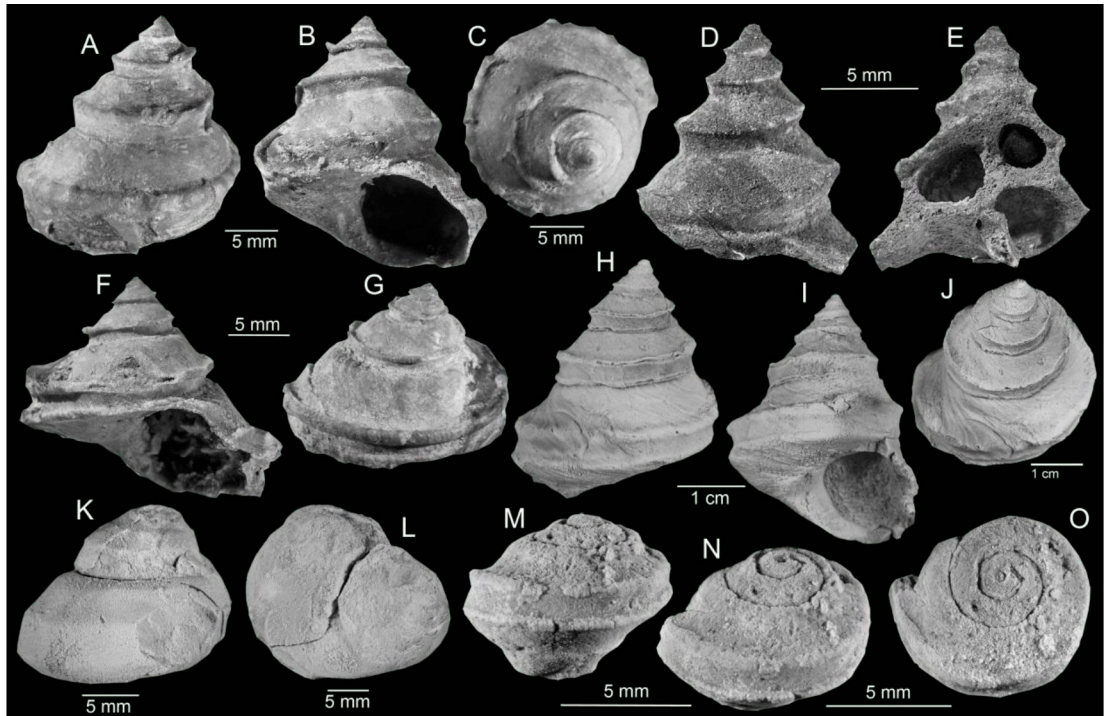


FIG. 1. A-E: *Chartronella pacifica* (Jaworski, 1923); A-C: AMNH No. 35552; A-B: lateral and apertural views; C: apical view; D-E: AMNH No. 26530; D: lateral view; E: columellar view; F-G: *Chartronella wortheniaeformis* (Cox, 1949), AMNH No. 26531; F: lateral and apertural view; G: apical view; H-J: *Chartronella gradata* Ferrari (2014a and b), MCF-PIPH 552; H-I: lateral and apertural views; J: apical view; K-L: *Chartronella atuelensis* Ferrari, 2014b MLP (8); K: lateral view; L: basal and apertural view; M-O: *Chartronella paganiae* Ferrari, 2011, MPEF-PI 4022; M: lateral view; N-O: apical views.

**Description:** Dextral, conical, gradate, trochiform and slightly low- spired shell, with a height of 17.1 mm and a width of 20.81 mm. The protoconch is not clearly visible; the teleoconch consist of five whorls. The sutural ramp is narrowly horizontal and more developed toward mature growth stages. The flank of whorls is slightly convex to flat; the outer face is vertical, and straight to slightly concave. Last teleoconch whorl is more expanded than spire whorls. The angulation is delimited by a strong spiral keel which is stronger on last whorl. The peripheral spiral keel bears weakly elongated nodes. A second abapical spiral cord is visible on last whorl and covered by subsequent whorls on the spire. The shell surface is covered by fine crowded prosocline growth lines. The base is flattened without ornamentation and bordered by an abapical spiral keel. The aperture is subcircular with the outer lip indented by the peripheral spiral keel; the inner lip is crescent- shaped.

**Affinities:** *Chartronella wortheniaeformis* com. nov. is very similar to *C. pacifica*; however, it has a lower spire, the peripheral keel is more acute and stronger, and the nodes on the peripheral keel are less elongated and weaker. *C. wortheniaeformis* resembles also *C. gradata* (see above); even though the Argentinean

form has a higher spire, the peripheral keel is weaker and lacks the elongated nodes.

### Family Eucycloscalidae Gründel, 2007

#### Genus *Eucycloscala* Cossmann, 1885

**Type species:** *Trochus binodosus* Münster, 1844 from the Late Triassic of St. Cassian Formation.

**Occurrence:** Late Triassic-Late Cretaceous; Europe and South America.

**Remarks:** Bandel (2010, p. 437) proposed an updated diagnosis of *Eucycloscala* consisting on a 'slender conical shells; axis of coiling of the planispiral protoconch may deviate from the axis of coiling of teleoconch; first teleoconch whorl ornamented by simple axial costae; later teleoconch whorls are ornamented with strong axial ribs, which are crossed by spiral ribs forming sharp nodes; ornament of base is spiral and sometimes with umbilicus; and the aperture simple, circular and with a continuous peristome'. The material described by Haas (1953) from the Late Triassic of Perú, fits in the diagnosis of Bandel (2010). Moreover, Haas (1953) included *Eucycloscala* in the family Turbinidae Rafinesque and Bandel (2010) in Eucycloscalidae. Here, the classification of Bandel

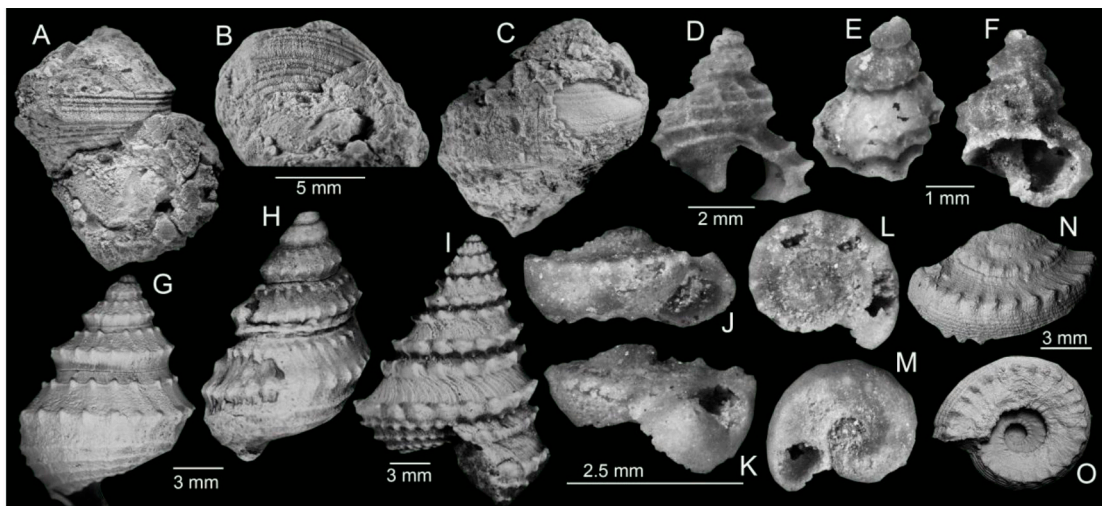


FIG. 2. A-C: *Chartronella spiralis* Ferrari, 2011, MPEF-PI 3590; A, C: lateral and apertural views; B: basal view; D-F: *Eucycloscala pascoensis* Haas, 1953; D: AMNH No. 26510A, holotype, lateral view; E-F: AMNH No. 26510B, paratype; E: lateral view; F: lateral and apertural views; G-H: *Calliotropis (Riselloidea) keideli* Ferrari et al., 2014; G: MPEF-PI 1160, holotype, lateral view; H: MPEF-PI 4132, lateral view; I: *Ambercyclus? isabelensis* Ferrari et al., 2014, MLP 18822, holotype, lateral view; J-M: *Colpomphalus Peruvianus* (Haas, 1953), AMNH No. 27543, holotype; J-K: lateral views; L: apical view; M: basal view; N-O: *Colpomphalus musacchioi* Ferrari, 2014a; N: MPEF-PI 4041, holotype, lateral view; O: MPEF-PI 4018, paratype, basal view.

(2010) is followed, considering that the genus diagnosis fits with the updated characterization of the family Eucycloscaliidae proposed by Gründel (2007).

***Eucycloscala pascoensis* Haas, 1953**

Fig. 2D-F

**Material examined:** Holotype, No. 26510A AMNH; well preserved teleoconch. Paratype, No. 26510B AMNH; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 21 km E, 3.5 km SSE of Huanco Jenks Lot 26, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, conical to slightly cyrtconical, trochiform, very small-sized and relatively high-spired shell, with a mean height of 3.66 mm and a mean width of 2.8 mm. The protoconch consists of one convex, dome shaped and smooth whorl that slightly deviates from the coiling axis of the teleoconch. The first teleoconch whorl is strongly convex and smooth; the ornament becomes more visible from second teleoconch whorl toward the mature whorls. On mature growth stages axial and spiral elements are present; prosocline to prosocyrt axial ribs are intercepted by three to four regularly spaced spiral cords, forming acute nodes at the crossing points. The ramp of whorls is widely flattened and horizontal to slightly sloped; the outer face becomes strongly convex. Suture is visible in a concave furrow. The aperture is holostomatous and circular; basal details are not preserved.

**Affinities:** Regarding related eucyclid-like forms from South America, *Eucycloscala pascoensis* Haas (1953, p. 102, pl. 6, figs. 61, 69, 72-76) slightly resembles *Calliotropis* (*Riselloidea*) n. sp. Ferrari *et al.* (2014) (Fig. 2G-H) from the Early Jurassic (late Pliensbachian-early Toarcian) of Chubut and Neuquén provinces; the Argentinean form, however, differs from the Peruvian species in being larger, having more distinct axial ribs on the shell surface, and a more circular aperture. Moreover, *E. pascoensis* possesses a characteristic reticulate pattern which is not present in *Calliotropis* (*R.*) n. sp. Other comparable species to *E. pascoensis* is *Ambercyclus*? n. gen. et n. sp. Ferrari *et al.* (2014) (Fig. 2I), also from the Early Jurassic of Argentina; however, *Ambercyclus*? n. gen. et n. sp. has strongly acute and spinose nodes, a larger shell and more distinct prosocline and opisthocyrt axial riblets. *Eucylus subtiliscostatus* Gründel (2001a, p. 49 pl. 2, figs.

8-10) from the Early Jurassic of Chile, also resembles *E. pascoensis*; however, Gründel's species has a more gradate outline, two strong spiral ribs delimiting the angulation of whorls forming a concave area in between; and strongly opisthocyrt collabral ribs on the shell surface. *Eucycloscala tortulosa* Bandel *et al.* (2000, p. 79, pl. 2, figs. 11-13) from the Early/Middle Jurassic of New Zealand is very similar to the Peruvian species; but, *E. tortulosa* has a less convex and more angulated outline toward mature whorls, and has a more developed spiral striation.

**Family Discoheliciidae Schöder, 1995**

**Genus *Colpomphalus* Cossmann, 1906**

**Type species:** *Straparollus altus* D'Orbigny, 1853, from the Middle Jurassic of France.

**Occurrence:** Late Triassic-Middle Jurassic; Europe and South America.

**Remarks:** The genus *Colpomphalus* Cossmann is common in Early and Middle Jurassic marine deposits of the Tethyan region. According to Gründel (2005), members of *Colpomphalus* share a discoidal, small- to medium-sized shell, with few whorls rapidly increasing in width, lateral side high and oblique, umbilicus relatively narrow, abapical keel with less and more acute nodes than the sutural keel, and growth lines on the lateral side of last whorl. Gründel (2001a) and Ferrari (2009, 2014a) reported representatives of the genus in the Early Jurassic of South America. Gründel (2001a) described *Colpomphalus toarciensis* Gründel from the Toarcian of Chile, and later Ferrari (2014a) reported *Colpomphalus musacchio* Ferrari from coeval deposits of Patagonia. Haas (1953) described a very small *Colpomphalus*-like species from the Late Triassic of Perú and included it into *Phymatifer* de Koninck (family Euomphalidae de Koninck). Haas's species, however, shows the typical characters of *Colpomphalus*; thus, here it is reassigned to this genus and included in the family Discoheliciidae.

***Colpomphalus Peruvianus* (Haas, 1953) comb. nov.**

Fig. 2J-M

1953 *Phymatifer Peruvianus* Haas: p. 32, pl. 2, figs. 5, 6, 12, 13.

**Material examined:** Holotype, AMNH No. 27543; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 7.5 km SSE Jenks Lot 31, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, discoidal, auriform, very small- sized and low- spired shell, with a height of 1.48 mm and a width of 2.45 mm. The protoconch is not clearly visible. The teleoconch consists of three whorls slightly gradate in outline; last whorl is more expanded than spire whorls. The sutural ramp of last whorl is widely horizontal, and flattened to slightly concave, and its periphery is delimited by a row of acute and slightly elongated nodes. The peripheral nodes coincide with the angulation of last whorl; the outer face is markedly convex to angular, ornamented by very fine and almost imperceptible spiral lines which are intercepted by fine growth lines. The base is flat to concave and bordered by a row of about 14 acute and pointed nodes. The umbilical area is widely opened and funnel- shaped, with a narrow umbilicus. The aperture is holostomatous, and the peristome oblique with a quadrangular outline.

**Affinities:** *Colpomphalus Peruvianus* com. nov. shows striking resemblance to *Colpomphalus musacchio* Ferrari (2014a, p. 11, fig. 5a-j) (Fig. 2N-O), from the Early Jurassic (late Pliensbachian-early Toarcian) of Patagonia; the Argentinean form, however, has a larger shell, less elongated and more rounded nodes on the angulation of last whorl, six to seven regularly spaced spiral threads and sigmoidal growth lines on the outer face, and a high number of nodes (24) on base. Another South American species comparable to *C. Peruvianus* is *Colpomphalus toarciensis* Gründel (2001a, p. 46, pl. 1, figs. 9-13), from the Early Jurassic (Toarcian) of Chile; both are similar in shell shape and ornamentation; however, Gründel's species is bigger, has high and pointed nodes on the angulation of last whorl, and a third row of nodes surrounds the umbilicus.

### Family Ptychomphalidae Wenz, 1938

#### Genus *Ptychomphalus* Agassiz, 1837

**Type species:** *Helicina compressa* Sowerby, 1813 from Early Jurassic of France.

**Occurrence:** Late Triassic-Lower Jurassic; Europe, northern Africa, South America.

**Remarks:** Bandel (2009) included representatives of *Ptychomphalus* in the Jurassic family Ptychomphalidae, suggesting that its placement in the family

Eotomariidae (proposed by Bouchet and Rocroi, 2005) is erroneous; even though the Ordovician *Eotomaria* somewhat resembles members of *Ptychomphalus*. This genus is also represented in the St. Cassian Formation (Bandel, 2009) and *Ptychomphalina* Fischer, 1885, is a closely related Peruvian Triassic form described by Haas (1953) and assigned by that author to the family Pleurotomariidae. In the present paper, I propose considering the genus *Ptychomphalus* as an anterior synonymous of the Peruvian *Ptychomphalina* following the updated classification of the genus proposed by Bandel (2009). The genus was recently revised by Gründel (2011).

#### *Ptychomphalus? discoidea* (Haas, 1953) comb. nov. Fig. 3A-C

1953 *Ptychomphalina? discoidea* Haas: p. 27, pl. 1, figs. 46, 47, 54-58.

**Material examined:** Holotype, AMNH No. 27693; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 24.5 km SSE, 0.5 km W of Ninacaca Jenks Lot 86, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, sublenticular, biconical, widely phaneromphalous, lens- like, very small- sized and low- spired shell, with a height of 1.69 mm and a width of 2.15 mm. The protoconch is fragmentary and consists of one convex and smooth whorl. The teleoconch comprises three to four convex whorls; ramp of whorls is convex becoming slightly concave toward the outer face of last whorl. Last teleoconch whorl is markedly more expanded than the spire. Ornament is not present on the shell surface and the selenizone is not completely visible either. Suture is clearly impressed in a weakly deep spiral furrow. The base is strongly convex and smooth, with a widely opened and funnel- shaped umbilicus. The aperture is holostomatous and circular, and the peristome continuous.

**Affinities:** The species described by Haas (1953) as *Ptychomphalina? discoidea*, shows the typical diagnostic features of *Ptychomphalus*, including a sublenticular shell, with low spire, convex base and smooth surface. However, other diagnostic features of the genus, such as, a peripheral selenizone and an umbilicus covered by a callus are absent in the Peruvian form; thus, the open nomenclature is also kept in the updated description of the species. It

also shows the diagnostic characters of *Cryptaenia* Eudes-Deslongchamps, 1864 (see diagnosis in Gründel, 2011); however, an opened umbilicus is not a typical character of the former genus.

*Ptychomphalus? discoidea* com. nov. resembles *Cryptaenia sudamericana* Ferrari, 2014b (Fig. 3D-E), from the Early Jurassic (late Pliensbachian-early Toarcian) of Argentina; however, the Argentinean material is bigger than the Peruvian species, the selenizone is narrow, concave and peripheral on last whorl, two weak spiral cords are present at the angulation of whorls, the aperture is subquadrate and the umbilicus completely covered by a callus. *Cryptaenia globosa* Ferrari, 2014b (Fig. 3F-H), also from the Early Jurassic (Pliensbachian) of Argentina, differs from *P.? discoidea* in being much bigger, strongly globose, with the periphery forming a rounded angulation.

**Family Nododelphinulidae Cox, 1960**  
**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:** Upper Triassic (Norian)-Early Jurassic (Sinemurian-Pliensbachian); Europe, New Zealand and South America.

**Remarks:** Haas (1953) described many species of this genus from the Late Triassic of Perú and defined *Trochus retulus* Stoliczka, 1861 as its genotype, including the most representative forms into the family Trochonematidae Zittel. Gründel (2004) assigned *Guidonia* to the family Liotiidae H. Adams and A. Adams. In contrast, Szabó (2009), on the basis of the bicarinate whorls and the gradate shell outline, included the genus into the family Nododelphinulidae Cox. Szabó (2009) pointed out that the shell shape of *Guidonia* resembles also the typical *Chartronella*, and suggested accommodation in another family. The similarities between *Guidonia* and *Chartronella* were also stated out by Ferrari (2011). The classification of *Guidonia* in Nododelphinulidae was subsequently followed by Gatto and Monari (2010). Here, I adopt the proposal of Szabó (2009) and Gatto and Monari (2010) based on the similarities in shell shape of *Guidonia* with the representatives of the family Nododelphinulidae.

***Guidonia Peruviana* Haas, 1953**

Fig. 3I-O

**Material examined:** Paratype No. 35535A AMNH; 'well preserved' and replaced teleoconch. Syntype, No. 26500A AMNH; 'well preserved' and replaced teleoconch.

**Occurrence:** Cerro de Pasco locality, 24.5 km SSE, 0.5 km W of Ninacaca Jenks Lot 86 and 18.75 km S, 7.75 km W of Ninacaca Jenks Lot 70, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, trochiform, gradate to step-like, moderately low-spired and small-sized shell. The protoconch is not preserved; the teleoconch comprises about five strongly gradate whorls, with a mean height of 7.48 mm and a mean width of 7.98 mm. Earliest teleoconch whorls are slightly convex and become straight and angular to mature growth stages. The sutural ramp on adult whorls is slightly flat to concave; the outer face is straight, vertical and concave. The periphery of last whorl is delimited by a strong spiral keel which forms an angulation; a second weak and abapical spiral cord is visible on last whorl but covered by subsequent whorls on the spire. Collabral ornament appears on the outer face of last whorl; it consists of fine and crowded prosocline growth lines. The base is slightly convex, narrowly phaneromphalous, with a deep and funnel-shaped umbilicus. The aperture is holostomatous and circular; the outer lip is indented by external angulation; the basal lip is flat and slightly expanded abapically, and the columellar lip is thickened forming a crescent-shaped callus. Fine and spaced collabral ribs are also visible on base.

**Affinities:** According to the diagnosis of Bandel *et al.* (2000), the species described by Haas certainly shows the typical characters of *Guidonia*. *Guidonia Peruviana* Haas (1953; p. 65, pl. 4, figs. 1-3, 5-9, 11-18, 20, 32, 42), however, is very similar in general shell morphology to *Chartronella paganiae* Ferrari (2011; p. 69, fig. 7.1-10) (Fig. 1M-O), from the Early Jurassic of Patagonia; but, the Argentinean form has a less gradate outline, a more convex sutural ramp, and lacks umbilicus. The absence of umbilicus is the reason for keeping *C. paganiae* separately from *Guidonia*. A new specimen tentatively assigned to *Guidonia disciformis* Ferrari, 2014b (Fig. 3W-Y) has been recently reported from the Early Jurassic (Pliensbachian) of the Neuquén Basin (Argentina) (Ferrari, 2014b), however, has a smaller size, a

lower spire and a less gradate outline, very weak and prosocline growth lines on the ramp of last whorl, base flatter with three to four spiral keels, and the umbilical area flat with the umbilicus not deeply developed.

Bandel *et al.* (2000) pointed out the difference between *Guidonia riedeli* Bandel *et al.* (2000; p. 82, pl. 4, figs. 1-3, 5), from the Early Jurassic of Kaiwara Valley (New Zealand), and *G. Peruviana*, showing that the latter has a less developed spiral and axial ornament in comparison to the New Zealand form. Moreover, *G. riedeli* differs also from the Peruvian form in having a less gradate and lower spire, with a strongly horizontal sutural ramp, a larger and wider funnel-shaped umbilicus, and a subcircular aperture. *Guidonia pseudorotula* Gatto and Monari (2010; p. 786, text-figure 6H-N), from the late Sinemurian of Austria, has a ramp moderately oblique, less concave outer face, a wider umbilicus, and growth lines prosocline and straight on the ramp and outer face, slightly prosoclyt on the abaxial region of the base and opisthoclyt on the umbilical region.

### ***Guidonia bifasciata* Haas, 1953**

Fig. 3P-S

**Material examined:** Paratypes, AMNH No. 26502D, No. 26502S; 'well preserved' and silicified teleoconchs. Syntype, AMNH No. 26502H; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 24.5 km SSE, 0.5 km W of Ninacaca Jenks Lot 86, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, trochiform, slightly gradate, small-sized and moderately low-spired shell. The protoconch is not preserved; the teleoconch consists of about four whorls, with a mean height of 5.18 mm and a mean width of 5.83 mm. Earliest whorls are convex and become angular and gradate in mature growth stages. Suture is impressed. From third to mature whorls, two acute spiral keels become visible; the weaker adapical one borders the suture, and the stronger is peripheral and delimits the angulation. Fine and regularly spaced spiral keels are present on the ramp of last whorl, between the adapical and peripheral spiral keels; the specimen 26502H has four well preserved and regularly spaced spiral ribs on the outer face of last whorl. The third and fourth whorls have very weak axial ribs intercepting the spiral elements and forming weak nodes at the intersection

points. Base is slightly convex ornamented by five regularly spaced spiral keels. The umbilical area is bordered by the inner spiral keel; the umbilicus is deep and narrow. The aperture is holostomatous and circular; the outer lip indented by peripheral spiral keel and the columellar lip crescent-shaped.

**Affinities:** *G. bifasciata* Haas (1953; p. 74, pl. 4, figs. 76-78, 81-85, pl. 5, figs. 1-3) is very similar in general shell morphology to *G. Peruviana*; however, *G. bifasciata* has a slightly more conical and less gradate shell, five regularly spaced spiral keels on base, and its columellar lip is slightly thickened in comparison to *G. Peruviana*. The present species also resembles *Chartronella spiralis* Ferrari (2011, p. 71, fig. 9.1-6) (Fig. 2A-C), from the Early Jurassic of the Chubut Province, in ornament pattern, having well developed spiral keels on base; however, the Argentinean form has also strong spiral keels on the shell surface crossed by fine prosocline collabral lines, and a more expanded and subcircular aperture.

### ***Guidonia planetecta* Haas, 1953**

Fig. 3T-V

**Material examined:** Paratype, AMNH No. 35538G; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 18.75 km S, 7.75 km W of Ninacaca Jenks Lot 70, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, gradate, step-like, low-spired and very small-sized shell, with a height of 4.24 mm and a width of 6.66 mm. The protoconch is not preserved; the teleoconch consists of three gradate whorls. The sutural ramp on adult whorls is flattened and horizontal; the outer face is sharp straight and strongly concave, bordered by two acute spiral keels. The two acute spiral keels are equally developed, completely visible on last whorl, and coincide with the angulation; they appear to have small and very weak nodes. No collabral ornament is observed on the shell surface. The base is flat to slightly convex, smooth, and widely phaneromphalous, with a deep and funnel-shaped umbilicus. The umbilical area lacks the typical bordering spiral keel. The aperture is holostomatous and circular; the outer lip indented by the external angulation. Basal lip slightly expanded abapically, and columellar lip crescent-shaped.

**Affinities:** The species here described is very similar in shell shape and ornamentation to *Chartronella*

*paganiae* (Fig. 1M-O) and *Guidonia disciformis* Ferrari, 2014b. (Fig. 3W-Y), both from the Early Jurassic of Argentina (see above). *G. planetecta*, however, is smaller than *C. paganiae*, has a more step-like shell and an open umbilicus; and *Guidonia disciformis* has a more depressed shell.

**Family Cirridae Cossmann, 1916**  
**Subfamily Hesperocirrinae Haas, 1953**  
**Genus Hesperocirrus Haas, 1953**

**Type species:** *Hesperocirrus triasicus* (Cox, 1949), from the Upper Triassic of Perú.

**Occurrence:** Late Triassic; Perú.

**Remarks:** Haas (1953) proposed the subfamily Hesperocirrinae to include the genera *Hespero-*

*cirrus* and *Sorocula*, both form the Late Triassic of the Pucará Group. The author considered *Hesperocirrus* as one of the less diversified genera within the Peruvian fauna, which is represented only by five species. Bandel (1993) pointed out the differences between *Hesperocirrus* with the coeval *Cassianocirrus* Bandel and *Zardinicirrus* Bandel from the St. Cassian Formation, differing from the Peruvian form in shell profile and sculpture. The author also compared the Jurassic *Hamusina* Gemmellaro with *Hesperocirrus* and emended the subfamily diagnosis to include the genera *Heperocirrus*, *Sorocula* Haas, *Hamusina* and *Sensuitrochus* Quintero and Revilla. The classification of Bandel was subsequently followed by Ferrari (2014a) and also adopted here.

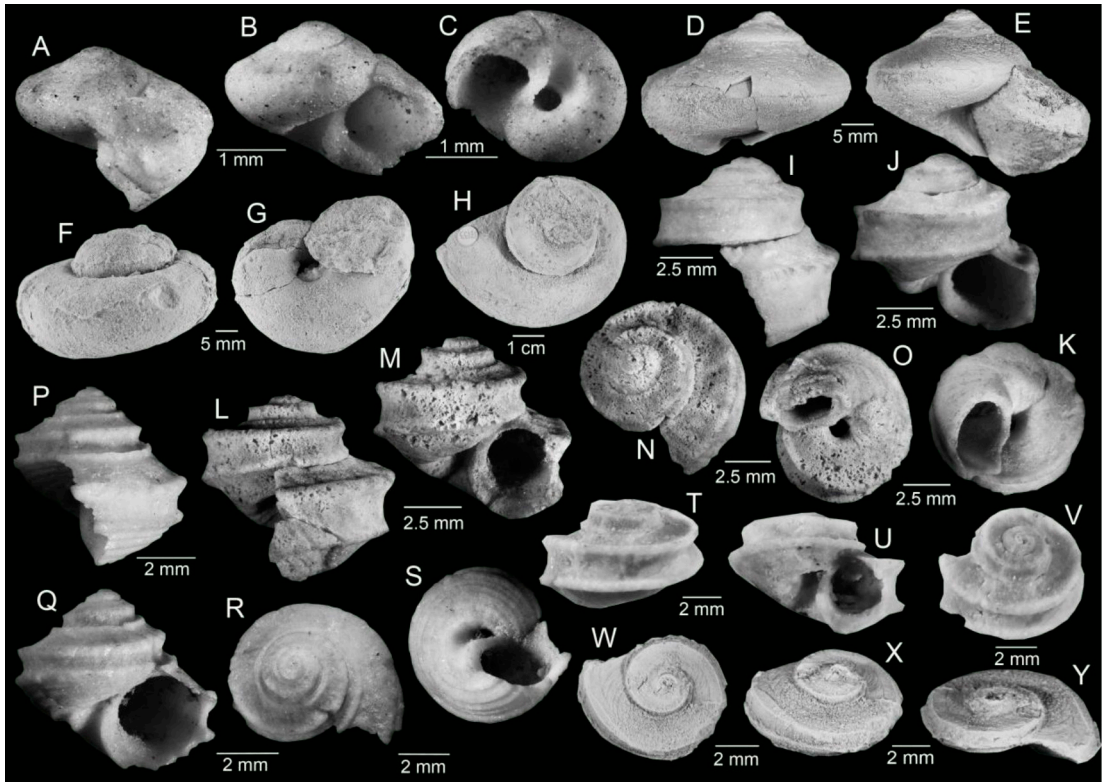


FIG. 3. A-C: *Ptychomphalus? discoidea* (Haas, 1953), AMNH No. 27693, holotype; A: lateral view; B-C: apertural and basal views; D-E: *Cryptaenia sudamericana* Ferrari, 2014b, MCF-PIPH 698, lateral and apertural views; F-H: *Cryptaenia globosa* Ferrari, 2014b, MLP (13a); F: lateral view; G: basal view; H: apical view; I-O: *Guidonia Peruviana* Haas, 1953; I-K: AMNH No. 26500A, syntype; I: lateral view; J: lateral and apertural views; K: basal view; L-O: AMNH No. 35535A, paratype; L: lateral view; M: lateral and apertural view; N: apical view; O: basal view; P-S: *Guidonia bifasciata* Haas, 1953, AMNH No. 26502S, paratype; P: lateral view; Q: lateral and apertural views; R: apical view; S: basal view. T-V, *Guidonia planetecta* Haas, 1953, AMNH No. 35538G, paratype; T-U: lateral and apertural views; V: apical view; W-Y: *Guidonia disciformis* Ferrari, 2014b, MCF-PIPH 703; W-X: apical views; Y: lateral views.

***Hesperocirrus robusteornatus* Haas, 1953**

Fig. 4A-B

**Material examined:** Syntype, AMNH No. 34406; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 18.75 km S, 7.75 km W of Ninacaca, Jenks Lot 69, Central Perú; Late Triassic, Pucará Group.

**Description:** Sinistral, trochiform, conical to slightly gradate, medium-sized and relatively high-spired shell. The protoconch is not preserved. The teleoconch consists of six whorls, with a height of 23.28 mm and a width of 18.52 mm. Earliest teleoconch whorls are fragmentary and last whorl slightly more expanded than the spire. Suture is impressed in a deep spiral furrow. The ramp of whorls is narrowly horizontal; the outer face is strongly convex and ornamented by two acute nodose rows; the adapical is stronger and has more acute nodes than the abapical. The outer face is strongly concave between the spiral rows. Weak opisthocline collabral ribs are present on the shell surface; they are opisthocline on the upper portion of the outer face and become prosoclyt toward the lower portion. The base is angular and flattened, with a relatively wide umbilicus. The aperture is strongly circular and the peristome continuous.

**Affinities:** The resemblance between *Hesperocirrus robusteornatus* Haas (1953, p. 42, pl. 2, figs. 35-37, 41, 43, 44, 47-49, 51-53, 58) and *Hamusina? wahnishae* Ferrari (2014a, p. 10, fig. 4n-u) (Fig. 4L-P), from the Early Jurassic of Patagonia, was discussed by Ferrari (2014a) who stated that *Hesperocirrus robusteornatus* differs from the Argentinean species in having axial and nodular elements, more conspicuous spiral threads, and a wide umbilicus. Another similar form to *H. robusteornatus* is *Hamusina maxwelli* Bandel (1993, p. 58, pl. 4, figs. 9, 10; pls 5, 1-5; Bandel *et al.*, 2000, p. 77; pl. 2, figs. 1-6) from the Early Jurassic of New Zealand; however, *H. maxwelli* is much smaller, has stronger axial riblets which are inclined toward the base and lacks nodose rows on the outer face.

***Hesperocirrus striatus* Haas, 1953**

Fig. 4C-G

**Material examined:** Paratype, AMNH No. 34427; 'well preserved' teleoconch. Syntype, No. 34428; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 24.5 km SSE, 0.5 km W of Ninacaca, Jenks Lot 86, Central Perú; Late Triassic, Pucará Group.

**Description:** Sinistral, trochiform, gradate, small- to medium-sized and relatively low-spired shell, with a mean height of 6.77 mm and a mean width of 6.26 mm. The protoconch is typical of vetigastropods, consisting of one convex and smooth whorl; the teleoconch consists of five gradate whorls. First teleoconch whorl strongly convex, ornamented by regularly spaced axial ribs; mature whorls become angular. The ramp of whorl is flat to slightly concave; the outer face become straight, vertical and concave. Suture is impressed in a weak spiral furrow. The angulation of whorls is bordered by a row of pointed and separate nodes; nodes are more acute and stronger on the peripheral spiral keel. A weaker adapical spiral cord with less conspicuous nodes borders the suture. Thin axial ribs connect the nodes of adapical and peripheral spiral keels. The base is angular and flattened, and ornamented by irregularly spaced spiral threads. The aperture is holostomatous and circular, with a thin outer lip; the basal lip is flattened and the columellar lip thickened. The umbilicus is very narrow and deep, partially covered by a thin columellar callus and ornamented by fine and weak collabral ribs.

**Affinities:** *Hesperocirrus striatus* Haas (1953, p. 48, pl. 2, figs. 42, 46, 54, 56, 57, 60) resembles *H. robusteornatus* (see above). The present form, however, is smaller, has a more gradate outline shell, less rounded and more acute nodes at the periphery of the shell, less developed collabral ribs, a lower spire and a narrower umbilicus, which is covered by a thin columellar callus. *Hamusina? wahnishae* (see above; Fig. 4L-P), is slightly larger, has a more conical outline shell, stronger spiral cords on the flanks of whorls, sutures feebly impressed, lack axial and collabral elements, lacks of umbilicus, and the aperture is quadrangular instead of circular. *H. maxwelli* (see above), is also very similar to *H. striatus* in shell shape and ornamentation; however, the species from New Zealand lacks pointed nodes and has a subangular aperture.

**Genus *Sororcula* Haas, 1953**

**Type species:** *Sororcula gracilis* Haas, 1953, by original designation, Upper Triassic of Perú.

**Occurrence:** Late Triassic; Perú.

**Remarks:** This genus was proposed by Haas (1953) to include sinistral, slender and small shells, with flank of whorls flattened to slightly concave, ornamented by distinct transverse ribs, sutures incised in a spiral furrow, base nearly flat with a narrow umbilicus or

at least with an umbilical notch. According to Haas (1953) *Sororcula* differs from *Hesperocirrus* in 'being smaller, having a more slender shell, flat or even slightly concave whorl faces, shallower sutures, lower pleural angle, almost flat base, narrower umbilicus, and a more delicate ornamentation'. Haas (1953) designated *Sororcula gracilis* as the type species of the genus and considered *Sororcula* less common than *Hesperocirrus*, represented only by two species and 27 specimens.

***Sororcula gracilis* Haas, 1953**

Fig. 4H-K

**Material examined:** Syntype, AMNH No. 35517; 'moderately well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 9.5 km SSE, 2.72 km N of Pasco, Jenks Lot 67, Central Perú; Late Triassic, Pucará Group.

**Description:** Sinistral, conical, trochiform, small-sized and slightly high-spire shell, with a height of 6.16 mm and a width of 4.6 mm. The protoconch is not preserved; the teleoconch consists of five whorls; earliest whorls slightly convex, becoming flattened toward mature whorls stages. Sutures are weakly incised in a spiral furrow. The ornament is clearly visible on the flanks of mature whorls. It consists of five to six fine, regularly spaced and crowded spiral cords; two stronger nodular spiral elements, developed as keels, are located adapically and abapically on whorls; the abapical is stronger with more pointed nodes. The base is flattened, angular and smooth. The aperture is quadrangular; with the columellar lip thickened. The umbilicus is absent or with a umbilical notch.

**Affinities:** *Sororcula gracilis* Haas (1953, p. 52, pl. 3, figs. 28, 30, 31, 35, 36, 42-46) is very similar in shell shape and ornament to *Hamusina? wahnishae* (see above; Fig. 4L-P), from the Early Jurassic of

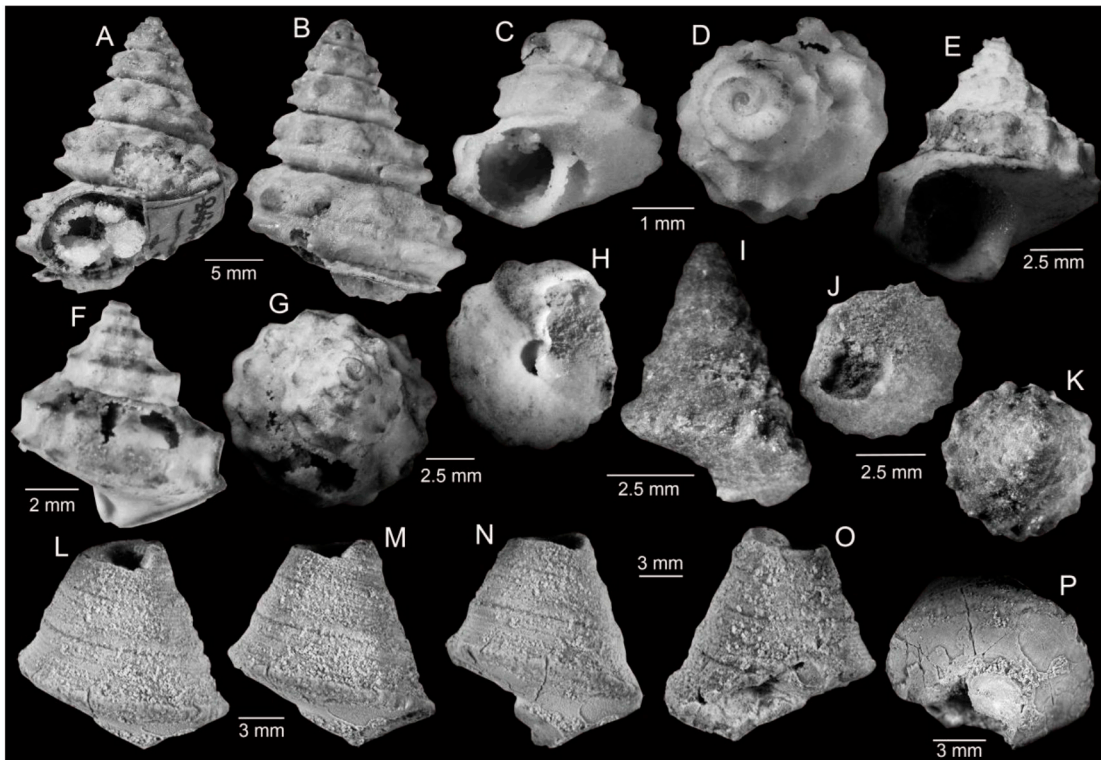


FIG. 4. A-B: *Hesperocirrus robusteornatus* Haas, 1953, AMNH No. 34406, syntype; A: apertural view; B: lateral view; C-G: *Hesperocirrus striatus* Haas, 1953; C-D: AMNH No. 34427, paratype; C: lateral and apertural view; D: apical view; E-H: AMNH No. 34428, syntype; E-F: lateral views; G: apical view; H: basal view; I-K: *Sororcula gracilis* Haas, 1953, AMNH No. 35517, syntype; I: lateral view; J: basal view; K: apical view; L-P: *Hamusina? wahnishae* Ferrari, 2014a, MPEF-PI 3592, holotype; L-N: lateral views; O: apertural view; P: basal view.

Patagonia. Both have a conical shell, with flattened flanks ornamented by five regularly spaced spiral cords on mature whorls, and lacks an umbilicus. However, the Peruvian form is slightly smaller and has two nodular spiral keels bordering the suture; nodes on *H.?* *wahnishae* are absent. Probably, *Hamusina?* *wahnishae* belong indeed to *Sororcula*. *Hamusina maxwelli* (see above) has more developed axial and nodular elements, and lacks spiral cords on the shell surface. The affinities between *S. gracilis* and *Hesperocirrus* were also noted by Haas (1953, p. 53). *Sororcula* differs from *Hesperocirrus* in being smaller, with a lower pleural angle, slender shell shape and not gradate in outline (see above).

#### Family uncertain

#### Genus *Jurassiphorus* Cossmann, 1915

**Type species:** *Jurassiphorus cailliaudanus* (D'Orbigny, 1853), Middle Jurassic (Callovian), France.

**Occurrence:** Late Triassic-Middle Jurassic (Callovian); North America, South America and France.

**Remarks:** *Jurassiphorus* was reported by Haas (1953) from the Late Triassic of the Pucará Group and included it in the caenogastropod family Xenophoridae Cossmann. Bandel (1994) listed this genus under the trochomorph vetigastropods and compared it with the similar coeval *Rolandomphalus armatus* (Zardini) from the St. Cassian Formation. Gründel (1997) described the protoconch of the type species *Jurassiphorus cailliaudanus* (D'Orbigny), and also included the genus in the trochomorph taxa. Nützel and Erwin (2004) classified species of *Jurassiphorus* in an uncertain family within vetigastropods, classification followed subsequently by Ferrari (2014a). Here, the classification proposed by Nützel and Erwin (2004) is adopted.

#### *Jurassiphorus triadicus* Haas, 1953

Fig. 5A-D

**Material examined:** Holotype, AMNH No. 26514A; 'well preserved' specimen.

**Occurrence:** Cerro de Pasco locality, 21 km E, 3.5 km SSE of Huanco Jenks Lot 26, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, discoidal, gradate, low-spired and small-sized shell, with a height of 3.97 mm and a width of 9.04 mm. The protoconch is not pre-

served; the teleoconch consists of four trochospiral whorls, with last whorl markedly expanded. The sutural ramp is flattened and horizontal; the outer face becomes vertical and straight to slightly convex, and ornamented by strong elongated nodes at the angulations. Spiral elements are not observed. A big flattened and horizontal crest is developed on last teleoconch whorl. The base is flat to slightly convex and ornamented by two spiral nodose keels. The aperture is circular and holostomatous, with the outer lip indented by external crest.

**Affinities:** Ferrari (2014a) described a congeneric species, *Jurassiphorus?* cf. *triadicus* Haas (Ferrari, 2014a, p. 13, fig. 5k-p) (Fig. 5E-J), from the Early Jurassic of Patagonia; the Argentinean form, however, lacks an external crest on the last teleoconch whorl. Another related form to the Peruvian species is the type *Jurassiphorus cailliaudanus* (D'Orbigny) from the Callovian of France; but the European form has one nodose spiral keel on the base instead of two (Gründel, 1997; p. 87, pl. 4, fig. 9-11).

#### Order Caenogastropoda Cox, 1959

#### Family Procerithiidae Cossmann, 1905

#### Genus *Paracerithium* Cossmann, 1902

**Type species:** *Paracerithium acanthocolpum* Cossmann, 1902, from the Early Jurassic (Hettangian) of France.

**Occurrence:** Late Triassic-Late Jurassic; Perú, Europe and New Zealand.

**Remarks:** Haas (1953) reported the first Triassic occurrence of the genus *Paraceithium* Cossmann in the Peruvian Andes. The author corroborated the occurrence of this genus in the Late Triassic by comparing the type species, *P. acanthocolpum*, with the similar counterpart '*Kotosira*' *seelandica* Kittl from the St. Cassian Formation, suggesting that both resemble in shell shape, apertural details and ornamentation. Haas, thus, included '*K.*' *seelandica* into *Paracerithium* and pointed out that the coeval forms from the Pucará Group certainly belong to *Paracerithium*. Bandel *et al.* (2000) described two new species of this genus from the Early/Middle Jurassic of New Zealand and considered as its most diagnostic features the presence of wide conical shell, an aperture oval with a well developed siphonal notch, whorls with strong spiral keels, and widely spaced axial ribs intercepting spiral elements and forming nodes at crossing points.

***Paracerithium tambosolense* Haas, 1953**

Fig. 5K-N

**Material examined:** Paratype, AMNH No. 26576C; ‘well preserved’ teleoconch. Syntype, AMNH No. 35710B.

**Occurrence:** Cerro de Pasco locality, 22 km SSE, 4.5 km W of Pasco, Jenks Lot 78 and 80 km SE, 4 km E of Tilarnioc Jenks, Lot 48, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, turriculate, conical, small-sized and high-spired shell, with a mean height of 5.58 mm and a mean width of 2.85 mm. The protoconch is not preserved; the teleoconch consists of about six to seven whorls. The sutural ramp is narrowly horizontal and the outer face becomes strongly convex in shape. The ornament consists of spiral and axial elements; five regularly spaced and rather weak spiral cords appear on the outer face of mature whorls. The spiral elements are intercepted by seven to eight strong and orthocline to slightly opisthocyrt axial

ribs. The base is convex and ornamented by two to three regularly spaced spiral cords. The aperture is holostomatous and oval, with a strongly convex and thickened outer lip and the columellar lip straight and parallel to the coiling axis. The basal lip is expanded as a siphonal notch.

**Affinities:** *Paracerithium tambosolense* Haas (1953, p. 225, pl. 15, figs. 25, 33-39) show close resemblance to *Procerithium (Rhabdocolpus) patagoniensis* Ferrari (2012, p. 329, figs. 4G-P, 5A-K) (Fig. 5O-R) from the Early Jurassic of Patagonia; however, the Argentinean form is slightly larger than *P. tambosolense*, has up to eight spiral cords on mature whorls, a high number of axial ribs which are stronger opisthocyrt, less developed sutural ramp and lacks the siphonal notch on base.

Other two related species to the one here described are those described by Bandel *et al.* (2000) from the Early/Middle Jurassic of New Zealand. *Paracerithium spinosum* Bandel *et al.* (2000, p. 87, pl. 5, fig. 5, pl. 7, figs. 1-2, 4) has 10-12 teleoconch whorls, a more

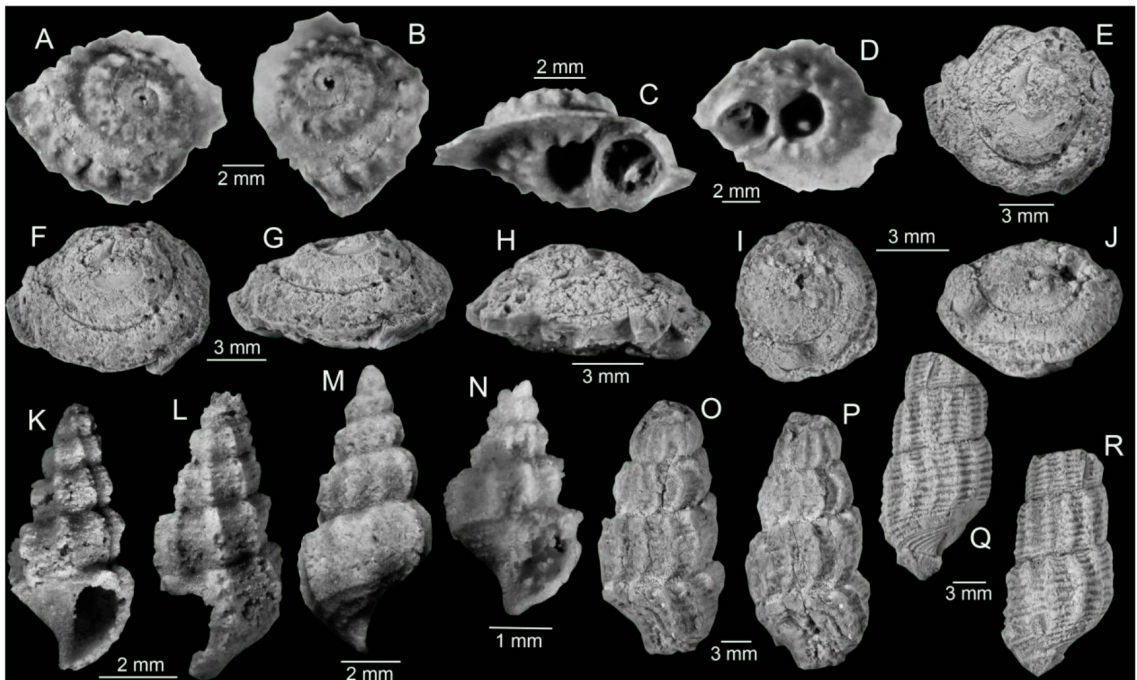


FIG. 5. A-D: *Jurassiphorus triadicus* Haas, 1953, AMNH No. 26514A, holotype; A-B: apical view; C-D: apertural and basal views; E-J: *Jurassiphorus? cf. triadicus* Haas, 1953 (Ferrari, 2014a); E-H: MPEF-PI 4023-1; E-F: apical views; G-H: lateral and apertural views; I-J: MPEF-PI 4023-2, apical views; K-N: *Paracerithium tambosolense* Haas, 1953; K-L: AMNH No. 35710B, syntype, apertural and lateral views; M-N: AMNH No. 26576C, paratype, lateral and apertural views; O-R: *Procerithium (Rhabdocolpus) patagoniensis* Ferrari (2012); O-P: MPEF-PI 3517, holotype, lateral and apertural views; Q-R: MPEF-PI 3518, lateral views.

step- like outline shell with a higher number (10-11) of axial ribs which are less opisthocyrt; the peripheral edge of the sutural ramp forms small nodes, and the base has an oblique and twisted anterior channel. *Paracerithium pacificum* Bandel *et al.* (2000, p. 87, pl. 6, figs. 1-3, 7) has a widely conical shell with a more convex appearance and two spiral keels located in a central position of the flanks with acute nodes at the crossing points with axial ribs.

***Paracerithium? vixstriatum* Haas, 1953**

Fig. 6A-D

1953 *Paracerithium vixstriatum* Haas: p. 230, pl. 15, figs. 57-64, 69, 70, 73-75.

**Material examined:** Syntype, AMNH No. 26580A; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 80 km SE, 4 km E of Tiliarnioc, Jenks Lot 48, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, turriculate, slender to strongly convex, very small- sized and high- spired shell, with

a height of 4.93 mm and a width of 2.41 mm. The protoconch is not clearly visible, probably consisting of one convex and smooth whorl. The teleoconch comprises seven strongly convex whorls. The sutural ramp is narrowly developed and horizontal, more clearly visible on mature whorls. Axial ribs are predominant and they appear in numbers of 11 toward mature growth stages. The axial ribs are acute and strongly developed giving the shell outline a strongly convex appearance; they are prosocline to strongly opisthocyrt. Spiral elements are absent on the shell surface. The base is flattened to angular and smooth, although delimited by a weak spiral cord. The aperture is holostomatous and oval, with the basal lip expanded abapically forming a weak siphonal notch. The outer lip is slightly reflected into the aperture, forming a weak adapical channel. **Affinities:** According to the characterization of Bandel *et al.* (2000), the species described by Haas (1953) seems to be a representative of *Paracerithium*, considering a wide to conical shell, convex in outline, aperture oval with a siphonal notch, and widely spaced axial ribs as its typical characters.

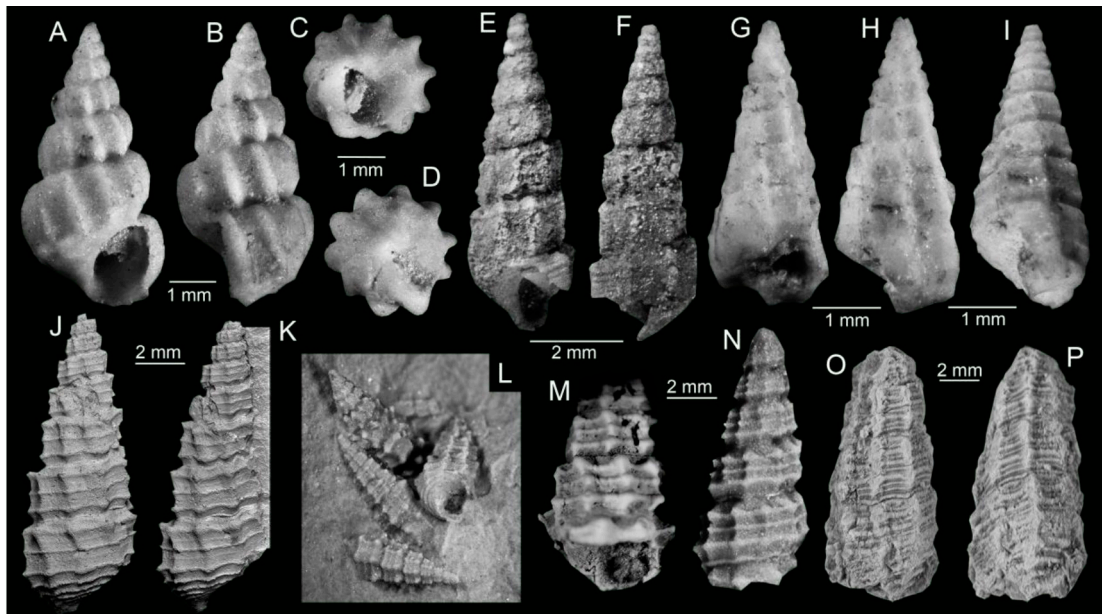


FIG. 6. **A-D:** *Paracerithium? vixstriatum* Haas, 1953, AMNH No. 26580A, syntype; **A-B:** apertural and lateral views; **C-D:** basal views; **E-F:** *Rhabdocolpus (Rhabdocolpus) praeco* Haas, 1953, AMNH No. 26594, paratype, lateral views; **G-I:** *Cryptaulax tilarniocensis* Haas, 1953, AMNH 26593F, paratype; **G-H:** apertural and lateral views; **I:** basal view; **J-N:** *Cryptaulax dambo-reneae* Ferrari (2009); **J-K:** MPEF-PI 1878b, holotype, lateral views; **L:** MPEF-PI 4036, four associated specimens in lateral and basal views; **M:** MPEF-PI 1877, apertural view; **N:** MPEF-PI 4013, lateral view; **O-P:** *Cryptaulax redelii* Ferrari (2012), MPEF-PI 3508, holotype, lateral views.

However, other diagnostic features such as strong spiral keels intercepting the axial elements and forming nodes at intersection points, are not visible in *Paracerithium? vixstriatum* Haas (1953, p. 230, pl. 15, figs. 57-64, 69, 70, 73-75). The Peruvian form also resembles members of *Zygopleura* Koken. Mesozoic zygopleurids are generally characterized by a high spired teleoconch ornamented with wavy axial ribs and without any spiral ornament. However, zygopleurid teleoconch can not be assigned to *Zygopleura* without knowledge of the protoconch, and the recognition of such characters relies on good preservation (Nützel and Erwin, 2004). In the single specimen here analyzed, the protoconch is not clearly visible. Here, I propose to keep the species in *Paracerithium* but I added question marks to express the uncertainty.

*Paracerithium? vixstriatum* resembles also members of *Protofusus* Bonarelli, 1921. Bonarelli (1921) proposed *Protofusus* for three species from Carabajal (Salta Province, Argentina).

### Genus *Rhabdocolpus* Cossmann, 1906

**Type species:** *Melania scalariformis* Deshayes, 1830-1932, from the Middle Jurassic of France.

**Occurrence:** Late Triassic-Late? Jurassic; Europe, New Zealand, Antarctica and South America.

**Remarks:** The diagnosis of *Rhabdocolpus* Cossmann was emended by Gründel (1999) and Bandel *et al.* (2000). The authors included in this procerithiid genus forms with a high- spired and flattened to slightly convex outline shell, with an horizontal to strong sloping subsutural ramp, opisthocyrt axial ribs on the teleoconch, forming nodes at the crossing point with spiral elements, and base with an adapical channel and lacking abapical notch. The genus is well known from the Jurassic of Europe, and Haas (1953) reported the first occurrence of *Rhabdocolpus* from the Late Triassic of South America.

#### Subgenus *Rhabdocolpus* (*Rhabdocolpus*) Cossmann, 1906

**Remarks:** Gründel (1999) retained the subgenus *Rhabdocolpus* (*Rhabdocolpus*) to include shells with a narrow and nearly horizontal subsutural ramp, whorls delimited against each other in a step- like appearance, and the outer face of whorls nearly

straight. Here, the classification of Gründel (1999) is followed considering that Haas's material belongs to the present subgenus.

#### *Rhabdocolpus* (*Rhabdocolpus*) *praeco* Haas, 1953 Fig. 6E-F

1953 *Rhabdocolpus praeco* Haas: p. 237, pl. 16, figs. 1-11, 13, 14, 27

**Material examined:** Paratype, AMNH No. 26594; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 80 km SE, 4 km E of Tilarnioc Jenks, Lot 48, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, turriculate, slender, very small- sized and high- spired shell, with a mean height of 6.3 mm and a mean width of 2.5 mm. The protoconch is not preserved; the teleoconch consists of about nine flattened to slightly convex whorls. Sutural ramp is narrowly horizontal and whorls have a step- like appearance. Suture is impressed in a weak spiral furrow. The ornament consists of spiral and axial elements. Regularly spaced spiral keels are present in numbers of six on each whorl; the spiral keels are intercepted by strong orthocline axial ribs which run from suture to suture. Acute nodes appear at the crossing points of axial and spiral elements; nodes are stronger at the intersection of the adapical spiral keel. The base is convex and smooth, delimited by two strong spiral keels. The aperture is holostomatous and oval, with the columellar lip thickened and the basal lip expanded abapically forming a siphonal notch.

**Affinities:** According to the characterization of Gründel (1999), the species described by Haas (1953) certainly belongs to the subgenus *Rhabdocolpus* (*Rhabdocolpus*), based on the presence of an horizontal subsutural ramp and a step- like appearance as the most diagnostic features. *Rhabdocolpus* (*Rhabdocolpus*) *praeco* Haas (1953, p. 237, pl. 16, figs. 1-11, 13, 14, 27) is more similar to *Procerithium* (*Rhabdocolpus*) *patagoniensis* Ferrari (see above; Fig. 5O-R) than to *Paracerithium tambosolense* Haas (see above; Fig. 5K-N). The Argentinean form, however, has a higher spire with a mean height of 12.42 mm, the teleoconch whorls are slightly more convex, have less developed subsutural ramp, the axial ribs are opisthocyrt and the base is ornamented by 10 regularly spaced spiral keels which are intercepted by prosocline growth lines, and the basal lip is flattened

without an abapical notch. *Rhabdocolpus? kowalkei* Bandel *et al.* (2000, p. 88, pl. 6, figs. 4-6, 8, 10), from the Early/Middle Jurassic of New Zealand, differs from the Peruvian species in being smaller with six teleoconch whorls, the axial ribs are stronger forming concave interspaces between each other, nodes at the crossing points of spiral and axial elements are stronger, and sutures are slightly more impressed. *Rhabdocolpus* sp. Edwards (1980, p. 38, fig. 2b; Thompson and Turner, 1986, p. 26, tb. 1) from the Early Jurassic (Sinemurian) of Antarctica, resembles also *R. (R.) praeco*; however, the Antarctic form is more similar to the representatives of *Rhabdocolpus (Infacerithium)* (see diagnosis in Gründel, 1999, p. 11), differing from *R. (R.) praeco* in having sloping subsutural ramps which are not delimited against each other as a step-like appearance, and has more spaced and orthocone axial ribs.

### Genus *Cryptaulax* Tate, 1869

**Type species:** *Procerithium (Xystrella) protortile* Cox, 1965, pro *Cerithium tortile* Hébert and Eudes-Deslongchamps, 1860, from the Middle Jurassic (Callovian) of France.

**Occurrence:** Late Triassic-Lower Cretaceous; Cosmopolitan.

**Remarks:** The species of *Cryptaulax* are cosmopolitan and common in the Jurassic. Haas (1953) reported the first certain representatives of *Cryptaulax* from the Late Triassic of Perú, though the same taxa were previously recorded by Jaworski (1923) but classified as *Promathildia* Andreae, 1887. Haas (1953) described two *Cryptaulax* species from the Late Triassic of Perú. In the present research, the genus concept expressed by Gründel (1999), Kaim (2004) and Bandel (2006) are followed to retain Haas's (1953) species in *Cryptaulax*.

### *Cryptaulax tilarniocensis* Haas, 1953

Fig. 6G-I

**Material examined:** Paratype, AMNH No. 26593F; 'well preserved' teleoconch. Syntype, AMNH No. 26593C; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 80 km SE, 4 km E of Tilarnioc Jenks, Lot 48, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, turriculate, slender, very small-sized and high-spired shell, with a mean

height of 3.06 mm and a mean width of 1.4 mm. The protoconch is fragmentary and convex, consisting of one smooth whorl; first teleoconch whorl angular, ornamented by one weak peripheral spiral keel. From second teleoconch whorl to mature whorls, orthocone axial ribs appear from suture to suture. Spiral ornament is weakly developed; strong adapical and abapical spiral keels appear on whorls and are intercepted by the strong axial ribs, forming rounded nodes at the crossing points. Secondary spiral ribs are almost imperceptible. The base is flattened to slightly angular and delimited by two acute spiral keels. The aperture is holostomatous and circular, without an abapical notch.

**Affinities:** *Cryptaulax tilarniocensis* Haas (1953, p. 250, pl. 16, figs. 60-71) shows close resemblance to *Cryptaulax damboreneae* Ferrari (2009, p. 452, fig. 3B-D; Ferrari, 2012, p. 325, fig. 2A-H) (Fig. 6J-N) and to *Cryptaulax redelii* Ferrari (2012, p. 327, fig. 2I-K) (Fig. 6O-P), both from the Early Jurassic (late Pliensbachian-early Toarcian) of Patagonia. *Cryptaulax damboreneae*, however, is slightly larger than the Peruvian form, has a more gradate shell, and two well developed secondary spiral ribs on mature whorls. *Cryptaulax redelii* differs from *Cryptaulax tilarniocensis* in being larger, having stronger axial ribs and more conspicuous nodes at the crossing points with spiral elements, and four (or probably more) secondary spiral ribs on mature whorls. *Cryptaulax cf. protortile* (Cox, 1969), from the Early/Middle Jurassic of New Zealand, is also comparable to Haas's species; but, Cox's form has more convex whorls, more developed axial and spiral elements, and a slightly more gradate shell (Bandel *et al.*, 2000, p. 89, pl. 6, figs. 9, 11-13).

### Order Ptenoglossa Gray, 1853

#### Family Ampullinidae Cossmann, 1919

#### Genus *Oonia* Gemmellaro, 1878

**Type species:** *Melania abbreviata* Cossmann Terquem 1855=*Pseudomelania hettangiensis* Cossmann, 1909, from the Early Jurassic of France.

**Occurrence:** Late Triassic-Middle Jurassic; Europe, South America.

**Remarks:** According to the characterization of Gründel (2001b), members of *Oonia* have an oval shell with pointed apex, the teleoconch lack of sculpture, subsutural ramp is absent, and growth lines, when present, are distinctly sinuous and prosocline.

Haas (1953) reported *Omphaloptycha jaworskii* Haas, from the Late Triassic of Perú and included it into the family Coelostylinidae Cossmann. Haas's species is very similar to the Jurassic *Oonia*. Here, I propose accommodation of *Omphaloptycha jaworskii* in the genus *Oonia* following the classification of Gründel (2001b), extending also the chronostratigraphic distribution of the genus into the Late Triassic.

***Oonia jaworskii* (Haas, 1953) comb. nov.**

Fig. 7A-E

1953 *Omphaloptycha jaworskii* Haas; p. 137, pl. 8, figs. 1-28, 31.

**Material examined:** Holotype, AMNH No. 26522D; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 24.5 km SSE, 0.5 km W of Ninacaca, Jenks, Lot 48, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, globose to strongly turbiniform, small-sized and moderately high-spired shell, with a height of 10.2 mm and a width of 6.68 mm. The protoconch is fragmentary and consists of one convex and smooth whorl and is slightly deviated from the coiling axis. The teleoconch comprises five strongly convex whorls. Suture is deeply impressed in a spiral furrow. The sutural ramp is slightly developed on earliest whorls; on mature whorls the ramp is very weak, narrowly horizontal and slightly concave. The outer face becomes strongly convex. The shell surface is smooth and lacks spiral ornament. On last whorl, sigmoidal collabral threads appear; on the upper portion of the outer face they are orthocone

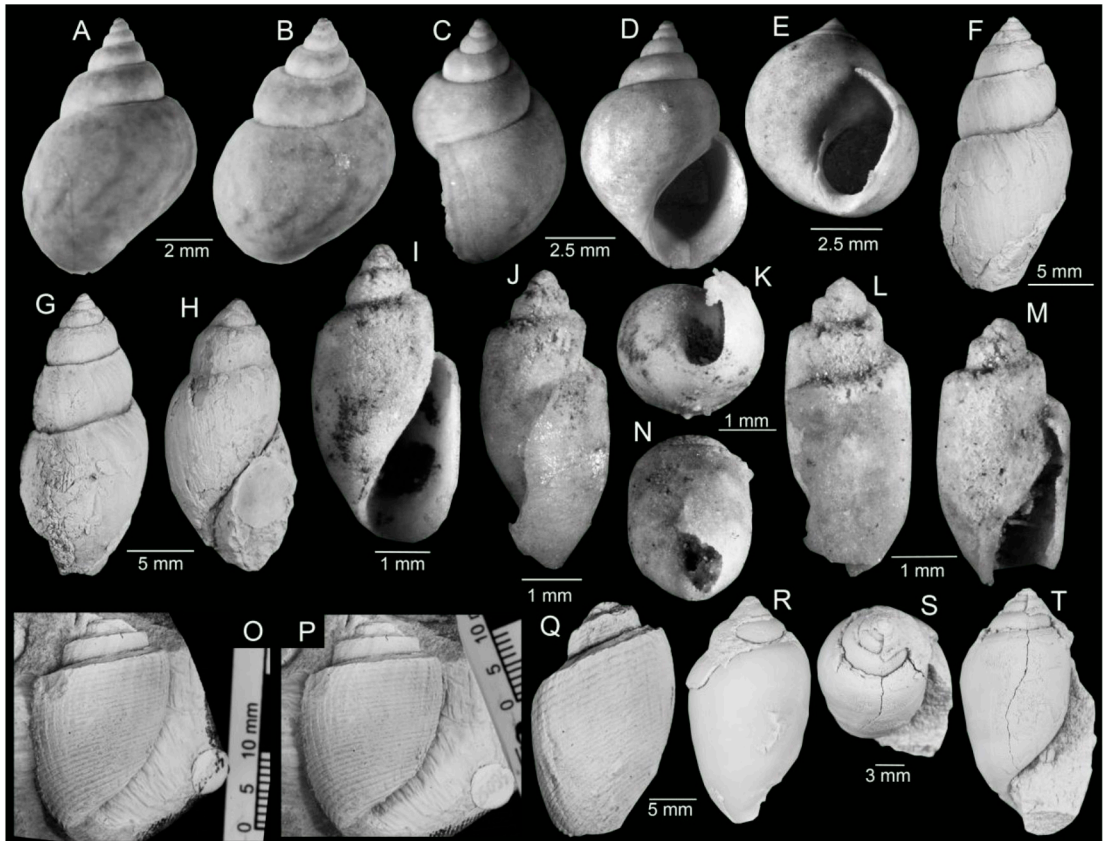


FIG. 7. A-E: *Oonia jaworskii* (Haas, 1953), AMNH No. 26522, holotype; A-C: lateral views; D-E: apertural and basal views; F-H: *Oonia?* sp., MLP 12159; F-G: lateral views; H: apertural view; I-N: *Cylindrobullina (Cylindrobullina) avenoides* Haas, 1953; I-K: AMNH No. 27634B, syntype; I-J: apertural and lateral views; K: basal view; L-N: AMNH No. 27634K, paratype; L-M: lateral and apertural views; N: basal view; O-Q: *Striactaeonina transatlantica* (Behrendsen, 1891), MLP 25094, lateral views; R-T: *Actaeonina ovata* Behrendsen (1891), MCF-PIPH 546; R: lateral view; S: apical view; T: lateral and apertural views.

slightly opisthocyrt, becoming strongly prosocline in the lower portion. The base is convex and expanded abapically, with a very narrowly opened umbilicus. The aperture is holostomatous and oval, with the basal lip flattened to concave; the columellar lip is thickened forming a callus which partially covers the umbilicus. A weak adapical channel is also developed. **Affinities:** *Oonia jaworskii* com. nov. shows close resemblance with Early Jurassic species from Chile and Argentina. For instance, cf. *Oonia* Gründel (2001a, p. 59, pl. 4, figs. 1-4), from the Early Jurassic (Hettangian-Pliensbachian) of Chile, differs from the Peruvian form in being bigger and in having less convex teleoconch whorls. The genus *Oonia* was also reported in the Early Jurassic of Argentina by Jaworski (1926) and Weaver (1931). The species *Oonia euspiroides* (Gemmellaro) (Jaworski, 1926, p. 200; Weaver, 1931, p. 371 as *O. cf. euspiroides*), however, has well developed growth lines on the shell surface. *Oonia?* sp. (Fig. 7F-H) was recently reported in the Early Jurassic (Pliensbachian) of Argentina and is also comparable to Haas's species; *Oonia?* sp., however, has a more acute shell shape and the last whorl is more expanded and elongated.

**Order Opisthobranchia Milne-Edwards, 1848**  
**Family Cyndrobullinidae Wenz, 1947**  
**Genus Cyndrobullina Von Ammon, 1878**

**Type species:** *Actaeonina fragilis* Dunker, 1846, from the Early Jurassic of Europe.

**Occurrence:** Late Triassic-Late Jurassic; Europe and South America.

**Remarks:** Bandel *et al.* (2000) defined representatives of *Cylindrobullina* by having egg-shaped, conical to step-like shells, with growth lines as the major sculptural elements, aperture elongated, oval, and lacks columellar folds, larval shell sinistral and twists into the teleoconch. Later, Gründel and Nützel (2012) emended the genus's diagnosis as 'the shell has cylindrical shape; the whorls embrace just below the subsutural ramp; the aperture is high and narrow; the spire is low; the whorls have a subsutural ramp with a rounded edge as transition to the almost straight flanks; the base is convex and has an evenly rounded transition to the whorl flanks; the whorls are smooth or weakly ornamented...there are no columellar folds; the protoconch is heterostrophic'. Haas's (1953) material fits with the characterization of Bandel *et al.* (2000) and Gründel and Nützel (2012); however,

Haas (1953) included the Late Triassic species in the family Acteonidae D'Orbigny, while Bandel *et al.* (2000) and Gründel and Nützel (2012) considered members of *Cylindrobullina* to belong to the family Cyndrobullinidae. Here, the classification of Bandel *et al.* (2000) and Gründel and Nützel (2012) is followed and the Late Triassic *Cylindrobullina* are accommodated into Cyndrobullinidae.

***Cylindrobullina (Cylindrobullina) avenoides* Haas, 1953**  
 Fig. 7I-N

**Material examined:** Paratype, AMNH No. 27634K; 'well preserved' teleoconch. Syntype, AMNH No. 27634B; 'well preserved' teleoconch.

**Occurrence:** Cerro de Pasco locality, 80 km SE, 4 km E of Tilarnioc, Jenks, Lot 48, Central Perú; Late Triassic, Pucará Group.

**Description:** Dextral, oval, cylindrical, egg-shaped, step-like, small-sized and slightly high-spined shell, with a mean height of 4.3 mm and a width of 2 mm. The protoconch is fragmentary; the teleoconch consists of five whorls, with the last whorls markedly more expanded than the spire. Sutural ramp is widely horizontal forming an angular to slightly convex demarcation with the outer face. The outer face becomes straight to slightly convex. Suture is weakly impressed in a spiral furrow. The shell surface shows fine, regularly spaced spiral furrow, more visible toward the outer face of last whorl; collabral ornament is not developed. The base is slightly convex to angular and strongly expanded abapically; the aperture is elongated and oval, and lacks columellar folds. A weak adapical channel is also visible.

**Affinities:** *Cylindrobullina (Cylindrobullina) avenoides* Haas (1953, p. 261, pl. 17, figs. 35, 36, 39-42, 46, 49-51, 58, 59) is comparable to *Cylindrobullina fragilis* Dunker (Jaworski, 1926, p. 205; Weaver, 1931, p. 389) from the Early Jurassic of Argentina; however, the last form is slightly bigger, has a more ovoid shell, and lacks spiral furrows. *Striactaeonina transatlantica* (Behrendsen, 1891) (Behrendsen, 1922; Möricke, 1894; Jaworski, 1926; Weaver, 1931; Gründel, 2001a), also from the Early Jurassic (Pliensbachian) of Argentina, resembles *Cylindrobullina (Cylindrobullina) avenoides*; however, the Argentinean species is bigger, has strongly developed spiral furrow on the shell surface, and has a more step-like shell (Fig. 7O-Q). *Striactaeonina atuelensis* Gründel (2001a; p. 66, pl. 4, figs. 7-8) from the early

Pliensbachian of Río Atuel (Mendoza) is also similar to the Peruvian species; but, *Striactaeonina atuelensis* has a sutural ramp nearly horizontal to sloped, and the shell outline is rather broader. *Actaeonina ovata* Behrendsen (1891, p. 383, pl. 22, fig. 7) (Fig. 7R-T), from the Early Jurassic of Argentina, is similar to *Cylindrobullina* (C.) *avenoides*; however, *A. ovata* has an ovoid shape and has smooth shell surface.

#### 4. Palaeobiogeography and Diversity

The distribution patterns of Mesozoic benthic marine gastropods in South America may be interpreted following the idea of a shallow marine connection along the eastern Paleo-Pacific sea way between Perú and the Andean region of Argentina during the Late Triassic (Norian-Rhetian)/Early Jurassic (Toarcian) boundary (Fig. 8). Vicente (2005) pointed out the evolution of the Jurassic Andean retroarc basin at a global scale for the Central Andes. The author systematically checked the time of the marine transgressions along the Andean region of South America and distinguished two main gulfs of passage through the arc from which waters have progressed at the same time northward and southward in a narrow retroarc furrow. One of these gulfs is located at 25°S and known as the Taltal; the Curepto Pacific gulf is found further south at 35°S. Both Pacific gulfs initiated 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 elongate basin from Chubut Province (Argentina) to northern Perú (Vicente, 2005) (Fig. 8).

Some gastropod taxa that are well known from the Late Triassic of the Pucará Group occur in Early Jurassic marine deposits of the Andean region of Argentina. In particular, the genera *Chartronella*, *Guidonia*, *Cryptaulax*, *Colpomphalus*, *Cryptaenia*, *Jurassiphorus*, *Oonia* and *Cylindrobullina* are distributed along the South American Andes, from Perú to Chubut Province and also have a chronostrotigraphic range from the Late Triassic (Norian-Rhetian) to the Early Jurassic (Toarcian). These genera are interpreted here to represent a component of survivors of the end Triassic mass extinction in South America. The ancient seaway from Perú to Argentina is considered the most plausible explanation for biotic exchange of these faunas across the Late Triassic/Early Jurassic boundary. On the other hand, the Peruvian genera *Hesperocirrus*, *Sororcula*, *Paracerithium*, *Rhabdocolpus*, *Eucycloscala*

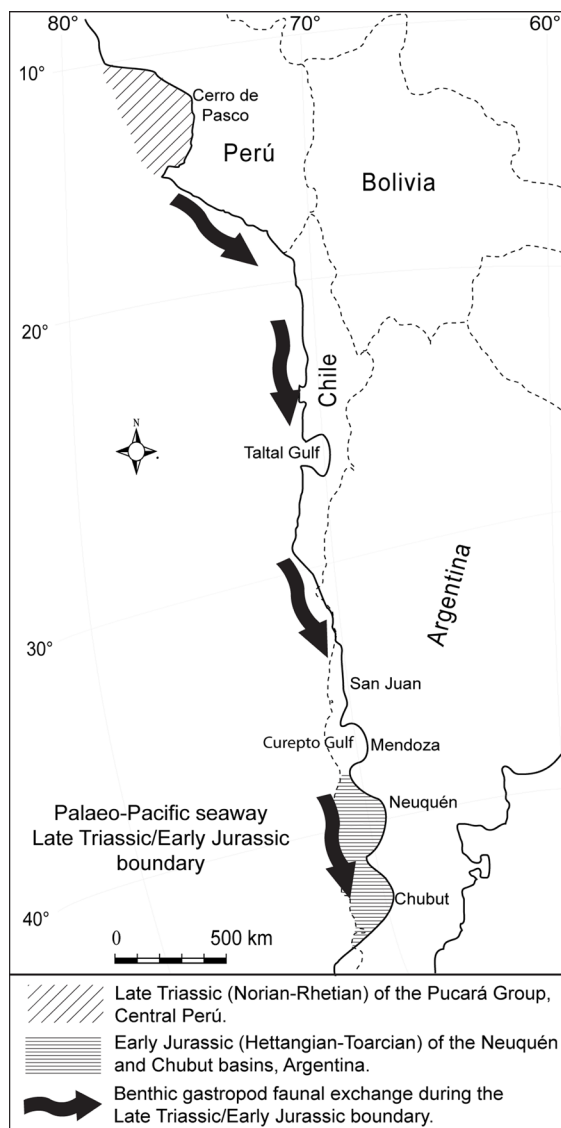


FIG. 8. Map of the Andean region of South America showing the palaeobiogeographical distribution of benthic gastropod faunas across the Late Triassic/Early Jurassic boundary.

are not represented in the Early Jurassic of Argentina but seem to have related counterparts. For instance, *Hesperocirrus* and *Sororcula* show close resemblance to *Hamusina* (see above); *Paracerithium* and *Rhabdocolpus* are also comparable to the genus *Procerithium* (see above); and *Eucycloscala* is related to the eucyclid genera *Calliotropis* and *Ambercycclus*, which are also reported in the Andean region of Argentina (see above). Figure 9 shows the taxonomic composition of the Peruvian and Argentinean Mesozoic marine gastropods across the Late Triassic/Early Jurassic

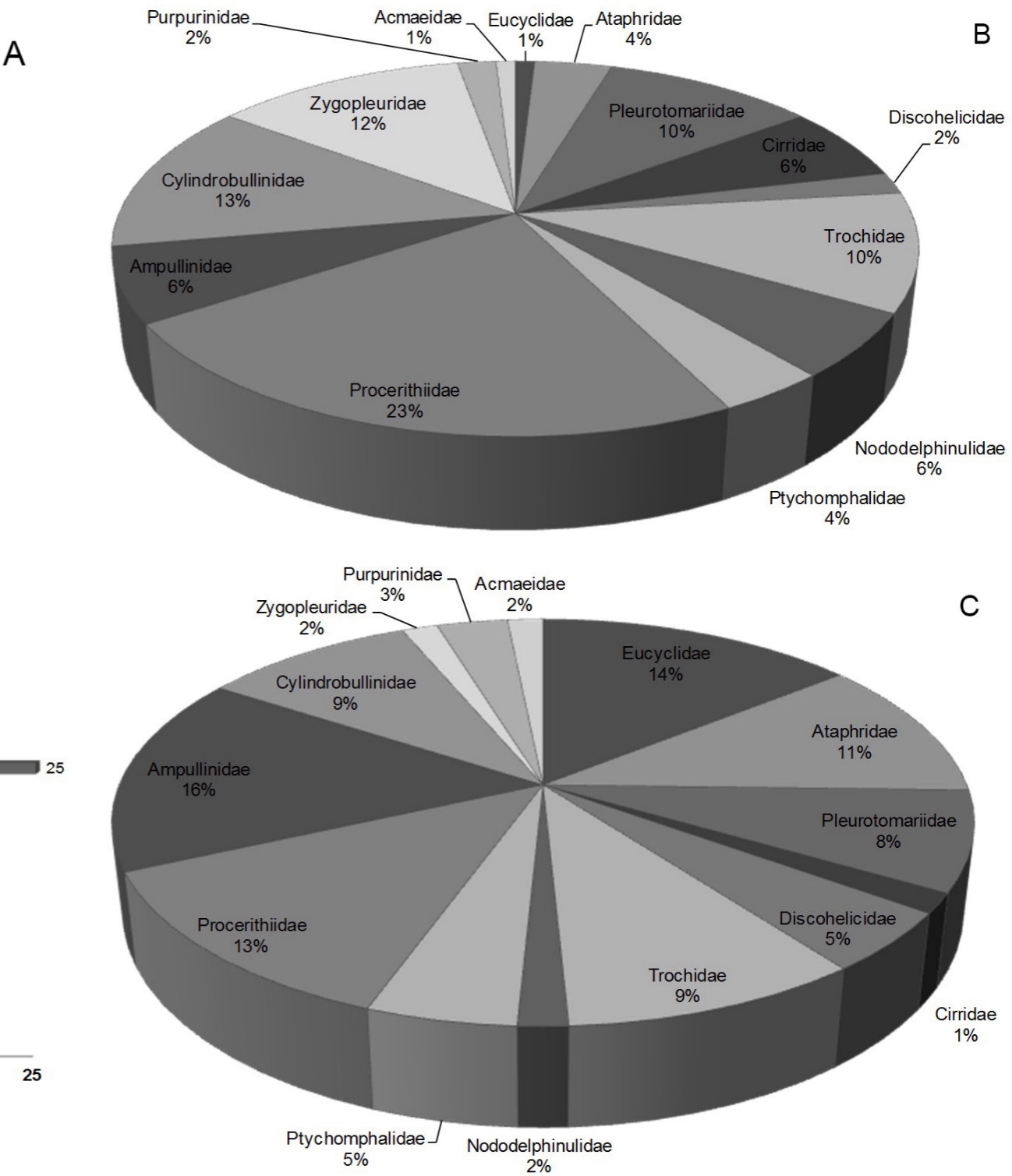
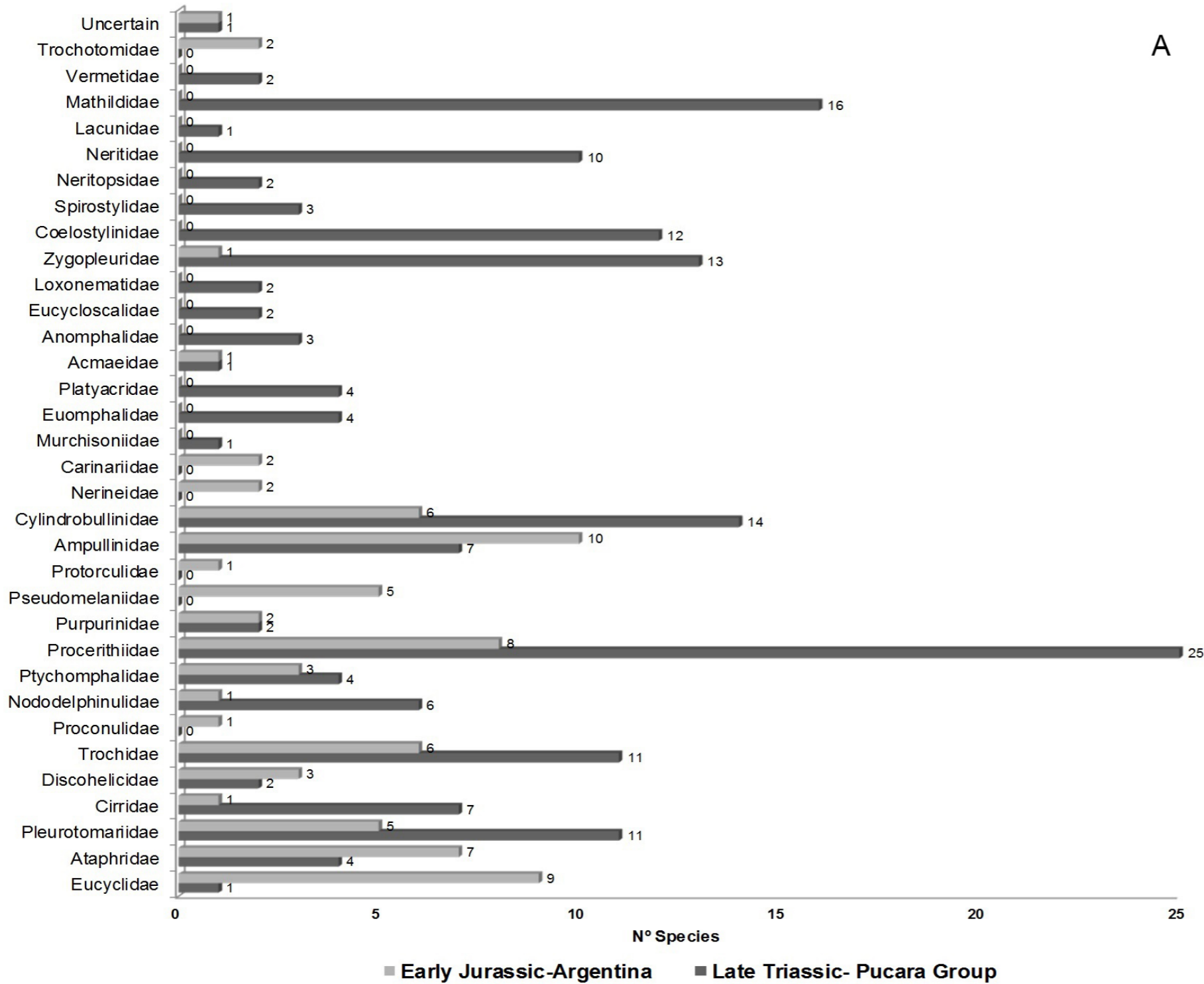


FIG. 9. A. Bar Graph showing the taxonomic composition (families) of the Peruvian and Argentinean Mesozoic marine gastropods across the Late Triassic/Early Jurassic boundary; B. Pie chart of families composition (%) from the Late Triassic of Perú; C. Pie chart of families composition (%) from the Early Jurassic of Argentina. Note that only the families Eucyclidae, Ampullinidae, Ataphridae and Discohelidae are far more diverse in the Argentinean Jurassic.

boundary. Note that several families are well represented in the Late Triassic of the Pucará Group (Perú) but are absent in the Early Jurassic marine deposits of Argentina; these are Vermetidae, Mathildidae, Lacunidae, Neritidae, Naritopsidae, Spirostylidae, Coelostylinidae, Loxonematidae, Eucycloscalidae, Anomphalidae, Platyacridae, Euomphalidae and Murchisoniidae. On the other hand, families such as Trochotomidae, Carinariidae, Nerineidae, Protorculidae, Pseudomelaniidae and Proconulidae seem to be characteristic in the Early Jurassic of Argentina but are not represented in the Peruvian Triassic. There are, however, several taxa that occur in both regions: Zygopleuridae, Acmaeidae, Cyndrobullinidae, Ampullinidae, Purpurinidae, Procerithiidae, Ptychomphalidae, Nododelphinulidae, Trochidae, Discohelicidae, Cirridae, Pleurotomariidae, Ataphridae and Eucyclidae. Regarding the latter families, only four (Eucyclidae, Ataphridae, Discohelicidae and Ampullinidae) are better represented in Argentina with a higher number of species (Fig. 9A, C). This suggests that some Late Triassic Peruvian gastropod taxa were probably more susceptible than others to the end Triassic extinction. The appearance of new gastropod genera and families in the Early Jurassic of Argentina, which are not represented in the faunal assemblages of the Pucará Group, also show a relatively rapid faunal recovery after the crisis. However, the Peruvian gastropod fauna is slightly more diverse and abundant than the Argentinean (Fig. 9).

In order to assess the gastropod diversity across the Late Triassic/Early Jurassic boundary, a biodiversity analysis was performed integrating all accessible data of marine gastropod faunas recovered thus far from the Late Triassic of Perú and from the Early Juras-

sic of Argentina. The analysis was based on PAST statistical software (Hammer *et al.*, 2001) which calculated Simpson, Shannon and Margalef indices for the included samples. The Simpson and Shannon diversity indices provide an estimate of the variation in abundance among species within an assemblage (Table 1); the Margalef indice estimate the biodiversity of a community based on the numerical distribution of individuals of different species. Margalef values above 5.0 are considered to be indicative of high diversity. The primary results of the analysis show that the gastropod faunal association from the Pucará Group displays the highest diversity during the Late Triassic (Table 1, Fig. 9). In contrast, the Early Jurassic marine gastropods from Argentina indicate a lower diversification during the Hettangian /Toarcian times, showing a smaller number of species and families at that time (Table 1, Fig. 9). It is indeed clear, that the Late Triassic mass extinction had an impact on the South American marine benthic gastropod faunal turnover.

Rarefaction analysis (PAST) have also been calculated for each accessible sample of marine gastropod taxa recovered thus far from Perú and Argentina in order to assess species richness in a function of the collection effort. The samples contained a total of 248 species representing 34 families. For the Peruvian association, a curve was calculated for the entire Haas's (1953) gastropod collection. The Argentinean curve displayed less diversity than the Haas's (1953) collection, although it represents a sample of widely distributed gastropod species which covers similar span of time. It is not surprising considering that the end Triassic crisis could have had a major incidence on the South American Early Jurassic faunal recovery. However, a more detailed research of Early Jurassic

**TABLE 1. DIVERSITY OF LATE TRIASSIC AND EARLY JURASSIC GASTROPOD FAUNAS IN COMPARISON: SPECIES RICHNESS, FAMILIES, SIMPSON, SHANNON AND MARGALEF DIVERSITY INDICES.**

	<b>Pucara Group</b>	<b>Argentina</b>
Families	28	21
Individuals	171	77
Simpson	0.93	0.92
Shannon	2.9	2.7
Margalef	5.2	4.6
Stage	Norian/Rhetian	Hettangian/Toarcian

gastropod faunas in Argentina, including the investigation of new fossiliferous localities and the collection of new gastropod material with accurate geographical and stratigraphical data is currently in progress.

Regarding other Mesozoic gastropod assemblages from the Southern Hemisphere, the Peruvian fauna shows also close resemblance to the Early/Middle Jurassic New Zealand gastropod associations and with Early Jurassic Antarctic species. Bandel *et al.* (2000) described many species from the Kaiwara Valley (New Zealand) which are treated here to be nearly coeval and related counterparts to the Peruvian and Argentinean forms. At least representatives of the genera *Guidonia*, *Hamusina*, *Eucycloscala*, *Paracerithium*, *Rhabdocolpus*, *Cryptaulax* and the families Mathildidae and Cyndrobullinidae show affinities with the South American taxa, and suggest palaeobiogeographical connections along the southern Paleo-Pacific ocean. The Early Jurassic Antarctic Procerithiidae show also close systematic affinities to the South American taxa.

### Acknowledgements

This work was supported by the Collection Study Grant Program awarded by the American Museum of Natural History, New York (AMNH). I thank the AMNH for this financial support. I also extend my gratitude to Ms. B. Hussaini (American Museum of Natural History, New York) and to Dr. N. Landman (American Museum of Natural History, New York) who allowed me access to the AMNH invertebrate collection. I specially thank B. Hussaini (American Museum of Natural History, New York) for taking the gastropod photographs. Critical reviews by H. Campbell (GNS Sciences, New Zealand), A. Kaim (Instytut Paleobiologii PAN, Warszawa, Poland) and A. Nützel (Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany) of an earlier version of this manuscript contributed to improve it and are gratefully acknowledged.

### References

- Agassiz, L. 1837. Grossbritanniens Mineral-Conchologie oder ausgemahlte Abbildungen und Beschreibungen der Schalthier-Überreste, welche zu verschiedenen Zeiten und in verschiedenen Tiefen der Erde erhalten worden sind, von James Sowerby: 689 p.
- Andreae, A. 1887. Die Glossophoren des Terrain à chailles der Pfirt. Abhandlungen zur geologischen Spezialkarte von Elsass-Lothringen 4: 1-45.
- Bandel, K. 1993. Evolutionary history of sinistral archaeogastropods with and without slit (Cirroidea, Vetigastropoda). *Paläontologie, Stratigraphie, Fazies* (1), Freiburger Forschungshefte C 450: 41-81.
- Bandel, K. 1994. Comparison of Upper Triassic and Lower Jurassic Gastropods from the Peruvian Andes (Pucará Group) and the Alps (Cassian Formation). *Palaeontographica* 233: 127-160.
- Bandel, K. 2006. Families of the Cerithioidea and related superfamilies (Palaeo-Caenogastropoda; Mollusca) from the Triassic to the Recent characterized by protoconch morphology-including the description of new taxa. *Paläontologie, Stratigraphie, Fazies* (14), Freiburger Forschungshefte C 511: 59-138.
- Bandel, K. 2009. The slit bearing nacreous Archaeogastropoda of the Triassic tropical reefs in the St. Cassian Formation with evaluation of the taxonomic value of the selenizone. *Berliner Paläobiologische Abhandlungen* 10: 5-47.
- Bandel, K. 2010. Relationships of the Triassic Eucycloidea Koken, 1897 (Mollusca, Gastropoda) to modern genera such as *Pagodatrochus*, *Calliotropis* and *Euchelus*, based on morphology of the early shell. *Bulletin of Geosciences* 85 (3): 435-486.
- Bandel, K.; Gründel, J.; Maxwell, P. 2000. Gastropods from the upper Early Jurassic/Early Middle Jurassic of Kaiwara Valley, North Canterbury, New Zealand. *Paläontologie, Stratigraphie, Fazies* (8), Freiburger Forschungshefte C 490: 67-132.
- Behrendsen, O. 1891. Zur Geologie des Ostabhanges der argentinischen Cordillere. Teil I. *Zeitsch. Deutschen Geologischen Gesellschaft* 43: 369-420.
- Behrendsen, O. 1922. Contribución a la geología de la pendiente oriental de la Cordillera Argentina. *Academia Nacional de Ciencias, Actas* 7: 161-227, Córdoba.
- Bonarelli, G. 1921. Tercera contribución al conocimiento geológico de las regiones petrolíferas subandinas del Norte (Provincias de Salta y Jujuy). *Annales de la Dirección Nacional de Geología y Minería* 15 (1): 96 p. Buenos Aires.
- Bouchet, P.; Rocroi, J.P. 2005. Classification and nomenclator of gastropod families. *Malacologia* 47 (1-2): 1-397.
- Chartron, C.; Cossmann, M. 1902. Note sur l'Infralias de la Vendée et spécialement sur un gisement situé dans la commune du Simon-la-Vineuse. *Bulletin Société géologique de France* 4 (2): 163-203.
- Cossmann, M. 1885. Contribution à l'étude de la faune de l'étage Bathonien en France (Gastropoda). *Mémoires de la Société Géologique de France* 3: 1-374.

- Cossmann, M. 1902. Rectifications de nomenclature. *Revue critique de Paléozoologie* 6: p. 223.
- Cossmann, M. 1905. Rectifications de nomenclature. *Revue Critique de Paléozoologie* 9 (1): 57-60.
- Cossmann, M. 1906. *Essais de Paléoconchologie Comparée*. Septième Livraison 7: 261 p. Paris.
- Cossmann, M. 1909. *Essais de Paléoconchologie Comparée*. Huitième Livraison: 248 p. Paris.
- Cossmann, M. 1915. Étude complémentaire sur le Charmoutien de la Vendée. *Mémoires de la Société linnéenne de Normandie*, Section géologique 33: 113-159.
- Cossmann, M. 1916. *Essais de Paléonconchologie comparée*. Chez l'auteur 10: 292 p. Paris.
- Cossmann, M. 1919. Supplément aux mollusques éocéniques de la Loire-Inférieure. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, sér. 3: 53-141.
- Cox, L.R. 1949. Upper Triassic Mollusca from Perú. *Boletín Instituto Geológico del Perú* 12: 50 p.
- Cox, L.R. 1959. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* 33: 239-261.
- Cox, L.R. 1960. Family Nododelphinulidae Cox, n. fam. In *Treatise on invertebrate paleontology* (Moore, R.C.; Pitrat, W.; editors). Geological Society of America, Boulder, Colorado and University of Kansas Press, Mollusca 1, Part I: p. 308. Lawrence, Kansas.
- Cox, L.R. 1965. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. *Bulletin of the British Museum (Natural History) Geology* 1: 137-209. London.
- Cox, L.R. 1969. Gasterópodes jurassiques du Sud-Est Tunisien. *Annales de Paléontologie (Invertébrés)* 55 (2): 243-268.
- Damborenea, S.E.; Manceñido, M.O.; Riccardi, A.C. 1975. Biofacies y estratigrafía del Liásico de Piedra Pintada, Neuquén, Argentina. In *Congreso Argentino de Paleontología y Bioestratigrafía*, No. 1, Actas 2: 173-228. Tucumán.
- Deshayes, G.P. 1830-1932. *Encyclopédie méthodique. Histoire naturelle des vers*. Paris.
- D'Orbigny, A. 1850-60. *Paléontologie Française. Terrain Jurassique II. Gastéropodes*: 622 p. Paris.
- De Stefani, C. 1880. I fossili triassici delle Alpi Apuane. *Rendiconti del Reale Istituto Lombardo di Scienze e Lettere*, serie II 13: 493-497.
- Dunker, W. 1846 Diagnosen einiger neuer Conchylien aus der norddeutschen Liasbildung. *Zeitschrift für Malakozoologie* 3: 168-171.
- Edwards, C.W. 1980. Early Mesozoic marine fossils from central Alexander Island. *British Antarctic Survey Bulletin* 49: 33-58.
- Eudes-Deslongchamps, E. 1864. Notes paléontologiques. Caen et Paris: 392 p.
- Ferrari, S.M. 2009. Cosmopolitan Early Jurassic marine gastropods from west-central Patagonia, Argentina. *Acta Palaeontologica Polonica* 54 (3): 449-461.
- Ferrari, S.M. 2011. Early Jurassic Ataphridae (Mollusca: Gastropoda) from Chubut, Argentina: paleogeographic and paleoecologic implications. *Ameghiniana* 48 (1): 64-78.
- Ferrari, S.M. 2012. The genera *Cryptaulax* and *Procerithium* (Procerithiidae, Caenogastropoda) in the Early Jurassic of Patagonia, Argentina. *Alcheringa* 36 (3): 323-336.
- Ferrari, S.M. 2013. New Early Jurassic gastropods from west-central Patagonia, Argentina. *Acta Palaeontologica Polonica* 58 (3): 579-593.
- Ferrari, S.M. 2014a. Patellogastropoda and Vetigastropoda (Mollusca, Gastropoda) from the marine Jurassic of Patagonia, Argentina. *Historical Biology* 26 (5): 563-581.
- Ferrari, S.M. 2014b. Early Jurassic marine gastropods from Argentina: a palaeobiogeographical analysis based on Vetigastropoda. *Journal of Systematic Palaeontology*. doi: 10.1080/14772019.2014.967319.
- Ferrari, S.M.; Kaim, A.; Damborenea, S.E. 2014. The genera *Calliotropis* Seguenza and *Ambercyclus* n. gen. (Vetigastropoda, Eucyclidae) from the Early Jurassic of Argentina. *Journal of Paleontology* 88 (6): 1174-1188.
- Ferrari, S.M.; Damborenea, S.E.; Manceñido, M.O.; Griffin, M. In press. Early Jurassic Trochotomidae (Vetigastropoda, Pleurotomarioidea) from the Neuquén Basin, Argentina. *Journal of Paleontology*.
- Fischer, P. 1885. *Manuel de conchyliologie et de paléontologie conchyliologique, ou Histoire Naturelle des Mollusques Vivants et Fossils* 9: 785-896. Paris.
- Gatto, R.; Monari, S. 2010. Pliensbachian gastropods from Venetian Southern Alps (Italy) and their paleobiogeographical significance. *Palaeontology* 53 (4): 771-802.
- Gemmellaro, G.G. 1878. Sui fossili del calcare cristallino delle montagne del Casale e di Bellampo nella Provincia di Palermo. *Giornale di Scienze Naturali Ed Economiche* 13: 116-212.
- Gray, J.E. 1853. On the division of ctenobranchous gastropodous Mollusca into larger groups and families. *Annals and Magazine of Natural History* 11: 124-132.
- Gründel, J. 1997. Zur Kenntnis einiger Gastropoden-Gattungen aus dem französischen Jura und allgemeine Bemerkungen zur Gastropodenfauna aus dem Dogger Mittel-und Westeuropas. *Berliner geowiss. Abhandlungen E* 25: 69-129. Berlin.

- Gründel, J. 1999. Procerithiidae (Gastropoda) aus dem Lias und Dogger Deutschlands und Polens. Freiburger Forschungshefte C 481: 1-37. Freiberg.
- Gründel, J. 2001a. Gastropoden aus dem Jura der südamerikanischen Anden. Freiburger Forschungshefte C 492: 43-84.
- Gründel, J. 2001b. Neritimorpha und Caenogastropoda (Gastropoda) aus dem Dogger Norddeutschlands und des nordwestlichen Polens. Berliner geowissenschaftliche Abhandlungen E 36: 45-99. Berlin.
- Gründel, J. 2004. Gastropodem aus dem oberen Bathonium von Luc-sur-Mer/Clavados (Normandie; Frankreich): Archaeogastropoda und Neritimorpha. Freiburger Forschungshefte C 502: 15-50. Freiberg.
- Gründel, J. 2005. Die Gattung Discheliella Dunker, 1847 (Gastropoda) und zur Fassung der Discheliellidae Schröder, 1995. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte: 729-748. Stuttgart.
- Gründel, J. 2007. Jurassische Gastropoden aus der Betakalkbank (oberes Sinemurium, obere Obtusum-Zone) Südwestdeutschlands. Stuttgarter Beiträge zur Naturkunde B 370: 1-29. Stuttgart.
- Gründel, J. 2008. Remarks to the classification and phylogeny of the Ataphridae Cossmann, 1915 (Gastropoda, Archaeogastropoda) in the Jurassic. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 250: 177-197.
- Gründel, J. 2011. Die Ptychomphalidae Wenz, 1938, (Ptychomphaloidea, Gastropoda) im Jura. Freiburger Forschungshefte C 539: 59-60.
- Gründel, J.; Nützel, A. 2012. On the early evolution (Late Triassic to Late Jurassic) of the Architectibranchia (Gastropoda: Heterobranchia), with a provisional classification. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 264 (1): 31-59.
- Hammer, O.; Harper, D.A.T.; Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electrónica 4 (1): 1-9.
- Haas, O. 1953. Mesozoic Invertebrate Faunas of Perú. Bulletin of the American Museum of Natural History 101: 321 p. New York.
- Hébert, M.; Eudes-Deslongchamps, M.E. 1860. Mémoire sur les fossiles de Montreuil-Bellay (Maine-et-Loire). Ire. partie. Céphalopodes et Gastéropodes. Bulletin de la Société linnéenne de Normandie 5: 153-240.
- Jaworski, E. 1923. Die marine Trias in Südamerika. Beiträge zur Geologie und Paläontologie von Südamerika (Steinmann, G.; editor). Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 47: 93-200.
- Jaworski, E. 1926. La fauna del Lias y Dogger de la Cordillera Argentina en la parte meridional de la provincia de Mendoza. Academia Nacional de Ciencias Argentina, Actas 9 (3-4): 137-316. Córdoba.
- Kaim, A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. Palaeontologia Polonica 62: 3-183.
- Kaim, A.; Jenkins, R.G.; Hikida, Y. 2009. Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan. Acta Palaeontologica Polonica 54: 463-490.
- Milne-Edwards, H. 1848. Note sur la classification naturelle des mollusques gastéropodes. Annales des Sciences Naturelles Zoologiques 3: 102-112.
- Monari, S.; Valentini, M.; Conti, A. 2011. Earliest Jurassic patellogastropod, vetigastropod, and neritimorph gastropods from Luxembourg with considerations on the Triassic Jurassic faunal turnover. Acta Palaeontologica Polonica 56: 349-384.
- Mörcke, W. 1894. Versteinerungen des Lias und Unteroolith von Chile. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband 9: 1-100.
- Münster, G.G. 1844. Petrefacta Germaniae, Dritter Theil. In Petrefacta Germaniae, Dritter Theil (Goldfuss, G.A.; editor). Arnz and Comp., Düsseldorf: 128 p.
- Nützel, A.; Erwin, D. 2004. Late Triassic (Late Norian) gastropods from the Wallowa Terrane (Idaho, USA). Paläontologische Zeitschrift 78: 361-416.
- Salvini-Plawen, L.V. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). Malacologia 19: 249-278.
- Schröder, M. 1995. Frühontogenetische Schalen jurassischer und unterkretazischer Gastropoden aus Norddeutschland und Polen. Palaeontographica A 238: 1-95.
- Sowerby, J. 1812-1822. The mineral conchology of Great Britain. Benjamin Meredith, London: 765 p.
- Stoliczka, F. 1861. Über die Gastropoden und Acephalen der Hierlatz-Schichten. Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlich-königlichen Akademie der Wissenschaften Wien 43: 157-204.
- Szabó, J. 2009. Gastropods of the Early Jurassic Hierlatz Limestone Formation; part 1: a revision of type collections from Austrian and Hungarian localities. Fragmenta Palaeontologica Hungarica 26: 1-108.
- Tate, R. 1869. Contributions to Jurassic Palaeontology. 1. *Cryptaulax*, a new Genus of Cerithiidae. The Annals and Magazine of Natural History 4: 417-419.

- Thompson, M.R.A.; Turner, T.H. 1986. Early Jurassic fossils from Central Alexander Island and their geological setting. *British Antarctic Survey, Bulletin* 70: 23-39.
- Vicente, J.C. 2005. Dynamic paleogeography of the Jurassic Andean Basin: pattern of transgression and localization of the main straits through the magmatic arc. *Revista de la Asociación Geológica Argentina* 15: 221-250.
- Von Ammon, L. 1878. Die Gastropoden des Hauptdolomites und des Plattenkalkes der Alpen, Separatabdruck des elften Beiheftes der Abhandlungen des zoologisch-mineralogischen Vereines in Regensburg 11: 1-72.
- Weaver, C. 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina. University of Washington, Memoir 1: 1-496.
- Wenz, W. 1938-1944. Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia *In* Handbuch der Paläozoologie (Schindewolf, O.H.; editor). Verlag Gebrüder Bornträger, Band 6: 1639 p. Berlin.
- Wenz, W. 1947. Zur Taxonomie der Euthyneura. *Archiv für Molluskenkunde* 76 (1): 33 p.