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EARLY JURASSIC ATAPHRIDAE (MOLLUSCA: GASTROPODA) FROM CHUBUT, ARGENTINA: PALEOGEOGRAPHIC AND PALEOECOLOGIC IMPLICATIONS

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Abstract. Three new species of the Ataphridae are described here: *Ataphrus mulanguiniensis* sp. nov., *Chartronella paganiae* sp. nov. and *Chartronella spiralis* sp. nov.; in addition, another doubtfully referred member of the family is recorded from the studied sections, i.*e., Lewisiella*? sp. The new findings here reported from the Early Jurassic of Chubut Province contribute towards the knowledge on the systematics of the family in Argentina, extending its paleogeographic distribution into the Jurassic of South America. An abundant and diverse invertebrate fauna found in association with the ataphrid genera indicates a littoral marine environment for the gastropod-bearing rocks.

Keywords. Ataphridae. Gastropoda. Early Jurassic. Chubut. Argentina.

Resumen. ATAPHRIDAE (MOLLUSCA: GASTROPODA) EN EL JURÁSICO TEMPRANO DE CHUBUT, ARGENTINA: IMPLICANCIAS PALEOGEOGRÁFICAS Y PALEOECOLÓGICAS. En el presente trabajo se dan a conocer tres nuevas especies de la Familia Ataphridae: *Ataphrus mulanguiniensis* sp. nov., *Chartronella paganiae* sp. nov. y *Chartronella spiralis* sp. nov.; y se describe otro miembro del grupo asignado con dudas al género *Lewisiella* (*Lewisiella*? sp.). Estos nuevos registros de Ataphridae provenientes del Jurásico Temprano de la Provincia del Chubut contribuyen al conocimiento sistemático de la familia en Argentina, permitiendo extender la distribución paleogeográfica de la misma en el Jurásico de América del Sur. En asociación a los atáphridos aquí descriptos se ha registrado una fauna abundante y diversa de invertebrados marinos lo cual ha permitido caracterizar un ambiente litoral para las rocas portadoras.

Palabras clave. Ataphridae. Gastropoda. Jurásico Temprano. Chubut. Argentina.

Gründel (2008) proposed a new classification of the family Ataphridae and considered the general morphology of the aperture and the peristome as the most diagnostic shell characters of this group. Gründel's classification differs from that proposed by Hickman and McLean (1990), which was based primarily on anatomical characters. Kaim *et al.* (2009) included the subfamily Ataphrinae within the Turbinidae Rafinesque.

In contrast to previous classifications (Knight *et al.*, 1960; Hickman and McLean, 1990; Monari *et al.* 1996 and Bouchet and Rocroi, 2005), Gründel (2008) placed Proconulidae near Ataphridae and included both in the Turbinoidea. According to Gründel (2008), two characters suggest this arrangement, *i.e.*, (1) both groups have a rounded apex; the initial whorls are very low-spired trochospiral to nearly planispiral, and (2) the outline of the peristome is very similar in both groups. However, ataphrids are characterized by the presence of a small or small-medium, turbiniform or trochiform shell, with flat to moderately convex whorls, a very low spire, and planispiral initial whorls. The teleoconch is smooth, usually forming a cyrtoconoid spire with an even outline. The base is convex, anomphalous, or possibly cryptomphalous in some forms. Apertures are mostly rounded with a crescent-shaped columellar lip and adaxial part of basal lip, which frequently has a furrow. In some genera this furrow has a knob at its adapical end. A number of the genera placed in this family have a true callus with a different morphology in adults; however, juveniles show the ataphrid columellar lip (Szabó *et al.* 1993; Gründel 2008).

The Ataphridae originated in the Early Triassic (Nützel, 2005; Kaim, 2009) and a rapid radiation occurred in the Early Jurassic. The most successful, diversified Jurassic group is represented by the Ataphrini (Gründel, 2008). Some ataphrid genera are represented by extant species, *i.e.*, *Collonia* Gray (Colloniini Cossmann in Cossmann and Peyrot), *Crossostoma* Morris and Lycett (Crossostomatini Cox in Knigth *et al.*), *Homalopoma* Carpenter (Homalopomatini Keen in Knigth *et al.*). Monari *et al.* (1996) considered the Ataphridae as synonym of Collonidae Cossmann. Gründel (2008) included Colloniini as a tribe of Ataphrinae, and Kaim *et. al.* (2009) included some Cretaceous memebrs of *Homalopoma* and *Cantrainea* Jeffreys within the tribe Colloniini (subfam-

ily Ataphrinae), stressing the similarity between them and others Jurassic and Cretacous repersentatives of Ataphrini. Molecular evidence provided by Williams *et al.* (2008) suggests that colloniids should be considered a disctinct superfamily of vetigastropods. The classifications followed here are those by Gründel (2008) and Kaim *et al.* (2009).

Ataphrids are common and widely distributed in the Mesozoic of Europe (Szabó, 1981, 1982, 2008; Szabó *et al.*, 1993; Monari *et al.*, 1996; Gründel, 2000, 2003, 2007, 2008; Kaim, 2004; Gründel and Kaim, 2006); and some members were recognized in other Asiatic and African Jurassic localities (Cox, 1965; Jaitly *et al.* 2000). In the Early Jurassic of Argentina, however, the only previously reported representative of this family was *Striatoconulus* sp. (Ferrari, 2009). Recent findings of new ataphrids in the Early Jurassic (Pliensbachian–Toarcian) of Chubut Province contribute towards increasing knowledge of the group in Argentina, also expanding its paleogeographic distribution in the Jurassic of South America. Four taxa —three of them new species—are described from Lomas Occidentales and Lomas de Betancourt, near Rio Genoa valley (Fig. 1). These are *Ataphrus mulanguiniensis* sp. nov., *Chartronella paganiae* sp. nov., *Chartronella spiralis* sp. nov. and *Lewisiella*? sp. An abundant and diverse invertebrate fauna found in association with the ataphrid genera suggests a littoral marine environment for the gastropod-bearing rocks.

GEOLOGIC AND STRATIGRAPHIC SETTING

Early Jurassic rocks in Chubut Province are exposed along a NW–SE belt of outcrops between 42º 30'– 44º 30' S and 69º 30'–71º W (Riccardi, 1983; Giacosa and Márquez, 1999). They rest unconformably over Late Paleozoic rocks of the Tepuel Group. In the southwestern region of Chubut Province, the Early Jurassic marine deposits crop out in two areas, *i.e.*, Ferraroti and Nueva Lubecka. They are known as Mulanguiñeu Formation (Fernández Garrasino, 1977), which was recognized by Suero (1952, 1953, 1958) as 'Serie marina con *Vola* y *Cardinia*'. The most extensive outcrops of this unit are on the western slope of Salar de Ferraroti and Lomas Occidentales near Río Genoa valley, and they lie unconformably over Late Paleozoic marine sediments referred to the Río Genoa Formation. The Mulanguiñeu Formation reaches a thickness of 490 m, and has been divided into two members according to its lithologic characteristics (Fernández Garrasino, 1977). The lower member is psamitic with

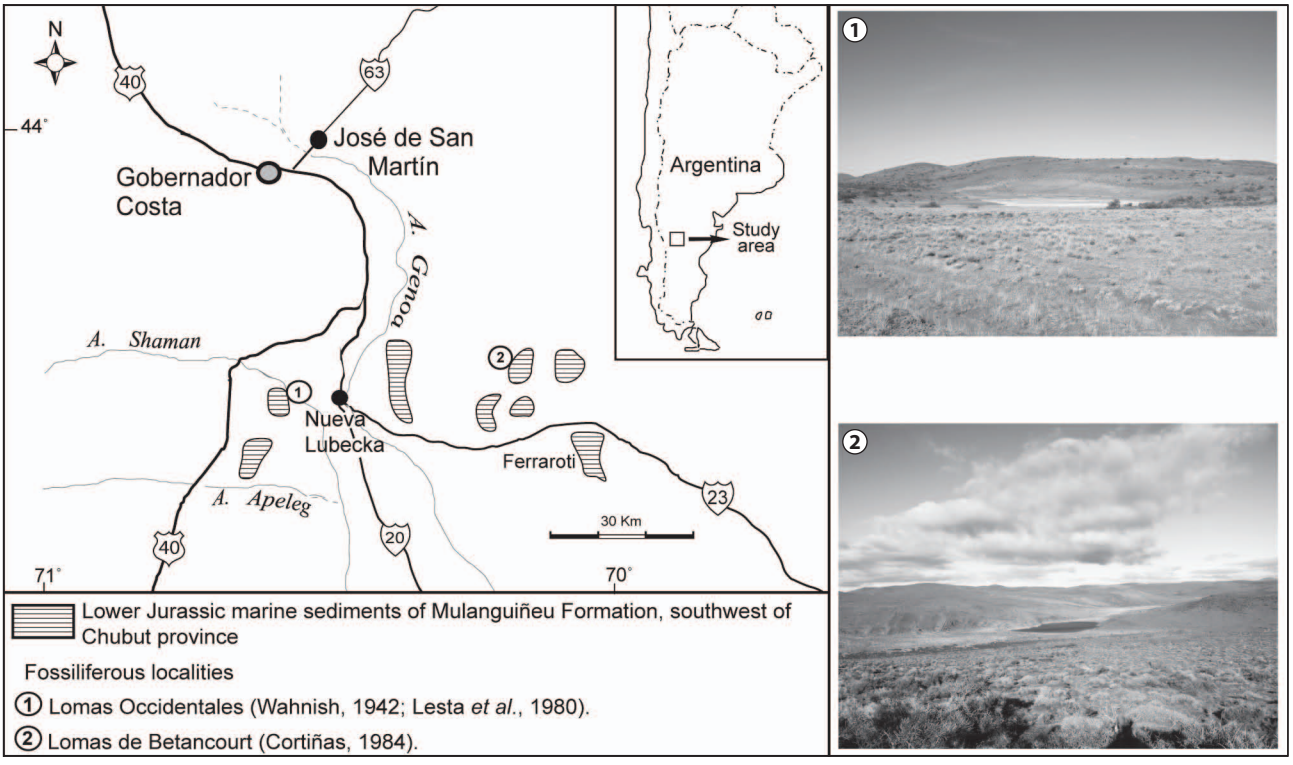

Figure 1. Location map of fossil localities in Lomas Occidentales and Lomas de Betancourt, southwestern Chubut Province, Argentina, and general views of each locality / *Mapa de localización de las localidades fosilíferas de Lomas Occidentales y Lomas de Betancourt al sudoeste de la provincia de Chubut, Argentina, y vista general de cada localidad.*

basal conglomerates, and the upper member is dominated by medium- to fine-grained sandstones, tuffs and carbonatic rocks. Lomas Occidentales (Wahnish, 1942; Lesta *et al.*, 1980) is located west of the old telegraphic station of Nueva Lubecka (Fig. 1.1). Early Jurassic marine rocks are also exposed at Lomas de Betancourt (Cortiñas, 1984) (Fig. 1.2), 15 km east and 4 km north of the same telegraphic station.

The Mulanguiñeu Formation was dated as Early Jurassic (Pliensbachian–Toarcian) based on marine invertebrate faunas including bivalves, ammonites and brachiopods (Fernández Garrasino, 1977).

MATERIAL AND METHODS

The material was collected in 2009 and belongs to the Museo Paleontológico Egidio Feruglio (MEF) collection. Teleoconchs were prepared by technical staff at the MEF laboratory. Photographs were made with a Sony digital camera at MEF. Systematic arrangement follows Gründel (2008) and Kaim *et al.* (2009). Morphologic terminology is based on Knight *et al.* (1960) and Gründel (2008).

Institutional abbreviations. ALUAR, Aluminio Argentino, Pto. Madryn, Chubut, Argentina; MPEF-PI, Museo Paleontológico "Egidio Feruglio", Trelew, Chubut, Argentina.

SYSTEMATIC PALEONTOLOGY

Order Vetigastropoda Salvini-Plawen, 1980

Superfamily Trochoidea Rafinesque, 1815

Family Ataphridae Cossmann 1915(= Colloniidae Cossmann 1916, according to Monari *et. al,* 1996)

Subfamily Ataphrinae Cossmann 1915
(= Helicocryptinae Cox, in Knight *et al.*, 1960; according to Szabó *et al.*, 1993)

Tribe Ataphrini Cossmann, 1915

Comments. A diagnosis of Ataphrini was published by Gründel (2008). Figure 2 shows the general shell morphology and ornament pattern of Ataphrinae and Ataphrini. Note that apertural and columellar characters have a diagnostic significance for the Ataphridae.

Genus ***Ataphrus*** Gabb, 1869

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

Diagnosis. In Kaim (2004) and Gründel (2008).

Stratigraphic and geographic range. Early Jurassic–Late Cretaceous; Europe, Asia, Africa and America.

Remarks. *Ataphrus* is the most diverse and abundant genus of Jurassic Ataphridae. According to Gründel (2008), the diagnostic characters of the *Ataphrus* group, its extent, and its suprageneric and generic subdivisions are also debatable. This is because of the incomplete knowledge on the general morphology of the peristome of *Ataphrus crassus*, the type species of the genus (it is missing details that are crucial for a correct systematic assignment whithin the *Ataphrus*-group). Gründel (2008) argued that many European Jurassic species included in *Ataphrus* clearly differ from the type species, rendering it doubtful whether these generic assignement are justified. *Ataphrus* shells are commonly missing any kind of ornamentation and the peristomes are quite complex with varied callus morphologies. Thus, morphology of the peristome seems to be one of the key diagnostic features for classification in this group.

The idea that the Mesozoic genus *Ataphrus* and family Ataphridae are similar to the Tertiary and Recent members of Trochaclididae Thiele was supported by Bouchet and Rocroi (2005) and Sasaki (2008). However (Kaim, 2004, 2009) suggested that a more systematic approach was needed to confirm this relationship, and that the Ataphrini are more closely related to the Colloniini.

Ataphrus mulanguiniensis sp. nov.

Figures 3.1–11, 4.1–6

Derivation of name. Refered to the Mulanguiñeu Formation, where the material was found.

Diagnosis. Shell turbiniform, anomphalous, low-spired; protoconch convex and planospiral; teleoconch whorls

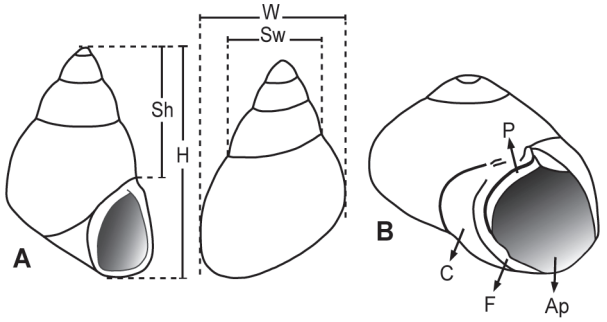

Figure 2. A. General shell morphology of Ataphridae / *Morfología general de la conchilla de Ataphridae*. Dimensions. **H**: maximum height/*altura máxima*; **Sh**: spire height/*altura de la espira*; **W**: maximum width/*ancho máximo*; **Sw**: spire width/*ancho de la espira*. **B.** Apertural and columellar characters of Ataphrini (modified from Gründel, 2008). **Ap**: aperture/*abertura*; **C**: crescent-shaped columellar lip/*labio columelar en forma de media luna*; **F**: furrow/*surco*; **P**: parietal lip/*labio parietal*.

convex; the last whorl more expanded; shell smooth; weak adapical keel sometimes present; base with spiral and colabral elements; aperture ovate to circular; columellar lip crescent-shaped.

Type material. Holotype MPEF-PI 3594 (Figs. 3.1–3). Paratypes: MPEF-PI 3593, 3595, 3597. Replaced teleoconchs .

Other material. MPEF-PI 3596, 3599, 3598, 3600, 4002, 4086. Fragmentary and replaced teleoconchs.

Geographic and stratigraphic range. Bed LO 29, Lomas Occidentales, Chubut, Argentina, Mulanguiñeu Formation, Early Jurassic (Late Pliensbachian–Early Toarcian).

Description. Shell small to medium-sized, turbiniform, low-spired, anomphalous, dextral, conical; fragmentary protoconch observed in specimen MPEF-PI 3597, consisting of one convex and planispiral whorl about 1 mm wide; teleoconch consisting of five whorls, the early ones more convex that the last ones; upper portion of basal whorls (below adapical suture) is strongly convex, becoming slightly convex to flat towards lower portion; last whorl of teleoconch more expanded than other whorls; sutures incised in weak spiral furrow; ornametation poorly developed, some specimens showing weak spiral keels bordering adapical suture and weak spiral ribs on last whorls; base convex to flat, ornamented with weak and regular spiral ribs (Fig. 4.4–5); spiral ribs on base crossed by fine opisthocline colabral threads; aperture circular to oval; columellar lip strongly thickenned forming a crescent-shaped callus.

Dimensions (in mm). See Table 1.

Remarks. The small-sized, turbiniform and poorly ornamented shell, slightly convex base with spiral ribs, and crescent-shaped columellar lip, suggest an assignment to *Ataphrus* (compare Kaim, 2004; Gründel, 2008). *Ataphrus mulanguiniensis* sp. nov. is the first record of this genus in the Early Jurassic of Argentina and South America.

This species is similar to *Ataphrus latilabrus* (Stoliczka, 1861) from the Early Jurassic (Sinemurian–Pliensbachian) of Europe. However, the latter, has fine prosocline colabral lines on the shell surface (Szabó, 2008; p. 56, fig. 49). *Ataphrus aciculus* (Hörnes, 1853) from the Early Jurassic (Sinemurian) of Europe differs from *Ataphrus mulanguiniensis* sp. nov. by having a more elongated spire, a concave and narrow furrow below the suture, and weak prosocline to prosocyrt growth lines on the shell surface (Szabó, 2008; p. 57, fig. 50). *Ataphrus*? *leviusculus* (Stoliczka, 1861) from the Early Jurassic (Pliensbachian) of Austria shares some features with *A. mulanguiniensis* sp. nov., but the European species, however, has a more conical to slightly cyrtoconoid shell with a rounded-angular periphery, and a strongly prosocline peristome (Szabó, 2008, p. 57, fig. 51). *Ataphrus (Ataphrus) acmon* (d'Orbigny, 1853) from the Middle Jurassic (Bajocian) of France has less convex whorls than the species from Chubut, and also a better developed colabral ornamentation (Gründel, 2008, p. 179, fig. 1, 8–9). *A. mulanguiniensis* sp. nov. is very similar to *Ataphrus folcoi* (Gemmellaro, 1911) from the Early Jurassic (Sinemurian?) of Sicily; this species, however, has prosocline growth lines and is probably cryptomphalous (Szabó, 1981, p. 62, pl. 2, fig. 14); the later characters are not observed in *A. mulanguiniensis* sp. nov. *Ataphrus naricopsiformis* Gründel (2007, p. 9, pl. 5, figs. 2–4) differs form *A. mulanguiniensis* sp. nov. by having a shell shape similar to *Naricopsina*, with a low spire and strongly convex last whorl, and a callus in the lower part of inner lip with a broad adapical end. *Ataphrus (Ataphrus) belus* (d'Orbigny, 1853) from the Middle Jurassic (Callovian) of India shares some features with the species described herein, but the first one

Table 1. *Dimensions (in mm) of* **Ataphrus mulanguiniensis** *sp. nov.. Abbreviations:* ***H****, maximum height/*altura máxima; ***Sh****, spire height/*altura de la espira; ***W****, maximum width/*ancho máximo; **Sw**, *spire width/*ancho de la espira.

Ataphrus mulanguiniensis *sp. nov.*	*H*	*Sh*	*W*	*Sw*
MPEF-PI 3593	*5,43*	*3,2*	*5,7*	*3,5*
MPEF-PI 3596	*12,3*	*8*	*10,8*	*8,5*
MPEF-PI 3595	*10*	*7,6*	*6,8*	*5,7*
MPEF-PI 3594	*9*	*7,8*	*6*	*5,4*
MPEF-PI 3597	*15*	*	*12,4*	*
MPEF-PI 3599	*12*	*8*	*11,2*	*8,5*
MPEF-PI 3598	*8,8*	*	*9,3*	*
MPEF-PI 3600	*13*	*	*10,5*	*

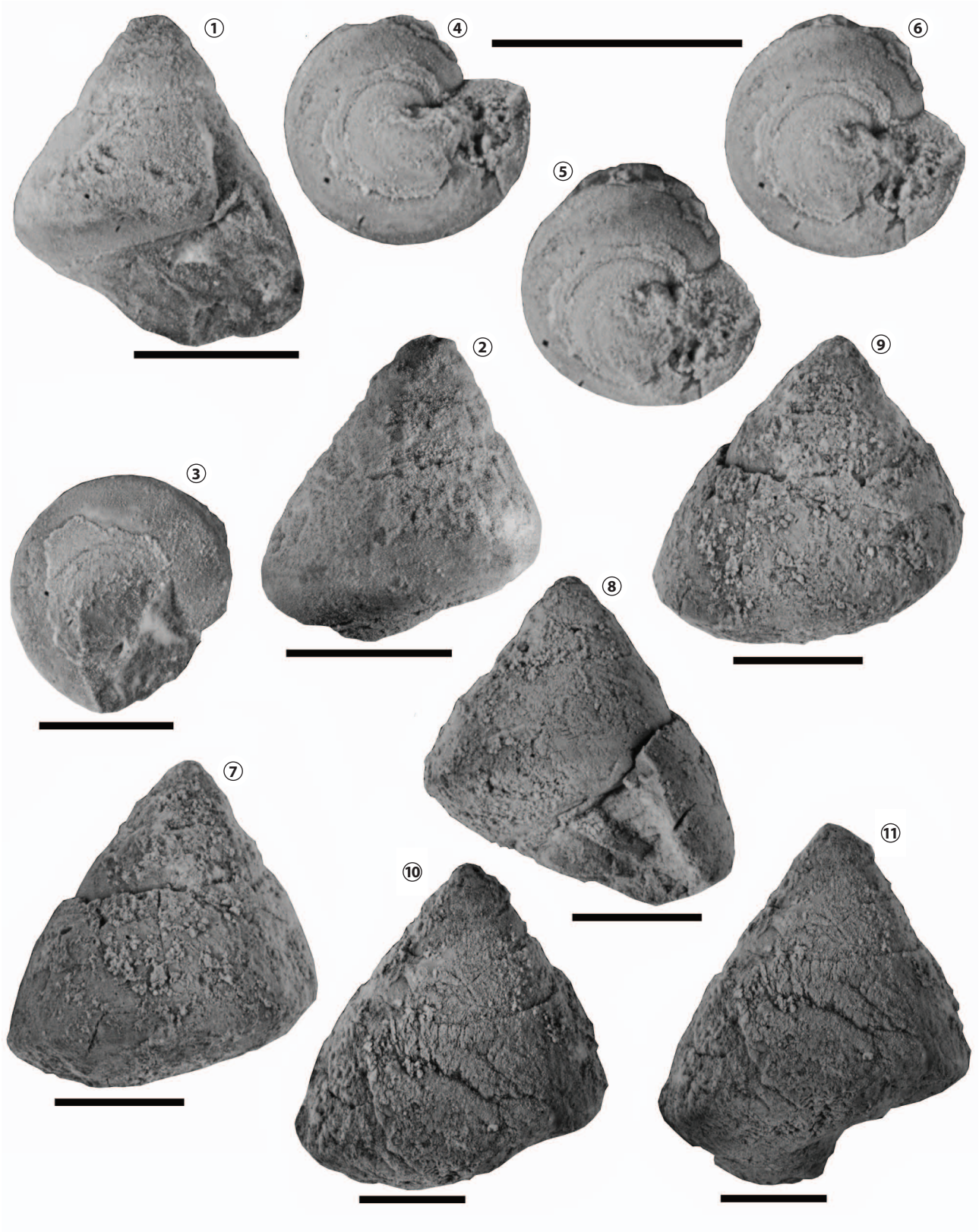

Figure 3. ***Ataphrus mulanguiniensis*** sp. nov. **1–3**, MPEF-PI 3594, holotype/*holotipo*; **1–2**, lateral view/*vista lateral*; **3**, basal view/*vista basal*. **4–6**, MPEF-PI 3593, paratype, basal view/*paratipo, vista basal*. **7–9**, MPEF-PI 3599, lateral and apertural view/*vista lateral y apertural*. **10–11**, MPEF-PI 3597, paratype, lateral view/ *paratipo, vista lateral*. Scale bar / escala = 5 mm.

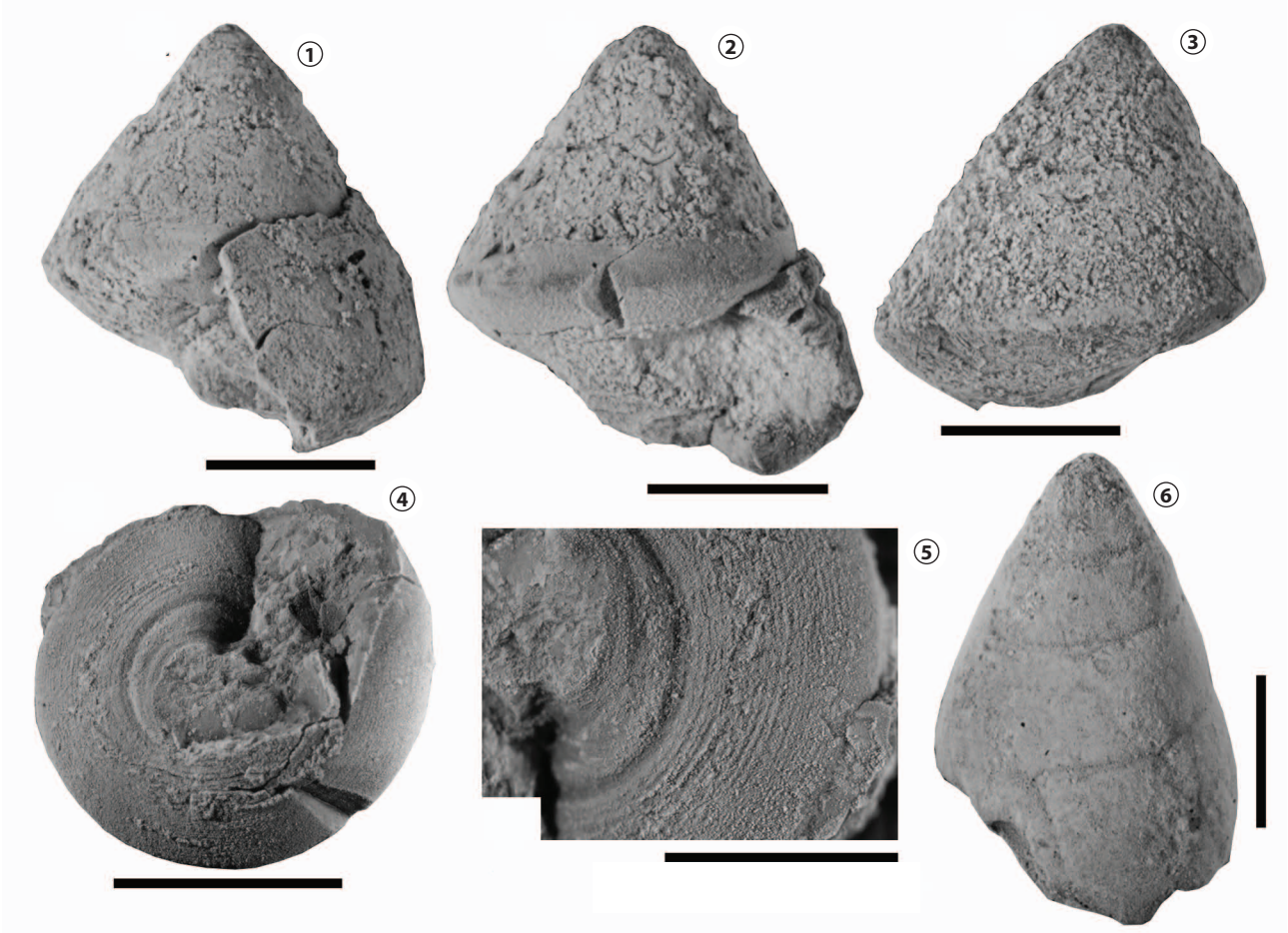

Figure 4. ***Ataphrus mulanguiniensis*** sp. nov. **1**, MPEF-PI 3599, lateral view/*vista lateral*. **2–5**, MPEF-PI 3596; **2**, lateral and apertural view/*vista lateral y apetural*; **3**, lateral view/*vista lateral*; **4**, basal view/*vista basal*; **5**, basal ornamentation detail/*detalle de la ornamentación basal*. **6**, MPEF-PI 4086 (SEGEMAR 5010), lateral view/*vista lateral*. Scale bar / escala = 5 mm (Fig. 4.5=2.5 mm).

is externally smooth and has a prosocline peristome (Jaitly *et al.*, 2000, p. 51, pl. 5, figs. 1–3). *A. mulanguiniensis* sp. nov. is also similar to *Ataphrus* (*Ataphrus*) *acis* (d'Orbigny, 1853) from the Middle Jurassic (Callovian) of India; the latter, however, has a more elongated spire and less convex whorls (Jaitly *et al.*, 2000, p. 51, pl. 5 fig. 4) than the species here described. *Ataphrus* (*Ataphrus*) *kaladongarensis* Jaitly *et al.* (2000, p. 51, pl. 5, figs. 5–6) from the Middle Jurassic (Bajocian?) of India has a pseudumbilicus or is probably cryptomphalous, and fine growth lines are present on shell surface; such characters are not observed in *A. mulanguiniensis* sp. nov. *Ataphrus marschmidti* Gründel and Kaim (2006, p. 131, fig. 8) from the Upper Jurassic (Oxfordian) of Poland differs from the Chubut species by having a teleoconch with well developed fine spiral ribs, a small and deep umbilicus, and an expanded callus on the lower part of the inner lip. *Ataphrus* sp. 1 Gründel (2000, p. 232, pl. 7, fig. 4) and *Ataphrus* sp. 2 Gründel (2000, p. 232, pl. 7, fig. 9) from the Middle Jurassic (Bajocian–Bathonian) of Poland are similar to *A. mulanguiniensis* sp. nov. in general shell morphology, but the European species have small-sized shells.

Tribe Colloniini Cossmann, 1917

Comments. Members of Colloniini were included by Gründel (2008) in the Homalopomatini Keen in Knight. Hickman and McLean (1990) and Bouchet and Rocroi (2005) considered both tribes as synonyms. Figure 5 shows the general shell morphology, ornamentation pattern, and apertural and columellar characters of an extant member of Colloniini (*Homalopoma*).

Genus ***Striatoconulus*** Gründel, 2000

Type species. *Striatoconulus latus* Gründel, 2000 (= *Trochus* sp. cf. *virdunensis* Buvignier) from the Callovian of Poland.

Diagnosis. In Gründel (2000) and Kaim (2004).

Stratigraphic and geographic range. Early Jurassic (Toarcian)–Middle Jurassic (Callovian); Poland and Argentina.

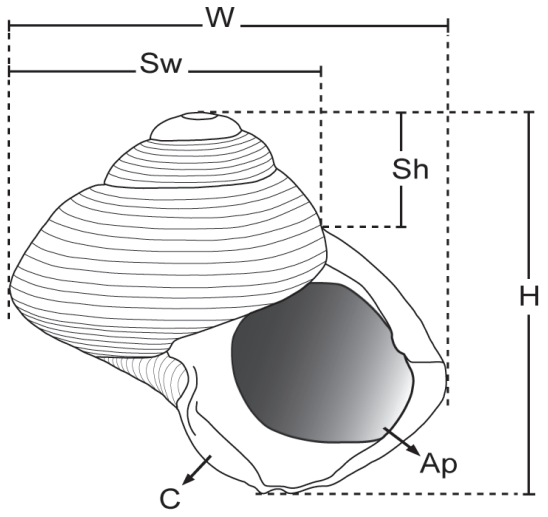

Figure 5. General shell morphology of Colloniini **(*Homalopoma*)**. Dimensions: apertural and columellar characters. **H**: Maximum height/*altura máxima*; **Sh**: spire height/*altura de la espira*; **W**: maximum width/*ancho máximo*; **Sw**: spire width/*ancho de la espira*; **C**: crescent-shaped columellar lip/*labio columelar en forma de media luna*; **Ap**: aperture/*abertura*.

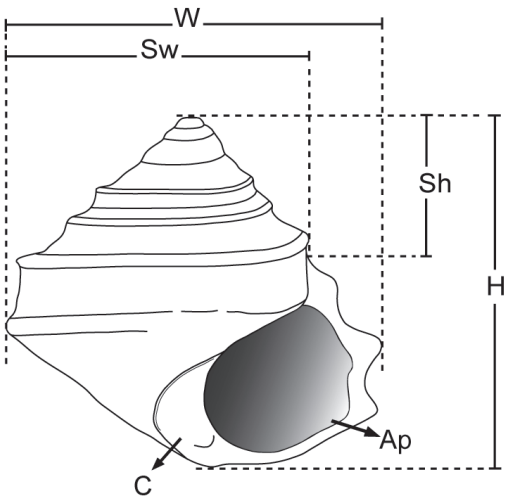

Figure 6. General shell morphology of Colloniini **(*Cantrainea*)**. Dimensions: aperural and columellar characters. **H**: Maximum height/*altura máxima*; **Sh**: spire height/*altura de la espira*; **W**: maximum width/*ancho máximo*; **Sw**: spire width/*ancho de la espira*; **C**: crescent-shaped columellar lip/*labio columelar en forma de media luna;* **Ap**: aperture/*abertura*.

Remarks. Gründel (2000) placed *Striatoconulus* in Proconulidae Cox; Kaim (2004) treated it under "family uncertain". The type species of the genus, *Striatoconulus latus* Gründel, has an ataphrid aperture, with shell shape and ornamentation comparable to those of *Homalopoma*. However, the type species of *Striatoconulus* differs from that of *Homalopoma* in having an angulation at the juntion of the whorl face and base, and the columellar lip forms a very small furrow at its periphery. Kaim (2004) treated *Trochus* and *Gibbula* as the most similar extant genera to *Striatoconulus*.

In the Early Jurassic of Argentina, members of *Striatoconulus* are represented by *Striatoconulus* sp., described by Ferrari (2009, p. 451, fig. 2C) from the Early Toarcian Osta Arena Formation (Chubut Province, Argentina).

Genus ***Chartronella*** Cossmann, 1902

Synonymy. Pro *Chartronia* Cossmann in Chartron and Cossmann 1902 (*non* Buckmann 1898) = *Chartroniella* Cossmann, 1916 (objective synonym).

Type species. *Chartronia digoniata* Cossmann in Chartron and Cossmann (1902), from the Early Jurassic (Hettangian) of France.

Stratigraphic and geographic range. Lower Triassic–Upper Jurassic; Europe, Asia, Africa, America.

Diagnosis. In Gründel (2008).

Remarks. Gründel (2008) included *Chartronella* in the tribe Costataphrini Gründel. But, according to Kaim *et al*. (2009), memebers of *Chartronella* are very closely related to the extant *Cantrainea* Jeffreys. Following Kaim *et al*. (2009), genus *Chartronella* is included herein in the Colloniini. Figure 6 shows the general shell morphology, ornament pattern, and apertural and columellar characters of an extant member of Colloniini (*Cantrainea*).

Chartronella paganiae sp. nov.

Figure 7.1–10

Derivation of name. Dedicated to Dr. María Alejandra Pagani (MEF).

Diagnosis. Shell turbiniform, anomphalous, angulated and low-spired; protoconch planospiral; teleoconch smooth, with two peripheral keels; base bordered by one spiral keel, with weak opisthocline colabral lines; aperture subcircular aperture; columellar lip crescent-shaped.

Type material. Holotype MPEF-PI 4022 (Fig. 7.1–3). Paratype MPEF-PI 3586–3588. Replaced teleoconchs preserved as secondary molds.

Additional material. MPEF-PI 3589. Replaced teleoconchs.

Geographic and stratigraphic range. Bed LO 29, Lomas Occidentales, Chubut Province, Argentina; Mulanguiñeu Formation, Early Jurassic (Late Pliensbachain–Early Toarcian).

Description. Shell small-sized, turbiniform, low-spired, anomphalous, dextral, angulate; protoconch and first whorls of the teleoconch planospiral; teleoconch consisting of four

Figure 7. ***Chartronella paganiae*** sp. nov. **1–3**, MPEF-PI 4022. holotype/*holotipo*; **1**, lateral view/*vista lateral*; **2**, apical and lateral view/*vista apical y lateral*; **3**, vista apical/*apical view*. **4**, MPEF-PI 3588, paratype, lateral view/*paratipo, vista lateral*. **5–7**, MPEF-PI 3587, paratype/*paratipo*; **5–6**, lateral and apical view/*vista lateral y apical*; **7**, basal and apertural view/*vista basal y apertural*. **8**, MPEF-PI 3586. **9–10**, MPEF-PI 3589; **9**, lateral view/*vista lateral*; **10**, basal and apertural view/*vista basal y apertural*. Scale bar = 5 mm.

whorls; upper portion of latter whorls flat to slightly convex, becoming concave towards the lower portion; sutural ramp observed on lower portion of last whorl, rendering shell outline angular; flank of last whorl becoming strongly vertical abapically, bordered by two keels; sutures weakly incised; ornamentation consisting of two strong peripheral spiral keels; abapical keel covered by subsequent whorl on all teleoconch whorls, and visible only on last whorl; shell surface smooth; base convex to angular, ornamented by fine opistocline colabral lines and bordered by strong spiral keel; aperture holostomatous and subcircular, with crescent-shaped columellar lip.

Dimensions (in mm). See Table 2.

Remarks. An angular-shaped shell, two strong peripheral keels (the abapical keel is covered by the subsequent whorl and is only visible on the last whorl), and a crescent-shaped columellar lip point towards inclusion of this species in *Chartronella* (see Gründel, 2008). *Chartronella paganiae* sp. nov. is the first record of the genus in the Early Jurassic of Argentina and South America.

At a first glance, *Chartronella paganiae* sp. nov. resembles some species of *Guidonia* de Stefani from the Peruvian Late Triassic–Early Jurassic faunas (Haas, 1953, p. 56, pl. 4), and *Guidonia riedeli* Bandel *et al.* (2000, p.82, pl. 4) from the Jurassic of New Zealand. However, one of the diagnostic characters of *Guidonia* is the presence of umbilicus (Bandel *et al.*, 2000), and none of the *Chartronella* specimens described herein shows an open umbilicus.

This new species from Chubut is very similar to the type species, *Chartronella* (*Chartronella*) *digoniata* (Cossmann, 1902) from the Early Jurassic (Hettangian) of France. However, the European species has a more elongated spire and a better developed spiral ornamentation (Gründel, 2008, p. 186, fig. 2, 10–11). *Chartronella* (*Tubertronella*) *tuberosa* Gründel (2000, p. 230, pl. 7, figs. 5–8; Gründel 2008, p. 186, fig. 2, 13–14) from the Middle Jurassic (Bathonian) of Germany differs from *C. paganiae* sp. nov. by having a more elongate spire and a conspicuous knob in the lower portion of the inner lip. *Chartronella mitoleensis* Cox (1965, p. 145, pl. 24, figs. 3a–b) from the Upper Jurassic (Kimmeridgian) of Tanganyka shares some features with *C. paganiae* sp. nov. However, the African species has a higher spire, the lateral face of the whorls (between the two keels) is concave, and a better developed colabral ornamentation pattern is present too. *Chartronella* (*Chartronella*) *philemon* (d' Orbigny, 1853) from the Early Jurassic (Hettangian) of Germany has a better developed spiral and colabral ornamentation pattern on the shell surface (Gründel, 2003, p. 18, pl. 5, fig. 6–9). Finally, *Chartronella noszky* Szabó (1982, p. 2, figs. 7–8) from the Jurassic of Hungary differs from the species described herein by having a higher spire, a third spiral keel on the periphery of the shell, stronger colabral ornamentation on the shell surface, and a prosocline outer lip.

Chartronella spiralis sp. nov.

Figure 9.1–6

Derivation of name. Referring to the strong spiral ornamentation on the lateral side of last whorl.

Diagnosis. Shell dextral, trochiform to turbiniform; teleoconch with flat upper portion and angular lower portion; sutural ramp present; ornamentation of five strong and regularly spaced spiral ribs crossed by prosocline colabral lines

Table 2. *Dimensions (in mm) of* ***Chatronella paganiae*** *sp. nov. Abbreviations:* ***H****, maximum height*/altura máxima; ***Sh****,* spire height/altura de la espira; ***W****, maximum width*/ancho máximo.

Chartronella paganiae *sp. nov.*	*H*	*Sh*	*W*
MPEF-PI 3588	*6,1*	*3,5*	*8*
MPEF-PI 3587	*4,3*	*2,7*	*6,7*
MPEF-PI 4022	*8*	*5*	*10*
MPEF-PI 3586	*10*	*6,2*	*11,8*
MPEF-PI 3589-1	*8,4*	*4,5*	*11,2*
MPEF-PI 3589-2	*10,7*	*6,4*	*12,2*
MPEF-PI 3589-3	*9*	*5*	*10,9*
MPEF-PI 3589-4	*9*	*6,4*	*10,8*
MPEF-PI 3589-5	*7,3*	*5,7*	*11,7*
MPEF-PI 3589-6	*8*	*6,5*	*12,8*
MPEF-PI 3589-7	*4,6*	*	*7,3*

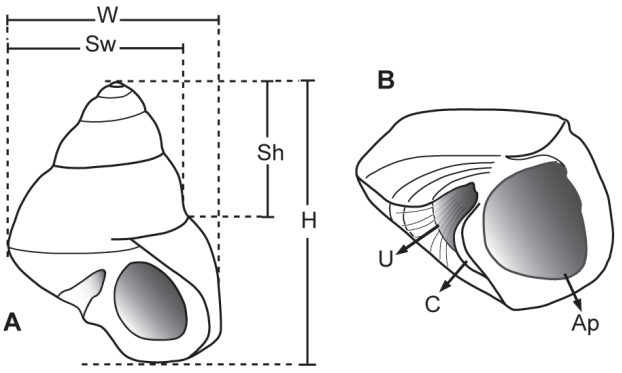

Figure 8. **A.** General shell morphology of Lewisiellinae. Dimensions. **H**: Maximum height/*altura máxima*; **Sh**: spire height/*altura de la espira*; **W**: maximum width/*ancho máximo*; **Sw**: spire width/*ancho de la espira*. **B.** Juvenile apertural, columellar and umbilical characters. **U**: umbilicus/*ombligo*; **C**: crescent-shaped columellar lip/*labio columelar en forma de media luna*; **Ap**: aperture/*abertura*.

(Fig. 9.5); last whorl of teleococnh more expanded than early whorls.

Type material. Holotype MPEF-PI 3590. Replaced teleoconch.

Geographic and stratigraphic range. Bed LO 29, Lomas Occidentales, Chubut Province, Argentina; Mulanguiñeu Formation, Lower Jurassic (Late Pliensbachian–Early Toarcian).

Description. Shell trochiform to turbiniform, dextral, small-sized, low-spired, anomphalous; protoconch not preserved; teleoconch consisting of four fragmentary whorls, upper portion flat and lower portion angular with sutural ramp rendering shell outline angular; lower portion of last whorls bordered by two keels; sutures weakly incised; ornamentation observed on flank and upper portion of last whorl; last whorl with weak and regularly spaced spiral ribs; flank (lateral side) of last whorl with five strong and regularly spaced spiral ribs (Fig. 9.5–6); fine and slightly prosocline colabral lines crossing spiral ribs; last whorl considerably more expanded than early whorls of teleoconch; base slightly convex to angular; aperture holostomatous, with outer lip convex; columellar lip straight and thickened, rendering aperture subcircular.

Dimensions (in mm). Maximum height: 12.3; spire height: 6.3; maximum width: 10.4

Remarks. Only one slightly broken specimen is available. Thus, some of the diagnostic features of the genus, such as a crescent-shaped columellar lip, can not be observed. However, the generally trochiform to turbiniform shell, angular whorls, two peripheral keels on last whorl, and an ornamentation pattern with spiral and colabral ribs suggest an assignment to *Chartronella*.

Chartronella spiralis sp. nov. differs from *Chartronella paganiae* sp. nov. by having better developed colabral and spiral elements on lateral side of last whorl.

Subfamily Lewisiellinae Gründel, 2008

Comments. Diagnosis in Gründel (2008). Figure 8 shows the general shell morphology, ornamentation pattern, and apertural, umbilical and columellar characters of Lewisiellinae.

Genus ***Lewisiella*** Stoliczka, 1868

Type species. *Pitonellus conicus* d'Orbigny, 1853 *sensu* Stoliczka, 1868 (*non* d' Orbigny), from the Early Jurassic of Europe (= *Lewisiella stoliczkai* Szabó, 2008).

Stratigraphic and geographic range. Early Jurassic (Sinemurian–Toarcian); Europe, America.

Generic diagnosis. In Gründel (2008).

Remarks. Members of this group show peculiarities in the morphology of the columellar callus. Its adapical portion is very narrow and may carry a furrow; in its abapical portion, at its transition to the lower edge of the aperture, the callus has a triangular shape or else it is broadly tongue-shaped. This differs from the typical callus morphology of Ataphrinae (Gründel 2008).

According to Gründel (2008), on mature specimens of *Lewisiella* the base center is covered by a strong and hemispherical callus bordered by a wide and deep furrow, a feature typical of this genus (see Gründel 2008, fig. 1.11). Juvenile specimens have an open umbilicus (see Gründel 2008, fig, 1.13). The widening of the columellar lip is slight, restricted to the middle and abapical portion of the columella, and shows a small, furrow-like depression. This morphology is observed in adult specimens of *Ataphrus* and suggests a phylogenetic relationship between *Ataphrus* and *Lewisiella*, even if the callus morphology is rather different in mature specimens of *Lewisiella*.

Szabó (2008) suggested that the material from Hierlatz referred to *Pitonellus conicus* d' Orbigny (Stoliczka 1861, p. 178, pl.3, fig.4; Gemmellaro 1911, p.230, pl.10, figs.7–9) was in fact misidentified and clearly different from the French specimens illustrated by d'Orbigny. For this reason, Szabó (2008) proposed a new species name for the Hierlatz material (*Lewisiella stoliczkai*), and included the reference of Stoliczka, 1861, in his synonymy. Stoliczka (1868) stated that he saw differences between d'Orbigny's (d'Orbigny, 1853) figures and he applied the morphology of the Hier-

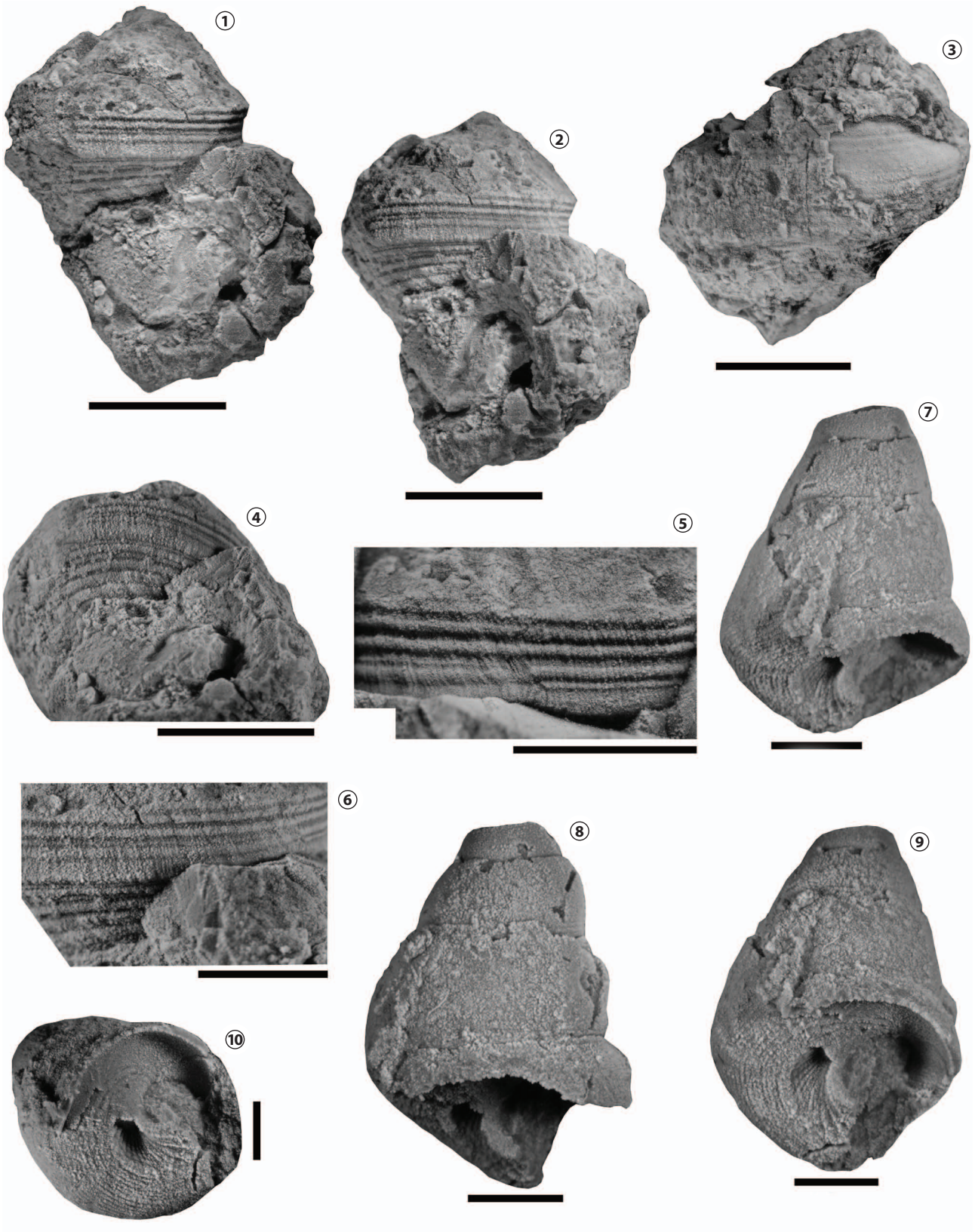

Figure 9. **1–6** ***Chartronella spiralis*** nov. sp., MPEF-PI 3590; **1–3**, lateral view/*vista lateral*; **4**, basal and apertural view/*vista basal y apetural*; **5–6**, last whorl ornamentation detail/*detalle de la ornamentación en la última vuelta*. **7–10**, ***Lewisiella?*** sp., MPEF-PI 4006; **7–8**, lateral view/*vista lateral*; **9–10**, basal and apertural view/*vista basal y apertural*. Scale bar: Figs. 9.1–4= 5 mm; Figs. 9.5–10=2.5 mm.

latz specimens to determine the diagnostic characters of his new genus, *Lewisiella* Stoliczka, 1868. According to Szabó (2008), *Pitonellus conicus* d'Orbigny, 1853, can not be included in *Lewisiella* because the base and columellar lip morphologies are entirely different from those in typical members of this genus.

Lewisiella? sp.

Fig. 9.7–10

Geographic and stratigraphic range. Bed BET 33, Lomas de Betancourt, Chubut province, Argentina; Mulanguiñeo Formation, Early Jurassic (Late Pliensbachian–Early Toarcian).

Material. MPEF-PI 4006; poorly preserved teleoconch.

Description. Shell turbiniform, small to medium-sized, low-spired, dextral, phaneromphalous; protoconch not preserved; teleoconch fragmentary, consisting of three whorls, two corresponding to spire; teleoconch whorls slightly convex; sutures well incised in spiral furrow; shell smooth or lacking conspicuous ornamentation; base flat to slightly convex, ornamented with about 14 regularly spaced spiral ribs or furrows; umbilicus small, deep and narrow, ornamented with strong and regularly spaced axial ribs crossed by weak spiral lines; aperture not preserved.

Dimensions (in mm). Maximum height: 9.4; spire height: 3.4; maximum width: 6.8; spire width: 4.4.

Remarks. Some diagnostic characters of the genus, such as a conical high-spired smooth (or with spiral furrows on base only) shell, and flat base with narrow umbilicus, resemble juvenile members of *Lewisiella* (see Gründel, 2008). However, basal, apertural and columellar features of mature specimens are not preserved. Until more complete specimens of different growth stages become available, the material is left in open nomenclature.

While its taxonomic position is rather uncertain, the material described herein as *Lewisiella*? sp. appears to be the first occurence of the genus in the Early Jurassic of Argentina and South America.

Lewisiella stoliczkai Szabó, 2008 (p.59, fig. 53) from the Early Jurassic (Sinemurian) of Austria, is similar to *Lewisiella*? sp. in general shell morphology and in the base ornamentation pattern with spiral ribs or furrows. Szabo's species, however, has a more angulate shell, a strongly thickenned callus, weak spiral ribs near the sutures, and fine and slightly prosocline growth lines on the shell surface. *Lewisiella*? *turbinata* Szabó, 2008 (p. 59, fig. 54; = *Lewisiella acicula* Hörnes in Szabó, 1983, p. 29, pl. 1, figs. 4–5) from the Early Jurassic (Sinemurian–Pliensbachian) of Hungary differs from the species from Chubut by having a strong spiral keel bordering the umbilicus, a more elongated spire, and ornamentation consisting of fine prosocline growth lines on the shell surface. *Lewisiella ventrocostata* Gründel (2007, p. 10, pl. 3, fig. 2–3) from the Early Jurassic (Sinemurian) of Germany shares some features with *Lewisiella?* sp., but the European species has a rounded callus bordered by a furrow.

Geographic and cronostratigraphic range of Ataphridae

The species of *Ataphrus*, *Striatoconulus*, *Chartronella* and *Lewisiella* described herein are the first records of Ataphridae in the Early Jurassic of Argentina. This extends the paleogeographic distribution of the group into the Jurassic of South America (Fig. 10).

Ataphrus is well represented in the Mesozoic of Europe, ranging from the Early Jurassic (Sinemurian) to the Early Cretaceous (Valanginian) (Szabó, 1981, 2008; Szabó *et. al*, 1993; Monari *et. al*, 1996; Kaim, 2004; Gründel and Kaim, 2006; Gründel, 2000, 2007, 2008). Members of the genus were recorded in other Jurassic marine localities of India and Africa (Cox, 1965; Jaitly *et al.* 2000); and in the Early and Late Cretaceous (Aptian–Maastrichtian) of Japan (Kase, 1984, 1990) and the United States (Gabb, 1869; Sohl and Koch, 1983). *Ataphrus mulanguiniensis* sp. nov. is the first occurrence of the genus in the Early Jurassic (late Pliensbachian–early Toarcian) of Argentina. *Striatoconulus* was originaly proposed by Gründel (2000) based on material from the Middle Jurassic (Callovian) of Poland, and Kaim (2004) later recorded it in the Bathonian. The occurrence of *Striatoconulus* sp. in the Jurassic of Argentina stretches the paleogeographic distribution of the group into South America, increasing its chronostratigraphic distribution from the Early Jurassic (Toarcian) to the Middle Jurassic (Callovian). The *Chartronella*-group was previously known from the Mesozoic of Europe, Africa, Asia and America, and its stratigraphic range spans the Lower Triassic to the Upper Jurassic (Cox, 1965; Batten and Stokes, 1986; Szabó 1982; Gründel, 2000, 2003, 2008; Nützel, 2005; Kaim, 2009). Like other members of the Ataphridae here reported, *Chartronella paganiae* sp. nov. and *Chartronella*? sp. are the first records of the genus in the Early Jurassic of Argentina. Finally, the species of *Lewisiella* have a more restricted geographic and chronostratigraphic range than other ataphrid genera here described, and at present they have been recorded in European Early Jurassic rocks of Sinemurian to Pliensbachian age (Szabó 1983, 2008; Gründel, 2007, 2008). The presence of

Lewisiella? sp. in Chubut Province is the first —albeit doubtful— record of the genus from the Early Jurassic (Pliensbachian–Toarcian) of Argentina.

According to Sha (2002), the break-up of Pangea —that began in the Triassic— during the Early Jurassic (Hettangian–Pliensbachian) opened a trans-Pangean seaway, changing the paleogeographical pattern and providing an oceanic corridor for gene exchange between Western Tethys and Eastern Palaeo-Pacific by means of migration and dispersion of the biota living then in these areas. The Hispanic Corridor

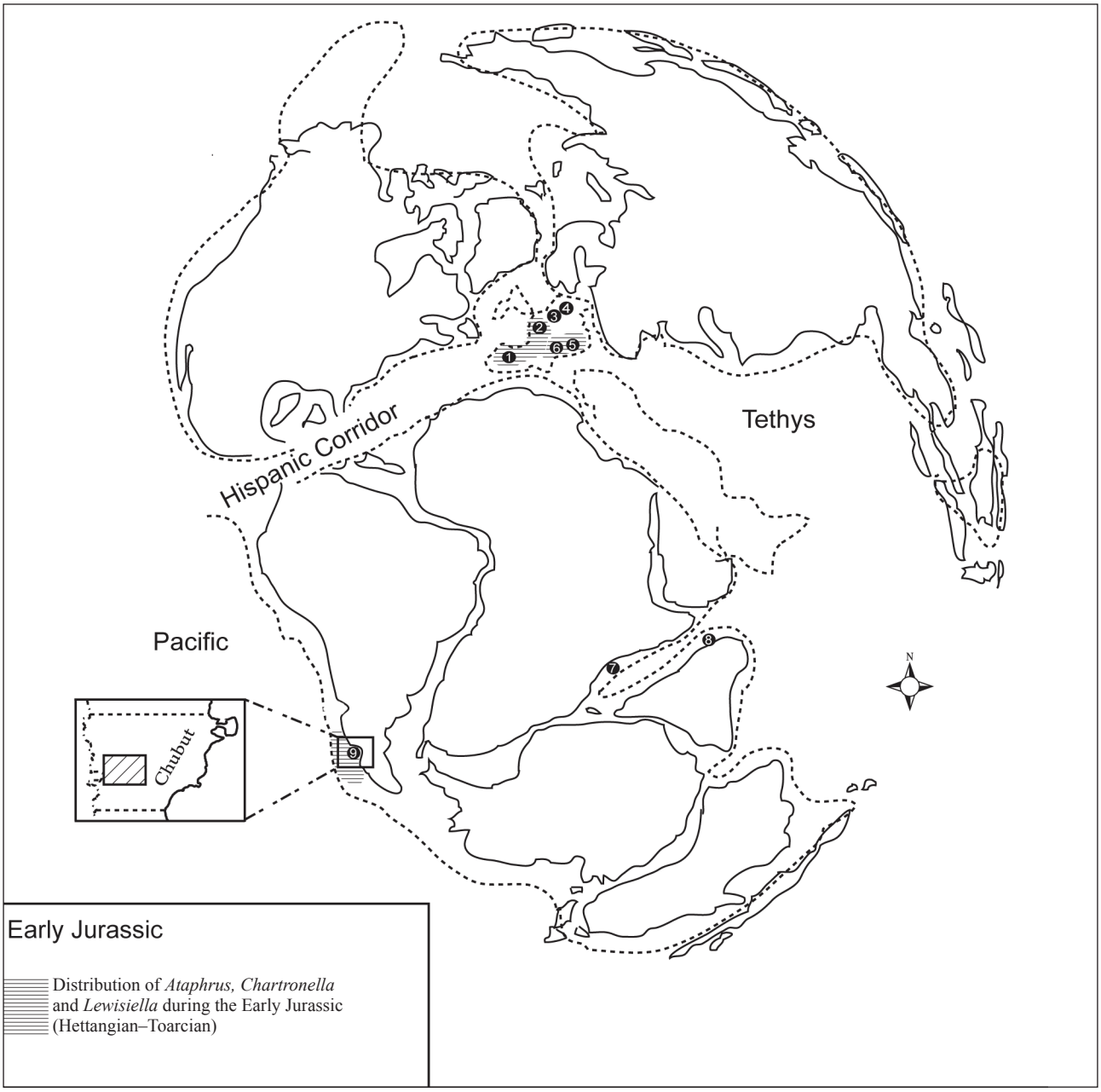

Figure 10. Map showing the paleogeographic distribution of the ataphrid genera here reported during the Jurassic. Note that the new ataphrid species in the Early Jurassic of Chubut province extends the paleobiogeographical distribution of the group in the Jurassic of Argentina and South America / *Mapa paleogeográfico mostrando la distribución, durante el Jurásico, de los géneros meniocnados aquí. Nótese que las nuevas especies del Jurásico Termprano descriptas extienden el rango de distribución del grupo en el Jurásico de Argentina y América del Sur*. **1,** Hettangian–Bajocian of France (Gründel 2008). **2,** Hettangian–Bathonian of Germany (Gründel 2000, 2003, 2007). **3,** Bajocian–Callovian of Poland (Gründel 2000; Kaim 2004). **4,** Oxfordian of Poland (Gründel and Kaim 2006). **5,** Sinemurian–Pliensbachian of Hungary (Szabó 1981, 1982, 2008). **6,** Sinemurian–Pliensbachian of Austria (Szabó 2008).**7,** Bajocian–Kimmeridgian of Tanganyika (Cox, 1965). **8,** Bajocian–Callovian of India (Jaitly *et al.*, 2000). **9,** Pliensbachian–Toarcian of Chubut province (here) (Modified from Damborenea and Manceñido, 1979; Sha, 2002)**.**

established along the Pangean rifting area separated North America, South America and Africa. It has been shown that the paloebiogeographic patterns of Jurassic pectinid bivalve faunas such as those of *Weyla, Chlamys* and *Camptonectes* (Damborenea and Manceñido, 1979; Sha, 2002) support the idea of a shallow marine connection between the western Tethys and the eastern Pacific at a date as early as in Pliensbachian times, with the opening of a Mid-Atlantic seaway. The geographic distribution patterns of the four ataphrid genera mentioned above may be the result of dispersal routes similar to those followed by the shallow-marine pectinid bivalve faunas during the Early Jurrasic (Fig. 10). The Hispanic Corridor may not have been the only dispersion route enabling gene flow among distant gastropod populations at that time. Peru (Haas, 1953) and New Zealand (Bandel, Gründel and Maxwell, 2000) were then closer to central Chubut than Europe, and thus may have been also possible avenues for biotic exchange with the Chubut basin during the Mesozoic.

PALEOECOLOGY OF ATAPHRIDAE

Members of Ataphridae are very closely related to the extant Turbinidae (see classification proposed by Kaim *et. al*, 2009). These forms are distributed worldwide and found at all latitudes and at depths ranging from intertidal to subtidal, with a few in the bathyal zone, but with a strong preference for carbonatic substrates; they are abundant and diverse in warm tropical and subtropical water (Hickman and McLean, 1990).

Homalopoma and *Cantrainea* are considered here as extant members of Ataphrinae (tribe Colloniini), very similar to the extinct *Striatoconulus* and *Chartronella*. These forms are epifaunal, herbivorous or suspensivorous feeders, mobile over consolidated substrates, and living at different depths, from shallow water to bathyal environments.

Members of Ataphridae are found in medium-grained to fine and green-yellow sandstones of the Mulanguiñeo Formation in Chubut. They are associated to an abundant and diverse invertebrate biota including corals, echinoderms, cephalopods, brachiopods, bivalves, and other gastropods. These fauna includes the gastropods *Calliotropis, Cryptaulax, Procerithium, Bathrotomaria*, *Pseudomelania, Talantodiscus?, Worthenia?, Hamusina, Scurriopsis ?, Lithotrochus?, Globularia*?; the bivalves *Ctenostreon, Myophorella, Frenguelliella, Jaworskiella, Groeberella, Weyla, Cardinia, Entolium, Neocrassina, Isocyprina, and* also scleractinians, belemnitids, and millericrinines. These faunas suggest a littoral marine depositional environment for the ataphrid-bearing rocks. Most extant Turbinidae and the Ataphridae reported here live in the nearshore zone where shallow water is dominant.

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