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Systematic palaeontology and taphonomic significance of the mollusc fauna from the Mata Amarilla Formation (lower Upper Cretaceous), southern Patagonia, Argentina

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ABSTRACT

Thirteen mollusc taxa are described from the Mata Amarilla Formation, a lower Upper Cretaceous unit exposed in southern Patagonia, Argentina. Of these, one is a new bivalve species, *Pterotrigonia flava* sp. nov. The fauna was collected from two sections representing different parts of the basin. Sedimentary characteristics at each one, together with the fossil content and taphonomic features of the preserved material, confirm that these localities represent littoral environments (lagoon). The two sections contain autochthonous elements, and beds with mixed autochthonous and parautochthonous fauna. The latter exhibits a marine shoreface influence, possibly owing to washover deposits. The possible age of the fossil-bearing rocks in the sections studied is late Albian–early Cenomanian.

1. Introduction

One of the most representative units of the Upper Cretaceous in the Austral Basin, the Mata Amarilla Formation comprises grey and whitish rocks that were first described as “Estratos de Mata Amarilla” (Feruglio in Fossa Mancini et al., 1938) and later as Formación Mata Amarilla (Leanza, 1972; Russo and Flores, 1972). It is equivalent to the unit named “Shehuenense” by Ameghino (1906). From a geotectonic point of view it belongs in the Austral Foreland Basin (Fig. 1), more precisely, the second phase of this basin. Thus it appears to be related to the closure of the Rocas Verdes Basin (Biddle et al., 1986).

The Mata Amarilla Formation reaches a thickness of approximately 350 m and comprises mainly grey to dark grey siltstones and claystones alternating with thin beds of medium to fine whitish and yellowish grey sandstones, all deposited in littoral to continental environments (Russo and Flores, 1972; Russo et al., 1980; Arbe, 1989, 2002; Poiré et al., 2004; Varela and Poiré, 2008). The lower section also incorporates thick beds with bioclastic accumulations (Goin et al., 2002; Poiré et al., 2004; Varela et al., 2008, 2011).

The type section is located on the southern margin of the Chalía River, about 23 km east of Tres Lagos, in the environs of Estancia Mata Amarilla (= Estancia La Soriana). The formation transitionally overlies the Piedra Clavada Formation and is overlain by the La Anita Formation (Varela and Poiré, 2008). It can be divided into three sections: a lower littoral section, a middle continental one and an upper one that ranges from littoral to continental depending on the location within the study area (Varela, 2011). This unit was deposited in the period spanning the latest Albian/early Cenomanian through the Santonian (Poiré et al., 2007; Varela, 2011; Varela et al., in press) (Fig. 2).

Among the fossils previously described from the Mata Amarilla Formation are the bivalves *Ostrea guaranitica*, *Trigonia aliformis* and *Corbula sehuena*, and the gastropod *Potamides* (*Pirenella*) *patagoniensis* (von Ihering, 1907; Wilckens, 1905; Bonarelli and Nágera, 1921; Feruglio, 1937, 1938; Piatnitzky, 1938). Santonian ammonites were recorded from this unit at Cerro Índice (Blasco et al., 1980). Remains of littoral and continental vertebrates are very common. These were described by Goin et al. (2002) and Cione et al. (2007), and include crocodiles, turtles, amphibians, and lungfish. The fauna also includes abundant remains of theropods and sauropods (e.g., the ornithischian *Talenkauen santacrusensis* and the sauropod *Puertasaurus reuili*; see Lacovara et al., 2004; Novas et al., 2004a, b, 2005, 2008). Recent collections in the lower section at Estancia La Blanca, located to the south of the study area, include plesiosaur vertebrae (O’Gorman and Varela, 2010).

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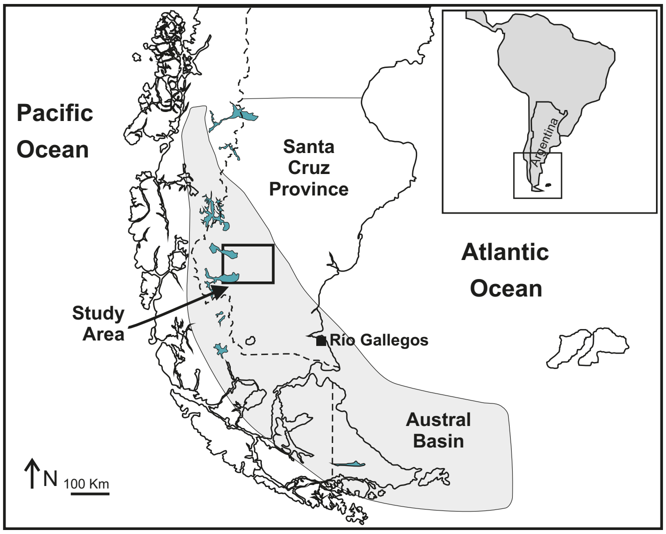


Fig. 1. Regional location map showing study area within the Austral Basin.

In addition, the Mata Amarilla Formation includes carbonaceous shale beds with an abundant flora of *Laucophyllum* sp. and *Araliaephyllum* sp. (Arrondo, 1983) and algae (*Botryococcus* sp., *Palambages* sp. and *Chizosporis reticulate*). Iglesias et al. (2007) recently described an abundant and very diverse angiosperm taphoflora contained within two plant beds. Poiré et al. (2004) and Zamuner et al. (2004, 2006) reported a petrified forest in life position known as “Bosque Petrificado María Elena” that mainly comprises gymnosperms of the family Podocarpaceae.

The aim of this paper is to describe the mollusc fauna contained in the lower section of the Mata Amarilla Formation, within a precise stratigraphic framework and a detailed sedimentological analysis. Concomitant with enhancing our knowledge of the fossil content, we assess the significance that the taxa described have on palaeoenvironmental interpretations regarding this stratigraphic unit at the localities studied.

2. Study area, material and methods

The study area lies in southwestern Santa Cruz, Patagonia, about 60 km east of Lake Viedma and close to the town of Tres Lagos, between Estancia Mata Amarilla and Estancia María Elena (Fig. 3). This paper is concerned with the lower section of the Mata Amarilla Formation in the area near its type section, i.e., localities Mafer and CME (Fig. 3) which for this depositional stage are located on the northern reaches of the basin (Varela et al., 2008). In this work we follow the stratigraphic criteria established by Goin et al. (2002).

All specimens studied were collected by one of us (AV). The material is housed in the Museo Provincial “Padre Manuel Molina”, Río Gallegos, Santa Cruz, Argentina MPM-PI. Reference material was examined at the following institutions in Argentina: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN); Museo de La Plata, La Plata (MLP); Instituto Superior de Correlación Geológica, San Miguel de Tucumán, Tucumán (INSUGEO); and Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Buenos Aires, Buenos Aires (CPBA).

3. Systematic palaeontology

Class Bivalvia Linné, 1758
Subclass Pteriomorphia Beurlen, 1944
Order Arcoida Stoliczka, 1871

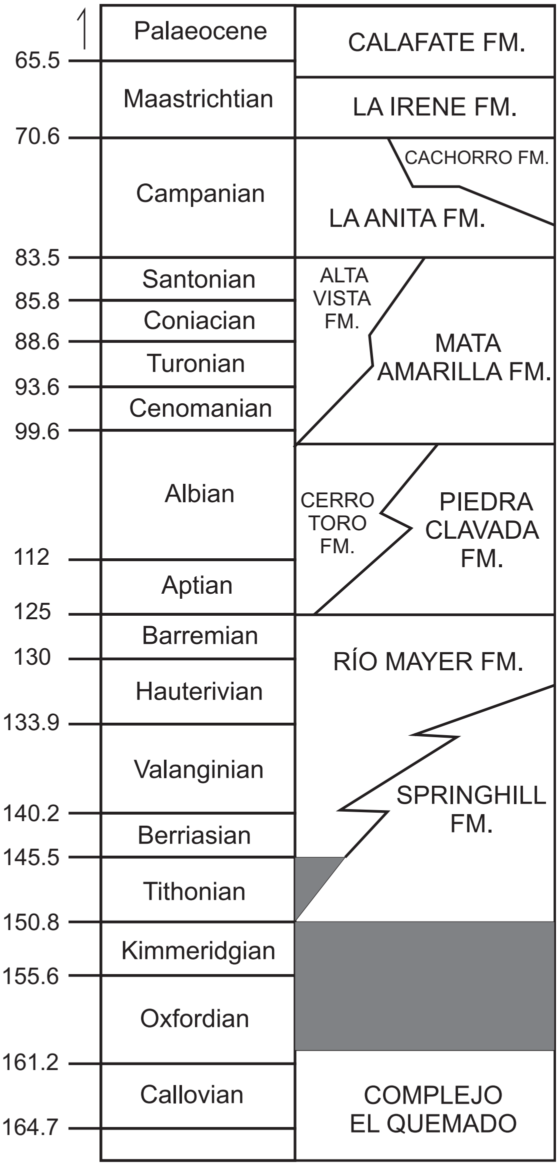


Fig. 2. Stratigraphic position of the Mata Amarilla Formation.

Superfamily Arcoidea Lamarck, 1809
Family Cucullaeidae Stewart, 1930
Genus *Cucullaea* Lamarck, 1801

Type species. *Cucullaea auriculifera* Lamarck, 1801 (by subsequent designation, Children, 1823).

Cucullaea? sp.
Fig. 5H

Material. MPM-PI-14181–14184; MPM-PI-14183 (see Fig. 5H); three internal moulds, one with part of the shell preserved, all from bed CME17.

Description. Small *Cucullaea* (largest specimen 35 mm high, 32 mm long and 20 mm wide) with subquadrate shells, inflated umbones placed at midlength of hinge; all specimens are internal moulds, only one with small fragments of shell matter preserved; one internal mould of left valve exhibiting a postumbonal furrow corresponding to an internal postumbonal ridge probably resulting from the buttressed posterior adductor muscle scar; one bivalve

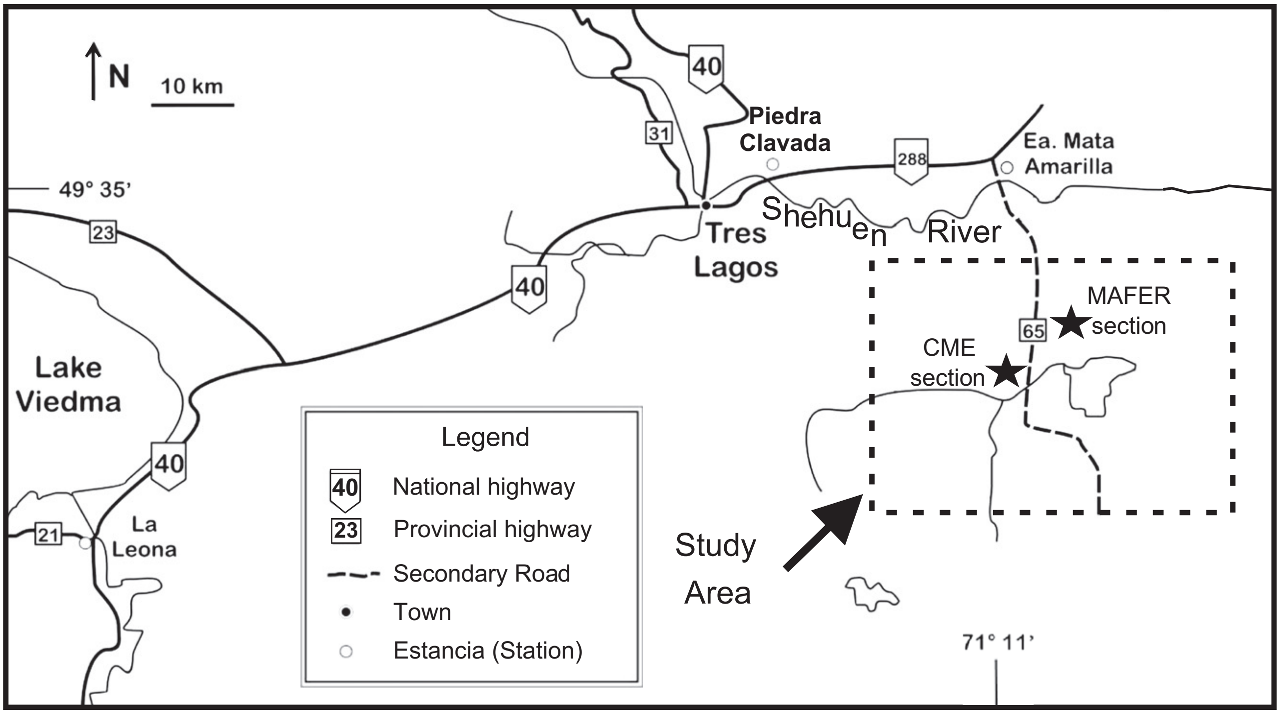


Fig. 3. Detail of study area.

internal mould showing vestiges of two straight lateral teeth at one (preserved) end of hinge and numerous very small vertical central teeth along the rest of preserved hinge margin; second bivalved internal mould with some remaining shell showing only regular growth lines.

Remarks. The only available specimens are fragmentary internal moulds, with almost no shell matter preserved. However, enough of the long horizontal lateral teeth remain in one of the hinges to confirm its taxonomic position within the Cucullaeidae. It is here tentatively included in *Cucullaea*, but better preserved material is necessary to confirm such a generic placement.

Order Pterioida Newell, 1965
Superfamily Ostreoidea Rafinesque, 1815
Family Gryphaeidae Vyalov, 1936
Subfamily Exogyrinae Vyalov, 1936
Tribe Nanogyrini Malchus, 1990
Genus *Amphidonte* Fischer von Waldheim, 1829

Type species. *Amphidonte humbodtii* Fischer von Waldheim, 1829; subsequent designation by Fischer, 1886.

Amphidonte guaranitica (von Ihering, 1899)
Fig. 6A–E

1899 *Ostrea guaranitica*; Ihering, pp. 63, 64.
1902 *Ostrea guaranitica* Ihering; Ihering, pp. 116, 117.
1906 *Ostrea guaranitica* Ihering; Ameghino, pp. 87, 89, fig. 7.
1907 *Ostrea guaranitica* Ihering; Ihering, p. 50.

Type material. MACN-PI-149: nine syntypes, from Pari-Aike (Parkaik, according to von Ihering, 1899), Santa Cruz (Ihering Collection). Ihering stated that the syntypes came from "Park-aik" on the Shehuen River. The locality referred to as Estancia Pari Aike or Cerro Pari Aike does not lie near the river, but the whole area is also known as Pari Aike region. It seems likely that the specimens came from virtually the same section as ours, as these are the only localities that match the content of the fossil-bearing beds as described by von Ihering (1902).

Material. MPPM-PI-14185–14192, from bed CME4 (see Fig. 6A–E); MPM-PI-14193, 14194, from bed CME17; MPM-PI-14198, from bed CME18.

Description. Small and strongly inequivalve *Amphidonte*; left valve subtriangular, with sharply opisthogyrous incurved umbones; ligament area sharply curved, narrow, deeply excavated; short straight chomata at both sides of umbones, more numerous anteriorly; subumbonal cavity deep; attachment area variably developed, small in some specimens and relatively large (up to 20% of shell surface) in others; shell surface with fine growth lines; some specimens with weak commarginal undulations; worn specimens with growth marks of chomata visible; posterior shelf fairly well developed, carrying chomata in well-preserved specimens; posterior adductor muscle scar circular, strongly impressed near posterior margin at about mid-height of shell.

Remarks. This species was first described by von Ihering (1899) based on material from Pari Aike. According to von Ihering (1902) it resembled *Exogyra*, or even *Amphidonte*, but some specimens had a curved umbone, while it was straight in others. Therefore, he placed it in *Ostrea*, a genus where it certainly does not fit because of its strongly opisthogyrous umbones, deeply cupped left valve, anterior shelf of left valve and compact lamellar shell structure. According to the shell shape, the posterior muscle scar shape and placement, the stegchomata on the anterior and posterior portions of shell margin of left valve, the opisthogyrous umbone, curved ligament area, and the flat to slightly concave right valve showing commarginal ornamentation only, it appears to fit better in *Amphidonte* Fischer von Waldheim, 1829, a genus well known from South American Upper Cretaceous and Palaeogene rocks (Casadío, 1998). *Amphidonte mendozana* (von Ihering, 1907) was originally

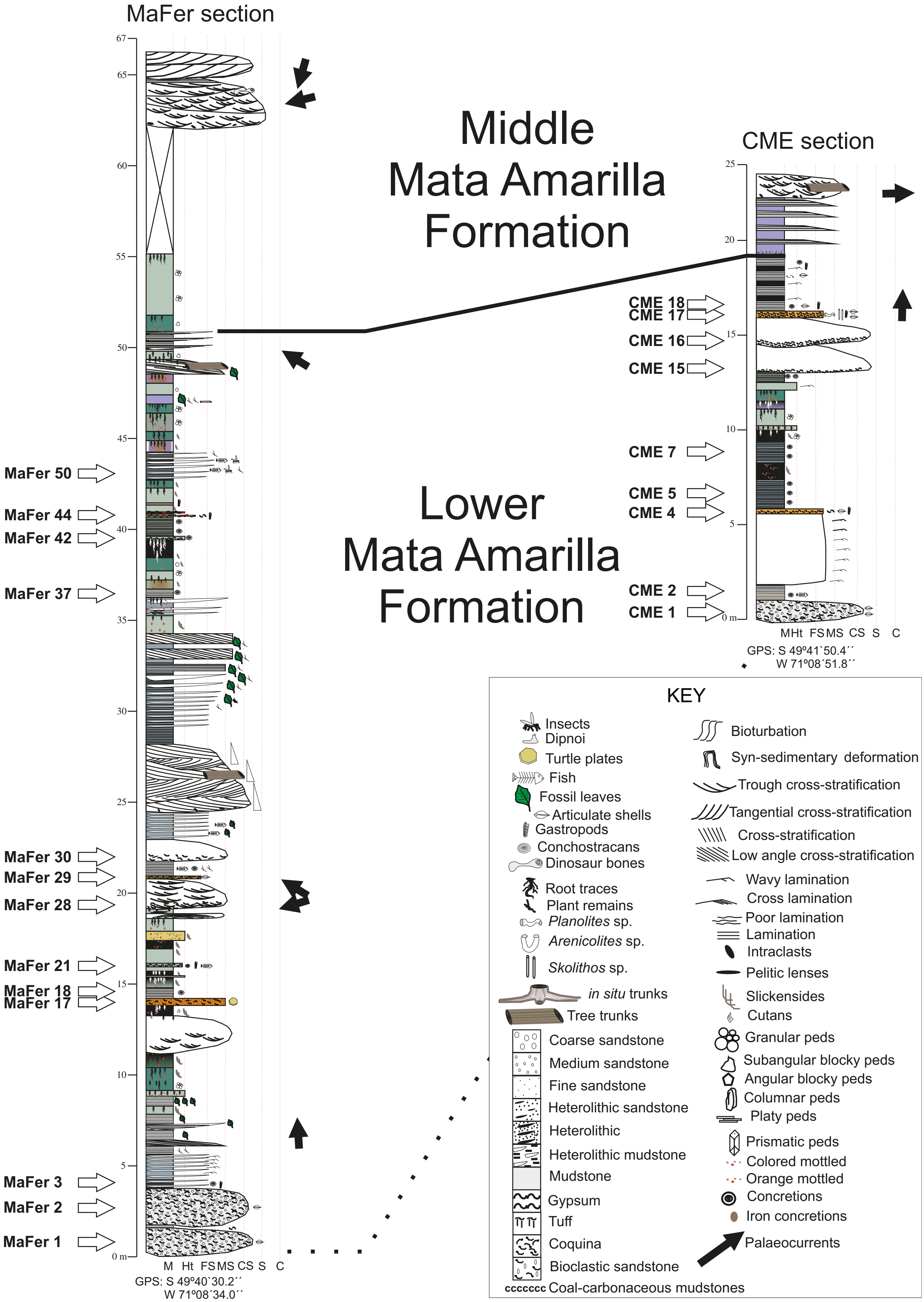


Fig. 4. Sedimentological sections and fossil-bearing beds of the Mata Amarilla Formation at the localities studied.

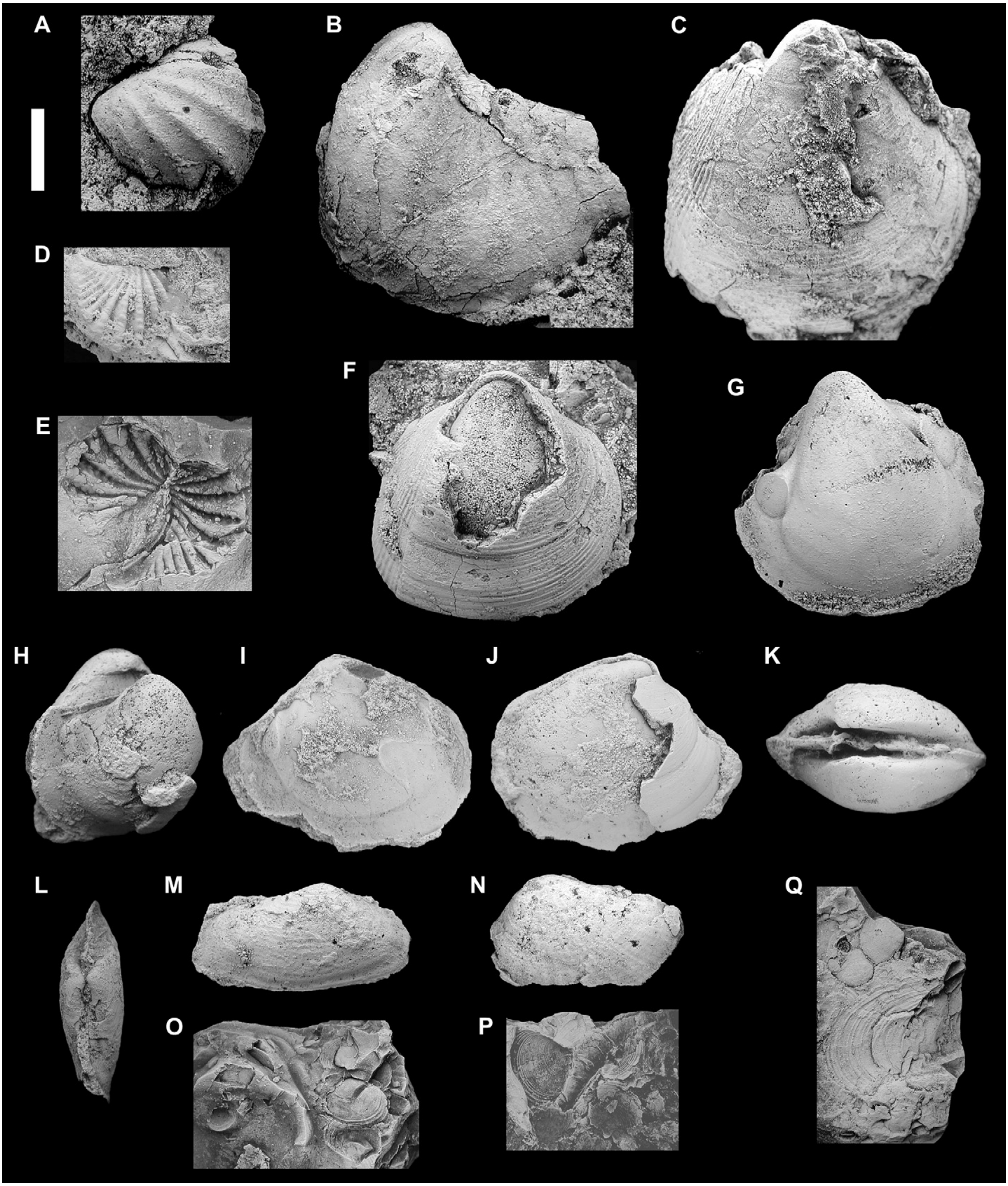


Fig. 5. A, B, D, E, *Pterotrigonia flava* sp. nov. A, MPM-PI-4199, paratype, LV internal mould. B, MPM-PI-4200, paratype, LV internal mould. D, MPM-PI-4201, holotype, RV, most shell preserved. E, MPM-PI-4209, paratype, open shell with conjoined valves. C, F, G, *Protocardia shehuenensis* Feruglio, 1936. C, MPM-PI-4218, paratype, RV, most shell preserved. F, MPM-PI-4213, holotype, RV, most shell preserved. G, MPM-PI-4214, paratype, internal mould. H, *Cucullaea*? sp., MPM-PI-4183, tilted view showing lateral tooth. I–K, Tellinidae indet. I, J, MPM-PI-4219, internal mould, shell partly preserved; I, LV; J, RV. K, MPM-PI-4220, internal mould, dorsal view. L, M, *Panopea*? sp., MPM-PI-4227. L, dorsal view. M, right valve view. N, ?*Pholadomya* sp., MPM-PI-4228, internal mould, left valve view. O, P, "*Corbula*" *sehuena* Ihering, 1907. O, MPM-PI-4222, external moulds of two specimens embedded in rock. P, MPM-PI-4223, one external mould. Q, Conchostraca indet.; MPM-PI- 4225. Scale bar represents 5 mm.

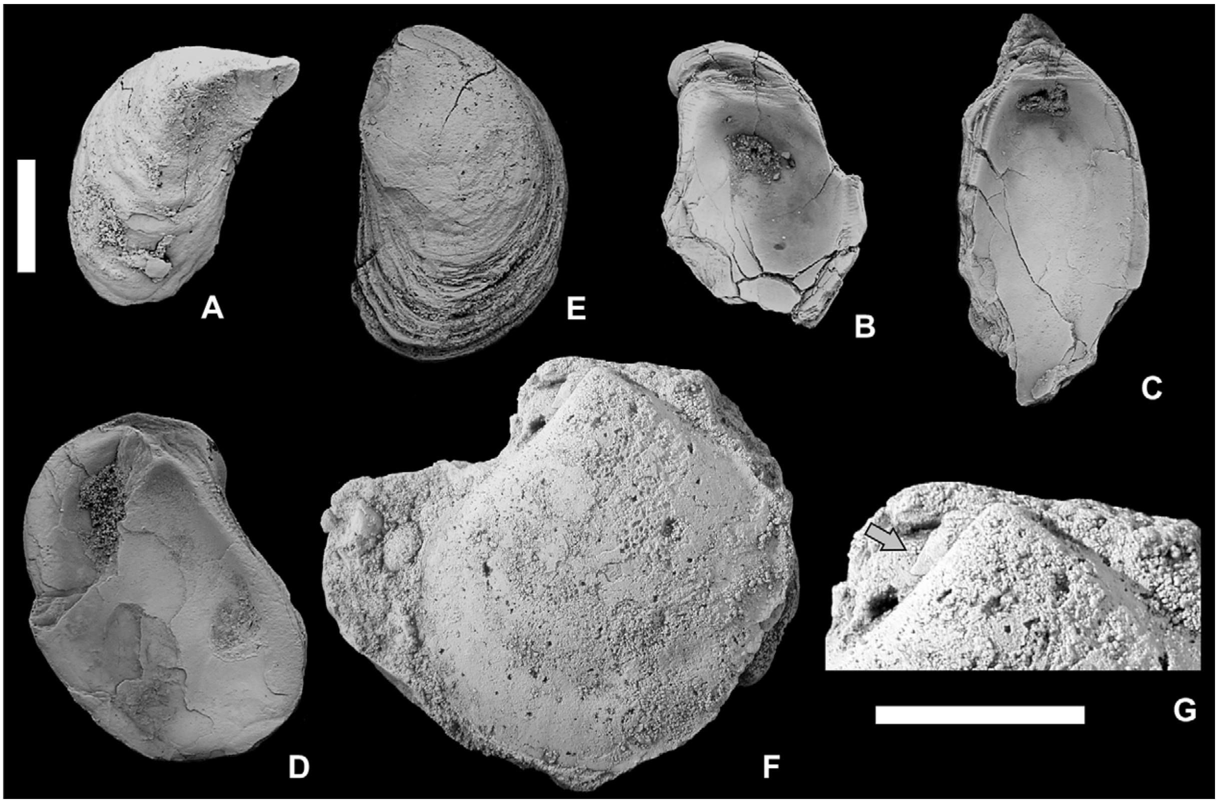


Fig. 6. A–E, *Amphidonte guaranitica* (von Ihering, 1899). A, MPM-PI-4189, LV exterior. B, MPM-PI-4187, LV interior. C, MPM-PI-4185, LV interior. D, MPM-PI-4186, RV interior. E, MPM-PI-4190, RV exterior. F, Pectinidae indet., MPM-PI-4231, LV internal mould with part of auricle preserved. G, enlarged view of umbonal area of same specimen. Scale bar represents 5 mm in A–F, 9 mm in G.

described as *Exogyra*, but a revision by Casadío (1998) provided data on shell anatomy and structure that warrant its inclusion in *Amphidonte*. However, although the two species share a similar morphology, the Late Cretaceous species has larger shells (up to 7.5 cm high and 5.5 cm long), which are thicker and show empty cavities in the umbonal area. These features are not evident in the material from the Mata Amarilla Formation. Malchus (1990) briefly revised this genus and provided a detailed description and discussion of *Amphidonte* (*Amphidonte*) *pyrenaicum* (Leymerie, 1851), a Late Cretaceous species he reported as occurring in France, Spain, Central Asia and Pakistan. The specimens from Egypt that he described and illustrated were included in a slightly different "forma nofretete". *Amphidonte guaranitica* appears quite similar to this species, except, again, for the smaller size of the Patagonian species. Also, the right valve of *A. guaranitica* also appears to be slightly more curved in the umbonal area and the ligamental area of the same valve is wider.

Order Pectinoida Wilckes, 1810
Superfamily Pectinoidea Rafinesque, 1815
Family Pectinidae Rafinesque, 1815

Pectinidae indet.
Fig. 2F, G

Material. MPM-PI-14231, CME17.

Remarks. The only specimen is a flat internal mould of a left valve. The umbo is anterior and the dorsal margin straight, although very badly preserved. The anterior margin is broadly excavated. The anterior auricle is preserved partly as shell and partly as mould and appears to show a well developed byssal notch (Fig. 2G). The mould is completely smooth, with no evidence of commarginal folds or internal ribs.

Subclass Palaeoheterodonta Newell, 1965
Order Trigonioida Dall, 1889
Family Trigoniidae Lamarck, 1819
Genus *Pterotrigonia* van Hoepen, 1929

Type species. *Pterotrigonia cristata* van Hoepen, 1929; original designation.

Pterotrigonia flava sp. nov.
Fig. 5A, B, D, E

Derivation of name. L, *flava*, yellow, alluding to the stratigraphic unit that bears the material.

Material. MPM-PI-14199–14208 (see Fig. 5A, B, D), from bed CME17; MPM-PI-14209 (see Fig. 5E), from CME2; MPM-PI-14210, from bed CME1; MPM-PI-14211, from bed MAFER2; MPM-PI-14212, from bed CME17; MPM-PI-14195, from bed CME1.

Diagnosis. Small *Pterotrigonia*, escutcheons narrow and finely ribbed, flank with 9–11 radial tuberculate ribs; tubercles about 15 on middle ribs.

Description. Shell relatively small (up to 45 mm long), very inflated anteriorly, rostrate; umbones opisthogyrous, placed near anterior end of shell; anterior margin evenly rounded, ventral margin slightly convex, posterodorsal margin deeply concave; escutcheon narrow, deeply concave, ornamented with very fine radial ribs only; flank ornamented by curved tuberculate radial ribs, numbering up to approximately 10; about 15 tubercles on middle ribs; ribs narrower than intercostal spaces; intercostals smooth.

Remarks. Species of *Pterotrigonia* have been reported from rocks of diverse age at localities scattered over a wide area of Patagonia. These have been reviewed by Leanza (1993), in a comprehensive study of all trigoniids from Patagonia.

This small species of *Pterotrigonia* resembles *Trigonia bustamantina* Feruglio, 1937 (pp. 196, 197, pl. 21, figs. 3, 4). Feruglio recorded his material as coming from the "Rocaniano" at Tetas de Pinedo, near Bahía Bustamante (Chubut). The exposures here include rocks of Maastrichtian and younger age, presently considered to be part of the Bahia Bustamante Member of the Salamanca Formation. The species from Chubut is based on fragmentary material, but it still exhibits the strongly rostrate posterior and the strong tuberculate ribs on the flank. These are similar to the ribs exhibited by *Pterotrigonia flava*, but the two species can be separated by the larger size of *Trigonia bustamantina*. In addition, the tubercles along the ribs of the species from Chubut are missing on the dorsal part of the ribs, while they can be observed throughout the entire length of the ribs of *Pterotrigonia flava* sp. nov. Also similar is *Trigonia wilckensi* Feruglio, 1937 (pp. 109, 110, pl. 12, fig. 11–12a, b) from the Senonian south of Lago Argentino, Santa Cruz. This is probably a synonym of *T. bustamantina*, as the only evident difference is the weakness or lack of tubercles on the ribs of the species from Santa Cruz, but this may be a taphonomic attribute, as previously suspected by Feruglio. Leanza (1993) grouped these species under *Pterotrigonia* (*Rinetrgonia*) *windhauseniana* (Wilckens, 1921). Wilckens (1905, p. 136, pl. 7, fig. 7) described this species based on material from Sierra de los Baguales in Santa Cruz, collected from rocks probably of Campanian/Maastrichtian age.

Subclass Heteroconchia Hertwig, 1895
Family Cardiidae Lamarck, 1809
Genus *Protocardia* von Beyrich, 1845

Type species. *Cardium hillanum* Sowerby, 1813 (by subsequent designation, Hermannsen, 1847).

Protocardia shehuenensis Feruglio, 1936
Fig. 5C, F, G

1936 *Protcardia shehuenensis*; Feruglio, pp. 289, 290, pl. 1, figs. 2a, b, 3a–c.

Type material. Five syntypes. These specimens could not be located among the material described by Feruglio and housed in the Università di Bologna (Italy). Additional material studied by Feruglio is housed in the Museo Argentino de Ciencias Naturales (Buenos Aires); however, the syntypes also are missing from this collection.

Type locality. According to Feruglio, the locality from where his specimens came is located SSW of Mata Amarilla, between the Shehuen and Pari Aike rivers. This indication, together with the accompanying fauna, suggests that it is the same section or one very nearby those we have studied (CME and MAFER).

Material. MPM-PI-14213–14218, all from bed CME17: MPM-PI-14213 (illustrated in Fig. 5C); MPM-PI-14214 (illustrated in Fig. 5F); MPM-PI-14218 (illustrated in Fig. 5G).

Description. Medium sized-shells (up to 45 mm long), subquadrate thick shells, with strong upwardly curved cardinal teeth; umbones prominent, posteroventral keel well developed; ornamentation of weak commarginal ribs, more strongly marked anteriorly and numbering about 10 in the last 10 mm along the margin; posterior flank behind keel bearing 21 narrow but fairly strong radial ribs.

Remarks. This species clearly fits in *Protocardia* von Beyrich, 1845, because of its shell outline, size and most importantly, its smooth outer shell surface except for the narrow and strong radial ribs it carries on the posterior flank. No similar species are known from Cretaceous rocks in Patagonia. It shows some resemblance to *Protocardia multistriata* (Shumard, 1854) (Perrilliat et al., 2006, p. 103, fig. 25) from the Coniacian/Santonian of Jordan, which, however, has more prominent umbones and the radial ribs on the posterior flank are stronger and number only 10. The shell outline of *Protocardia texana* (Conrad, 1857) from the Albian of North America is similar, but the commarginal ribs are much stronger and somewhat lamellose, and cover the entire shell surface, a feature that clearly separates it from *P. shehuenensis*.

Family Tellinidae de Blainville, 1814

Tellinidae indet.
Fig. 5I–K

Material. MPM-PI-14219 (see Fig. 5I, J), 14220 (see Fig. 5K), all from bed CME17; MPM-PI-14229, from bed CME17.

Description. Shells small, inflated (33 mm long; 27 mm high, 15 mm wide), umbones not conspicuous, placed at midlength of shell, gently prosogyrous; posterior dorsal margin gently convex and merging smoothly into widely rounded posterior margin; anterior margin gently concave; anterior end slightly tapering; shell relatively thick, reaching up to 1.8 mm near umbones; lunule smooth, not differentiated; escutcheon smooth; shell surface covered with closely spaced commarginal growth lines; short very faint radial striations superimposed on growth lines; internal mould showing hinge with two small divergent cardinal teeth and thickened hinge margins; anterior adductor muscle scar very weakly impressed; pallial line strong, with a conspicuous pallial sinus, pointing upwards and reaching near the midlength of shell; axis of sinus placed at 70° from vertical line at umbones; branches of sinus forming and angle of 35°.

Remarks. Only three specimens of this small shell are in our collection. Generic placement of this material is at present very uncertain because most hinge characters and external ornamentation are missing, preventing any attempt at further classification. However, the small divergent teeth and upward-pointing sinus show some resemblance to those present in *Arcopagella* Meek, 1872 (type species: *Arcopagella mactroides* Meek), from the Upper Cretaceous of North America. They do differ though by the more rounded and less vertical sinus of the North American species. In any event, meaningful comparisons will only be possible when better material becomes available that may allow a positive identification. The available information on the morphology of this species only indicates that it was a relatively deep burrower in soft sediment, a life habit consistent with sedimentological data.

Subclass uncertain
Family uncertain

"*Corbula*" *sehuena* Ihering, 1907
Fig. 5O–P

1897 *Astarte* sp.; Ihering, p. 316
1899 *Corbula* sp.; Ihering, p. 64

1902 *Corbula* sp.; Ihering, p. 209
1907 *Corbula sehuena* Ihering, pp. 51, 52, fig. 5

Material. MPM-PI-14221– 14223, from bed CME5; MPM-PI-14230, from bed MAFER3: MPM-PI-14222 (see Fig. 5O); MPM-PI-14223 (see Fig. 5P).

Description. Shell small (3–17 mm long), subtriangular to ovate, apparently very thin when preserved; umbos inconspicuous, placed in front of shell midlength; hinge unknown; outer shell ornamentation of commarginal asymmetrical ribs only; ribs fairly strong, separated by a deep furrow; inner surface apparently also covered with commarginal ribs.

Remarks. The specimens we have collected from the Mata Amarilla Formation agree well with the description and illustration of *Corbula sehuena* Ihering, 1907 (pp. 51, 52, fig. 5). The type series of this species comprises internal and external moulds that are very poorly preserved, collected at the locality known as "Par-Aïk" according to Ihering. The generic placement of this material has been the subject of controversy because it was initially classed by Ihering as *Astarte*. However, he later (von Ihering, 1902, 1907) followed Dall and Pilsbry's advice (von Ihering, 1907, p. 52) and placed it, albeit reluctantly, in *Corbula*. The fact is that neither Ihering's material nor most of ours show any preserved shell. Moreover, no internal characters, whether hinge or other, are available that may aid in its generic placement. In addition, the presence of internal commarginal ribs appears as a character that precludes its inclusion in *Corbula*. Even family-level affinities must remain doubtful until better preserved specimens are collected. Previous placement of this species in *Corbula* was probably based on the fact that in many instances it occurs alone and in rocks apparently reflecting brackish environments. Our material is associated with lagoon facies (Varela et al., 2011), deposited in brackish environments similar to those in which many extant species of *Corbula* live (Hartmann, 2002). While the material may be superficially similar, this or the fact that the environments are similar cannot be used as an argument for taxonomic placement.

Order Myoidea (Stoliczka, 1870)
Family Hiatellidae Gray, 1824
Genus *Panopea* Ménard de la Groye, 1807

Type species. *Panopea aldrovandi* Ménard de la Groye, 1807 (= *Mya glycymeris* Born, 1778); ICZN Opinion 1414, 1986.

Panopea? sp.
Fig. 5L, M

Material. MPM-PI-14226, 14227, from bed CME17: MPM-PI-14227 (see Fig. 5L, M).

Description. Small *Panopea* (up to 35 mm long and 15 mm high), subrectangular, elongate; umbones small, placed slightly behind shell midlength; posterior end gently tapering and narrowly rounded; posterior gap not evident; ventral margin almost straight; shell ornamentation unavailable, although one of the mould shows a few poorly developed commarginal undulations; hinge and other internal characters unknown.

Remarks. Represented by two small internal moulds, with no preserved shell or interior characters available. The generalized shell prevents any accurate identification. It resembles a number of taxa described from Cretaceous and Cenozoic rocks in southern South America. *Panoea simplex* Hupé, 1854 (p. 374, pl. 6, fig. 7) from the Maastrichtian of Quiriquina Island (southern Chile) is one of these, but it clearly differs by its more centrally located umbones and more conspicuous ornamentation. However, in no way can these features be taken as definite, as they may be a result of different taphonomic histories. Whether or not *Panopea simplex* belongs in *Panopea* was questioned by Griffin and Nielsen (2008, p. 285), who suggested it fitted better in *Mya*, albeit with reservations in view of the rather weakly inflated shell and the apparent lack of a posterior gap (two characters shared by the specimens from Mata Amarilla as well). The name *Panopea simplex* has also been applied to other material from Cretaceous rocks further south in Patagonia (Wilckens, 1905), but a definite generic position can only be achieved by careful study of shell interiors. Affinities among this group of common *Panopea*-like shells thus remain rather obscure at present.

Subclass Anomalodesmata Dall, 1889
Family Pholadomyidae Gray, 1847
Genus *Pholadomya* Sowerby, 1823

Type species. *Pholadomya candida* Sowerby, 1823; subsequent designation by Gray, 1847.

Pholadomya? sp.
Fig. 5N

Material. MPM-PI-14228 (see Fig. 5N), from bed CME17.

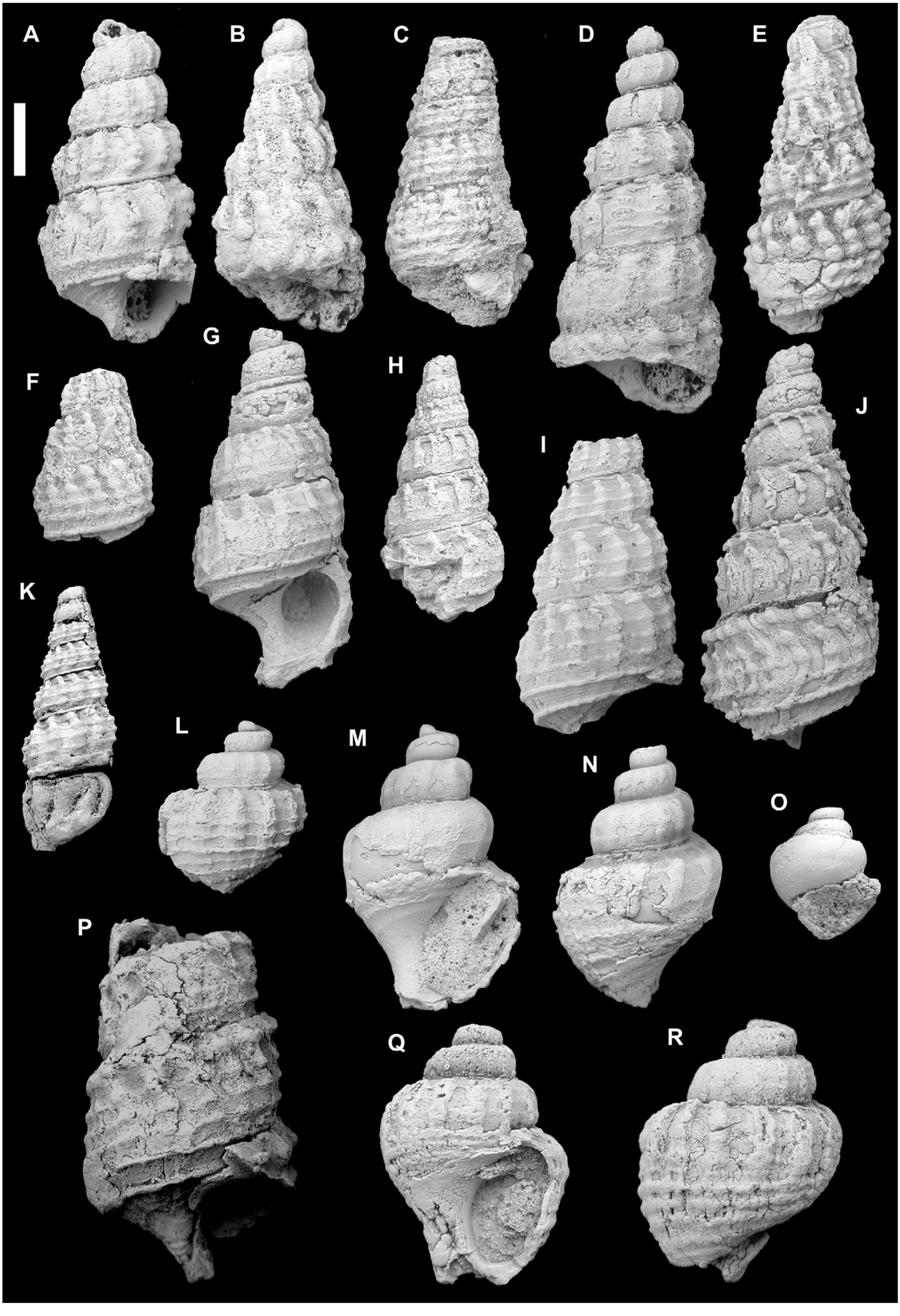
Description. Shell small (25 mm long and 14 mm high), compressed; inconspicuous umbones placed at 0.25 of total length from anterior end; anterior margin evenly convex, merging into gently convex ventral margin; posterior slightly truncated; posterior dorsal margin gently concave; ornamentation of 14 radial ribs on posterior two-thirds of shell; anterior progressively weaker towards posterior end; all ribs narrower than interspaces; hinge unknown.

Remarks. The only specimen is a poorly preserved mould in which very few characters are visible. However, the nature of the ornamentation and posterior gape tentatively suggest that it fits in *Pholadomya*, despite the small size of the specimen. Other members of the Pholadomyoidea from the Cretaceous of southern South America are more appropriately assigned to other genera. No similar material has been described from Cretaceous rocks in southern South America, and the true affinities of this specimen remain uncertain. The presence of a posterior gape, however, indicates that siphons were well developed and that it was probably a deep burrower in soft sediment, as are most anomalodesmatans.

Class Gastropoda Cuvier, 1797
Order Sorbeoconcha Ponder and Lindbergh, 1997
Superfamily Cerithioidea Fleming, 1822
Family Potamididae H. Adams and A. Adams, 1854
Genus *Potamides* Brongniart, 1810

Type species. *Potamides lamarcki* Brongniart, 1810 (by monotypy).

Remarks. Two different species of a tall-shelled gastropod are present in the rocks studied. They are both strongly ornamented with axial ribs and intersect spiral cords. Unfortunately, none of the specimens has the protoconch preserved and the apertural area in all cases is missing. Ihering described material from approximately the same locality as us and included it in *Potamides* Brongniart. However, generic assignment of his specimens and ours must remain uncertain at present until more complete material becomes available. Gastropods with a similar shell (size, apical angle,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ornamentation) have been included in several different genera, even in different families. As most of the characters used to separate the different groups have not been preserved in our material, we prefer to include them in the Potamididae, in view of the similarity they show in ornamentation with many of the species included in *Potamides*. This does not mean that such a placement should be definite.

This species also resembles some specimens included by Perrilliat et al. (2008) in *Melanatria*. This genus was placed within the Cerithiopsidae by Bouchet and Rocroi (2005), but not enough characters are available in our material in order to justify transferring it to that genus. Thus, we prefer to class it as *Potamides* s.l. with reservations, for the time being.

"Potamides" patagonensis Ihering, 1897
Fig. 7A, F

1897 *Potamides patagonensis* Ihering, p. 315, fig. 20
1907 *Potamides patagonensis* Ihering; p. 52

Material. MPM-PI-14232 (see Fig. 7A), 14233, 14234, from bed CME4; MPM-PI-14235, 14246 (see Fig. 7F), 14248, from bed CME18.

Description. Tall shell (largest preserved specimen 27 mm high and 10 mm wide), apical angle 30–35°; axial ornamentation of 12–15 opisthocyrt ribs; spiral ribs five: a weak one immediately adjacent to suture, followed by three strong ribs intersecting axials, and a fifth weak one posterior to axial ribs and running along suture too; spirals also observed on shell surface between axials; base of axial ribs sigmoid posteriorly and strongly nodose at intersection with spirals.

Remarks. This species was described by Ihering (1897, p. 315, fig. 20) based on a few specimens from Pari Aike. Comparison with the type material confirms that our specimens belong in this species, as they share all morphological traits available for observation, i.e., general outline of shell, type and number of axial and spiral ribs, and apical angle.

Most species of *Potamides* inhabit brackish to hypersaline lakes or lagoons (Plaziat, 1993), with those inhabiting more saline environments having the smoothest shells. This kind of environment agrees with that inferred for the rocks of the lower section of the Mata Amarilla Formation (Varela et al., 2011), from which our material was collected.

"Potamides" cf. *patagonensis* Ihering, 1897
Fig. 7B–E, G–I, K, P

Material. MPM-PI-14236 (see Fig. 7C), 14237, 14238 (see Fig. 7D), 14239 (see Fig. 7E), 14240 (see Fig. 7B); from bed CME4; MPM-PI-14241 (see Fig. 7G), 14242 (see Fig. 7H), 14243 (see Fig. 7I), 14244 (see Fig. 7K), 14245, 14247 (see Fig. 7P), from bed CME18.

Description. Tall shell (largest specimen 27 mm long and 12 mm wide), apical angle 20–25°; axial ornamentation of 12 slightly opisthocyrt ribs; spiral ribs four: posterior spiral strong and immediately adjacent to suture; two secondary spirals intercalated between two adjacent primary spirals; smooth weak posterior spiral running along suture; two strong spirals on shell base, the anterior one a prolongation of the smooth spiral running along suture.

Remarks. This species differs from "*Potamides*" *patagonensis* Ihering, 1897, by the nature of its ornamentation. Whilst in "*P.*" *patagonensis* the axial ribs are clearly opisthocyrt, they are very weakly so in "*P.*" cf. *patagonensis*. On balance, in "*P.*" *patagonensis* there are five spiral ribs, of which the three intersecting the axials are the strongest, while in "*P.*" cf. *patagonensis* they number four and the strongest of these is the posterior one. Assignment of these specimens to *Potamides* is provisional and follows the original assignment of von Ihering (1897), as they do not appear to belong in this genus. Specimens that preserve early whorls and apertures are necessary for an adequate generic placement.

Family Thiariidae Morrison, 1954
Genus *Pyrgulifera* Meek, 1872

Type species. *Melania humerosa* Meek, 1860, by monotypy.

Pyrgulifera? sp.
Fig. 7L–O, Q, R

Material. MPM-PI-14250 (see Fig. 7Q, R); MPM-PI-14253; from bed CME4; MPM-PI-14252, from bed MAFER3; MPM-PI-14249 (see Fig. 7L), 14251 (see Fig. 7M, N), 14252 (see Fig. 7O), from bed CME4.

Description. Shells small (19 mm high and 14 mm wide maximum), with rounded shoulders; axial ribs slightly opisthocline on shoulder, orthocline anterior to shoulder, reaching from one suture to the next; 12 axial ribs on last whorls; approximately 10 spiral ribs, weak posteriorly; basal ribs much stronger, six in number; suture bounded by a well-developed smooth spiral rib; secondary axial ribs intercalated.

Remarks. This small shell can probably be included in *Pyrgulifera*, because it resembles a number of taxa referred to this genus, including *Pyrgulifera humerosa* (Meek, 1860), from the Cretaceous Bear River Formation in Wyoming. The two species share the strong axial ribs and spiral cords, although they may be separated because the North American species appears to be taller and has a more concave shoulder, and there are up to fifteen ribs (White, 1895, p. 55, pl. 8, figs. 1–11, pl. 9, figs. 4–8). Likewise, *Pyrgulifera stantoni* White, 1895 (p. 56, pl. 9, figs. 1–3) has a much taller shell and the shoulder is not well defined. It should be mentioned, however, that one of our specimens appears to have a taller shell (Fig. 7N), but this feature may be only a result of intraspecific variation.

Pyrgulifera kahuitara Stilwell, 1998 (p. 70, fig. 16J, L) from the Santonian–Maastrichtian Kahuitara Tuff in the Chatham Islands (New Zealand) was reported as the only species of *Pyrgulifera* in the Southern Hemisphere. It appear quite similar to our material, but the shell shows 15 axial ribs, and the spiral cords appear to be stronger than in the Patagonian species. The apertural area is missing in our specimens, hindering comparison with the details described by Stilwell (1998). The only feature observable in this sense is the apparent slight elongation of the aperture in the New Zealand species, while it is more rounded in *Pyrgulifera*? sp. from the Mata Amarilla Formation.

4. Discussion

The unique fauna of the Mata Amarilla Formation has been very poorly known and therefore its usefulness as a biostratigraphic indicator or as a tool in palaeoenvironmental interpretations has

Fig. 7. A, F, J, "*Potamides*" *patagonensis* Ihering, 1897, MPM-PI-4232, 4234 and 4246 respectively. B–E, G–I, K, P, "*Potamides*" cf. *patagonensis* Ihering, 1897, MPM-PI-4240, 4236, 4238, 4239, 4241–4244 and 4247 respectively. L–O, Q, R, *Pyrgulifera*? sp. L, MPM-PI-4249, early whorls, shell partly preserved, abapertural view. M, N, MPM-PI-4251, internal mould of larger specimen with part of shell preserved; M, apertural view; N, abapertural view. O, MPM-PI-4252, small internal mould, shell mostly absent. Q, R, MPM-PI-4250, small specimen, shell partly preserved; Q, apertural view; R, abapertural view. Scale bar represents 5 mm.

been limited, although in some instances overestimated. The fossil assemblage described shares some elements (at a generic level) with the overlying La Anita Formation of Campanian (?) age. This is the case, for instance, with *Potamides* and *Corbula*. However, others are entirely missing, such as inoceramids, which are fairly common in the La Anita Formation. The trigoniids found in the Mata Amarilla Formation, while belonging in the same group as some of those from the La Anita Formation, are more similar to species common in other regions and in significantly younger rocks, e.g., Bahía Bustamante, Chubut (Feruglio, 1937). Other taxa occurring in this fauna are entirely unknown from rocks of similar age in other parts of South America. Such is the case of *Protocardia shehuenensis*. Species of *Protocardia* have been described from Cretaceous rocks in the Northern Hemisphere, but this is the first record from South America. *Amphidonte guaranitica* is similar to other oysters from Patagonia such as *Amphidonte mendozana* (Casadío, 1998). The relationship between these and the species from the Mata Amarilla Formation remains necessarily obscure until the latter is better understood. The exact significance of the gastropods contained in the Mata Amarilla Formation remains as yet uncertain, and whether they inhabited continental or marginally marine biotopes is still controversial. Similar gastropods can also be found in northern Argentina, in Maastrichtian rocks of the Salta Group exposed between Tucumán and Jujuy and further north into Bolivia (Bonarelli, 1927). The geological setting is, albeit, quite different, in addition to being younger (Marquillas et al., 2005, and references therein).

Some of the molluscs described herein belong to groups that have representatives living in brackish water. However, other related taxa are restricted to fully marine environments. Therefore, a taphonomic explanation for this mixture of fauna may lie in the palaeoenvironmental conditions in which the fauna or faunas lived and the origin of the deposits in which they were buried.

Of the taxa described from the Mata Amarilla Formation, some were found in facies interpreted as washover deposits (e.g., *Pholadomya* sp., *Protocardia shehuenensis*, *Cucullaea*) while others come from lagoon facies (e.g., *Corbula shehuena*, conchostracans, and possibly "*Potamides*" *patagonensis*; Fig. 5Q). The specimens of *Pterotrigonia flava* found in the lagoon facies were probably transported there from the washover deposits drawn from the marine areas they inhabited (Varela et al., 2011). It is noteworthy that sandy facies of the levels CME1 and Mafer 1 and 2 have articulated shells of *Pterotrigonia flava* in life position. These levels were interpreted by Varela et al. (2011) as deposits of barrier systems.

Summarizing, the fauna described herein, while having a low diversity and being far from well preserved, is important as a record of unusual environments and burial conditions of faunas of mid Cretaceous age, particularly in this area of South America. It draws attention to the fact that the utmost care should be taken when palaeoenvironmental interpretations are being made based solely on the fossil content, as different taphonomic processes could also be responsible in part for the unique faunal composition.

5. Conclusions

The fauna described confirms the marginally marine (paralic) setting traditionally assigned to the Mata Amarilla Formation. However, the mixed nature of this fauna in some of the beds suggests that there were different sub-environments within the basin at the time of deposition. Some of the taxa are clearly marine; this is the case for *Protocardia*, *Pterotrigonia*, *Cucullaea*, and pectinids, while others belong in groups that exhibit a tolerance to a wider range of salinity such as "*Corbula*", conchostracans, *Pyrgulifera* and probably "*Potamides*" cf. *patagonensis*. The Lower Section of the Mata Amarilla Formation in the northern sector of the basin was interpreted as a lagoon deposit (Varela et al., 2008, 2011), based on sedimentological and taphonomic data. Intercalated palaeosols with bioclastic deposits are a remarkable feature of this unit (Fig. 4). The lagoon was restricted by a system of sandbars. These sandbars were often overridden by episodic events. As a consequence of these events, invertebrate organisms living offshore were removed and transported towards the lagoon environments (e.g., *Protocardia*, *Pterotrigonia*, *Cucullaea*, pectinids). *Pterotrigonia* was found in life position in the sandbar facies, but in the sediments interpreted as lagoon deposits it occurrence is, as for the other marine fossils described from this part of the section, allochthonous or at most parautochthonous.

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