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# A novel late Early Miocene assemblage of terrestrial gastropods from Santa Cruz (Patagonia, Argentina)

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**Abstract.**—A remarkable fossil assemblage composed of five gastropod taxa is described from the Early Miocene of Santa Cruz (Patagonia, Argentina) in southernmost South America. The assemblage includes extinct and living genera South America, and on geographic distributions and represent background new information on spatial and across time distributions as well as identification of new taxa. A new taxon, *Patagocharopa enigmatica* n. gen. n. sp., is tentatively assigned to Charopidae. *Gastrocopta patagonica* n. sp. (Vertiginidae) represents the oldest record of *Gastrocopta* in Argentina and the southernmost record for the Americas. *Punctum patagonicum* n. sp. (Punctidae) represents the first record of *Punctum* for continental South America, and characterized by a protoconch with traces of axial costulae and a teleoconch with strong radial ribs. *Zilchogyra miocenica* n. sp. is the first Miocene record of the charopid genus *Zilchogyra*. Fragments of a possible *Scolodonta* (Scolodontidae) are recorded. Overall, the assemblage represents an important and useful paleoenvironmental tool. This fauna suggests that a more temperate and humid environment than today—with a more dense vegetation cover—was prevalent at this site during the Early Miocene.

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## Introduction

Patagonia is a region of great biogeographical interest because of its paleogeographical history and the endemic nature of its current biota. On this regard, Santa Cruz province in southern Patagonia harbours fossiliferous sites of extraordinary abundance and diversity of unique plants and animals. This is particularly true for the Santa Cruz Formation (Early Middle Miocene), which covers areas of eastern Austral Patagonian Cordillera and part of the Extra-Andean Patagonia, between Lake Buenos Aires and Río Turbio in the west, and the San Jorge Gulf and northern Tierra del Fuego in the east (Matheos and Raigemborn, 2012). Interestingly, this formation bears some of the most prolific continental deposits with fossil vertebrates of South America. These fossils have been addressed in many publications for over a century (Tauber, 1997a, 1997b, 1999; Vizcaíno et al., 2012; other references cited therein). The beds of the Santa Cruz Formation enclose a rich and diverse vertebrate fauna that includes mammals, birds, anurans, and reptiles; there are also insects, plant macro- and micro-remains (Tauber, 1994, 1999; Brea et al., 2012; Degrange et al. 2012; Fernicola and Albino, 2012; Krapovickas, 2012; Vizcaíno et al., 2012), coprolites (Tauber, 2005), as well as land gastropod shells (Rodríguez et al., 2012). This formation has also been highlighted as the foremost fossil-bearing deposit for

understanding the biological diversity and community structure of mammals in Patagonia prior to the Great American Biotic Interchange (Vizcaíno et al., 2012). The ‘Estancia La Costa’ Member, which is the lowermost within this formation, is the most significant in terms of specimen and taxon diversity, as well as by state of conservation of the fossils.

The historical development of terrestrial mollusks studies in Argentina is limited; a summary can be found in Parodiz (1969) and di Pasquo et al. (2008), highlighting both the surveys of Hermann von Ihering, who described a few species of large size mollusks (Strophocheilidae) (see Parodiz, 1996; Miquel and Bellosi, 2010) from the Tertiary of Patagonia around the early twentieth century.

Fossil records of land micromollusks from the Patagonian region are scarce. A unique Cretaceous record is that of Morton (1999), who recorded *Radiodiscus* but its taxonomy requires a re-assessment. The micromollusks from the deposits of Gran Barranca described by Miquel and Bellosi (2010) are Eocene taxa referred to Charopidae. The Strophocheilidae have been recorded in Paleocene rocks (Parodiz, 1969), and in Miocene beds from the Limay River area (Collón Cura Formation, Río Negro Province) (Miquel and Manceñido, 1999). The single record of land mollusks in the Santa Cruz Formation is a Charopidae specimen initially assigned to *Stephadiscus* Hylton Scott 1981 (Rodríguez et al. 2012) but later re-identified as a

species of *Stephacharopa* Miquel and Araya 2013. Adding to the information previously published by Rodríguez et al. (2012), we describe herein a remarkable land micromollusk assemblage from the Santa Cruz Formation including a new species of *Gastrocopta* (Vertiginidae), *?Scolodonta* (Scolodontidae), *Punctum* (Punctidae), *Zilchogyra* (Charopidae), and the new genus and species *Patagocharopa enigmatica*, tentatively assigned to Charopidae.

Fossil land snails are useful tools for paleoclimate interpretations and have been successfully studied in other areas as paleoenvironmental indicators. Particularly, terrestrial mollusks are good environmental indices and permit precise reconstructions of past environments (Rousseau and Wu, 1999). Land snail assemblages have provided reliable information on temperature and moisture conditions, allowing identification of climatic cycles from Quaternary loess sequences at Northern (Rousseau, 1989) and Western Europe (Rousseau, 1987; Rousseau and Puisségur, 1990, 1999; Rousseau et al. 1994; among others), and Southern Asia (Rousseau and Wu, 1999).

The importance of these groundbreaking records from Patagonia is significant from a paleoenvironmental standpoint. The taxonomic and distribution of the land snail communities can add independent and complementary source of evidence for habitat conditions during the Early Miocene, in support or in contrast with previous paleoenvironmental and paleoclimate settings based mainly on mammals.

### Geographical and stratigraphical provenance of the fossil terrestrial shells

The outcrop where the material was collected emerges between the Coyle and Gallegos inlets, on the Atlantic coast of Patagonia in southern Santa Cruz, and belongs to the Rousseau Santa Cruz Formation, of continental origin. This formation is exposed at many places in the eastern portion of southern Extra-Andean Patagonia (Russo et al. 1980; Fig. 1.1, 1.2) and was deposited during the late Burdigalian/early Langhian, as conceived in the International Stratigraphic Chart (between 18 and 15 Myr.; Marshall et al. 1986). The Santa Cruz Formation can be divided into two members, i.e. the Estancia La Angelina Member and the underlying Estancia La Costa Member. The materials described herein were recovered from a stratum of volcanic ashes within the Estancia La Costa Member. This member is 120 m thick and characterized by predominantly greenish epiclastic claystones, chonites, and limolitic sandstones, with mature and immature paleosols and low-sinuosity paleochannels (Tauber, 1994). According to Tauber (1999), there are 21 distinct fossiliferous levels. However, subsequent work by Fleagle et al. (2012) and Perkins et al. (2012) suggests that the lowest seven levels identified by Tauber (1997a) are a single sequence repeated at other northern coastal localities of the Santa Cruz Formation and that there is no temporal difference between them. Accordingly, a rectified age for PLC (paleontological site Puesto de la Estancia La Costa) sequence is estimated between 16.4 and 17.5 Myr. Yet, in this work the designation of the fossiliferous levels follows the nomenclature and the stratigraphical profile of Tauber (1999; Fig. 2) for ease of identification.

The material studied was collected at the paleontological site 'Puesto de la Estancia La Costa' (= Corriguen Aike; PLC: 51° 12' 8,2" S and 69° 03' 35,6" W; Fig. 1.1, 1.2). The bed yielding the fossil material is Tauber's fossiliferous Level 6 (Fig. 2), which consists of a brownish massive cineritic tuff, settled as a pyro-arenite layer. This level is distinguished by a significant amount of relatively complete skeletal remains of mammals and birds, and coprolites appearing at the exposed beds on the intertidal zone during low tide. The lithogenetic characteristics of the fossil-bearing rocks suggest low paleotopographic environments in proximity to floodplains, where the humidity input was high to moderate (Tauber, 1994).

### Materials and methods

The analyzed sample consisted of approximately 720 dm<sup>3</sup> of sedimentary rock. Land snail specimens were identified by washing and screenings through a series of mesh sizes down to 200 µm. The fraction retained was examined under a stereo microscope, with specimens retrieved by 'picking' with fine forceps. After metal-coating, specimens were imaged with a Scanning Electron Microscope (Philips XL 30 TMP) at the Servicio de Microscopía Electrónica de Barrido of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires.

The material available for this study includes 26 fragmentary specimens stored in the collection of the Museo Regional Provincial 'Padre Manuel Jesús Molina' (MPM), in the city of Río Gallegos (Santa Cruz Province, Argentina). Additional specimens studied were housed in the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN, Buenos Aires, Argentina).

The taxonomic classification we follow is that of Bouchet and Rocroi (2005).

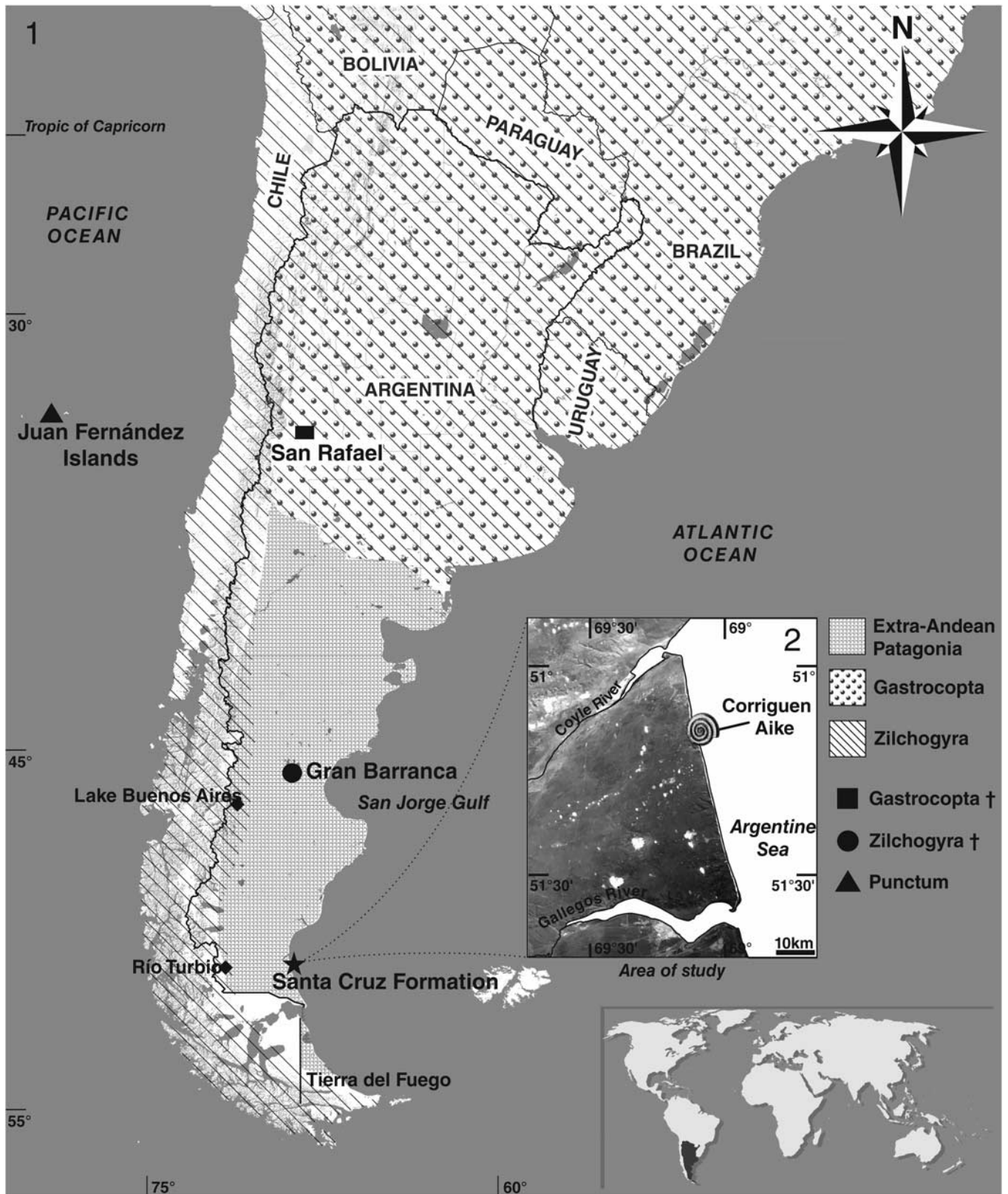
### Systematic paleontology

Superfamily Pupilloidea Turton, 1831  
 Family Vertiginidae Fitzinger, 1833  
 Subfamily Gastrocoptinae Pilsbry, 1918  
 Genus *Gastrocopta* Wollaston, 1878

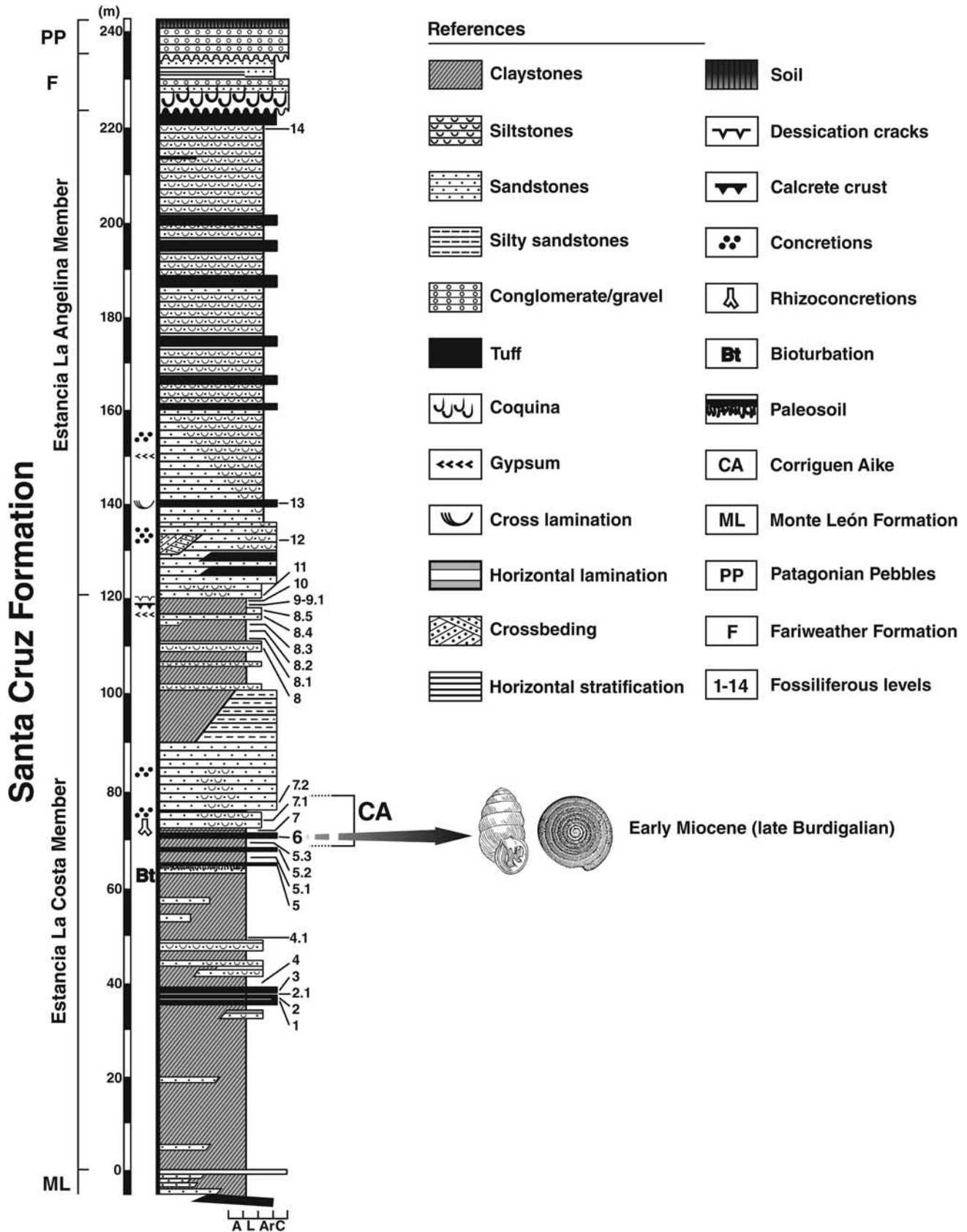
*Type species.*—*Pupa acarus* Benson, 1856, by subsequent designation of Pilsbry (1916).

*Occurrence.*—Both extant and fossil representatives of the genus *Gastrocopta* are known on the basis of records from extensive areas of the American continent, as well as the Galapagos Archipelago (Miquel and Herrera, 2014), but no living or fossil species has been recorded for Chile (Stuardo and Vega, 1985). Paleocene–Recent (Salvador and Simone, 2013).

*Occurrence in Argentina.*—Modern records indicate its occurrence from temperate and tropical regions of the north and central areas of the country down to the area over northern Patagonia, approximately at 34°S (Hylton Scott, 1963, 1968). Doering (1881) reported it from the banks of the Colorado River, in northern Patagonia. The new species described herein



**Figure 1.** Geographic distribution and location of extant and fossil specimens analysed in this study: (1) Distribution of extant *Zilchogyra* species extending down to the Colorado River (striped) in northern Patagonia, distribution of extant *Gastrocopta* species (dots), the square indicates the fossil record of *Gastrocopta* from the Pliocene of Mendoza province, the triangle indicates the record of *Punctum* from Juan Fernández Islands; (2) (inset), detail of the location of Corriguen Aike between Gallegos and Coyle rivers in Santa Cruz province.



**Figure 2.** Stratigraphic profile of Santa Cruz Formation (continental, late Burdigalian/early Langhian, between 18 and 15 Myr). Fossiliferous levels are indicated by arabic numerals. CA: outcropping fossiliferous levels at Corriguen Aike. The arrow indicates fossil-bearing Level 6 (after Tauber, 1999), from which land snail specimens were recovered. Modified from Tauber 1999.

is the oldest record of *Gastrocopta* from Argentina. The genus had been previously recorded from the Pliocene of Mendoza (Turazzini and Miquel, 2013, 2014) and the Holocene of Entre Ríos (Miquel and Aguirre, 2011). Miocene–Recent.

*Gastrocopta patagonica* new species  
Figure 3.1–3.4

**Diagnosis.**—Shell with more than four very convex whorls; two fused strong apertural lamellae (parietal and angular); columellar, palatal and basal lamellae and folds missing; surface of apertural callus covered by irregular calcareous pustules.

**Etymology.**—Feminine. From Patagonia, region where the material was found.

**Examined material.**—MPM PI 3314: Holotype. MPM PI 3315: 1 Paratype.

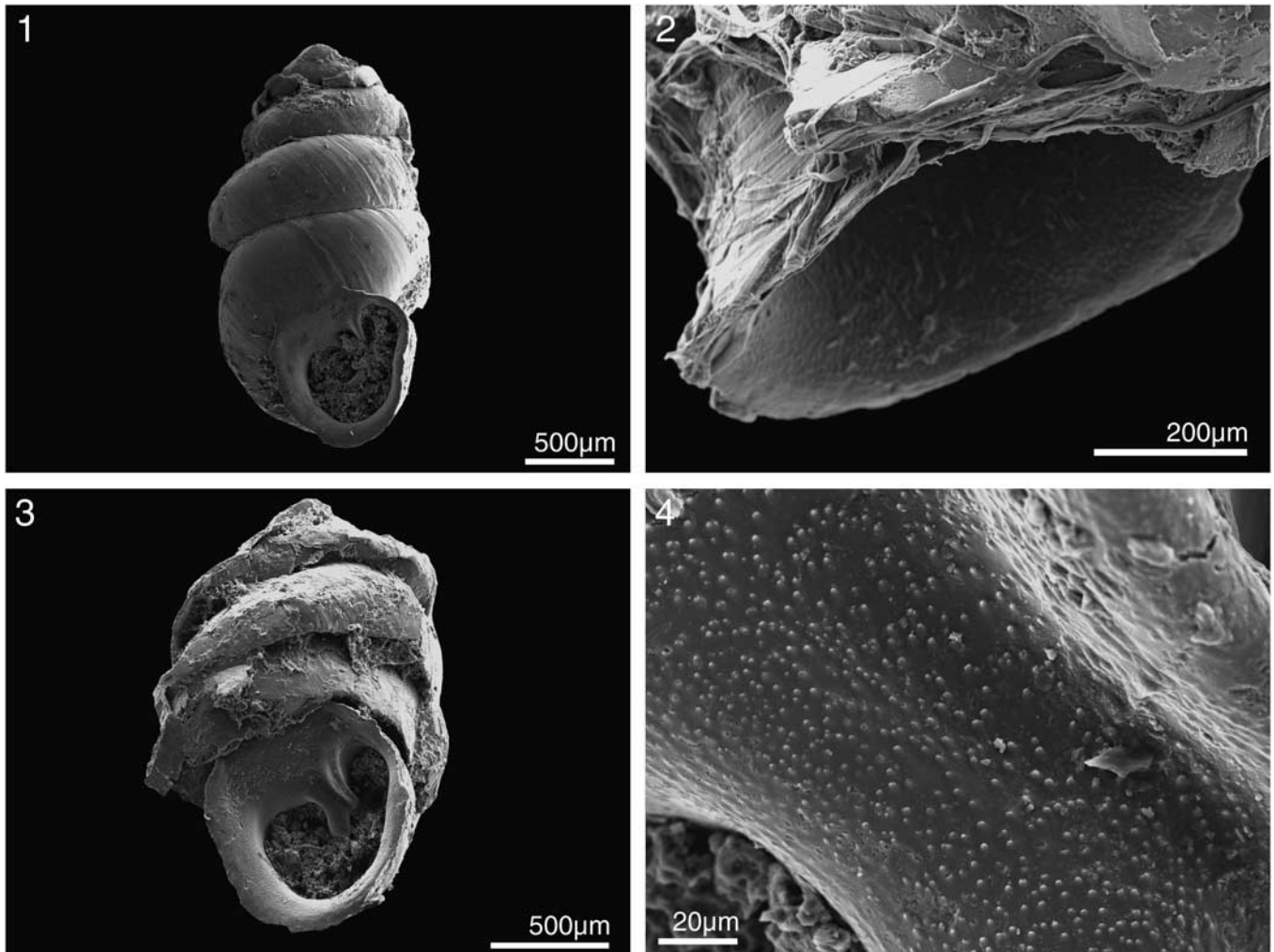
**Geographical provenance.**—‘Puesto de la Estancia La Costa’ (=Corriguen Aike; 51° 12’ 8.2” S and 69° 03’ 35.6” W), between the Coyle and Gallegos Inlets.

**Stratigraphical provenance.**—Santa Cruz Formation, late Burdigalian/early Langhian, Early–Middle Miocene (between 18 and 15 Myr.). Fossiliferous Level 6 of Tauber (1997a), late Burdigalian, ~17.5 Myr. (Fleagle et al. 2012).

**Description.**—Shell typically pupoid, with more than four very convex whorls, with marked axial growth lines; suture very deep; aperture rounded, with partially fused, strong parietal and angular lamellae but lacking columellar, palatal and basal lamellae and folds; labral edge expanded, with a notch toward the interior of the aperture; inner walls ornamented with microscopic calcareous pustules, irregularly arranged. Apex lost in both specimens.

**Measurements.**—Holotype: 2.5 × 0.8 mm, 4+ whorls.

**Comparative remarks.**—*Gastrocopta* sp. was recently described from the Early Pliocene of Mendoza (Turazzini and Miquel, 2014), but cannot be assigned to a species because of the erosional loss of apertural teeth which are of prime taxonomic importance in these vertiginids. *Gastrocopta patagonica* n. sp. differs from Paleocene species from Itaboraí (Brazil) by the



**Figure 3.** *Gastrocopta patagonica* n. sp.; (1) MPM PI 3314, holotype, apertural view; (2–4) MPM PI 3315, paratype: (2) apertural view; (3) apertural view and detail of teeth; (4) detail of the pustulae. Scale bars represent 500 µm (1, 3), 200 µm (2), and 20 µm (4).

shell form and the partial fusion of the parietal and angular lamellae in the aperture (Salvador and Simone, 2013). The absence of other apertural lamellae distinguishes *G. patagonica* from extant Argentine species with more numerous apertural barriers: *G. nodosaria* (Orbigny, 1835), *G. crucifera* Hylton Scott 1948, and *G. pulvinata* Hylton Scott 1948, living in the northern and central areas of Argentina (Hylton Scott, 1945, 1948; Miquel and Aguirre, 2011). The pustule-covered inner surface of the shell is a common feature of many land snails, but it is not a common feature of South American vertiginids; only *G. clausa* (Reibisch, 1892) from the Galápagos Islands (Miquel and Herrera, 2014) shows similar structures.

*Remarks.*—*Gastrocopta patagonica* n. sp. is the southernmost record for genus *Gastrocopta* in South America.

Family Scolodontidae H.B. Baker, 1925  
Genus *Scolodonta* Doering, 1875

*Type species.*—*Streptaxis (Scolodonta) semperi* Doering 1875.

*Occurrence.*—Brazil, Bolivia, Paraguay, Uruguay, and Argentina. Pleistocene–Recent (Miquel and Aguirre, 2011).

?*Scolodonta* sp.  
Figure 4.1–4.3

*Examined material.*—MPM PI 3316. One specimen.

*Geographical provenance.*—‘Puesto de la Estancia La Costa’ (=Corriguen Aike; 51° 12’ 8.2” S and 69° 03’ 35.6” W), between the Coyle and Gallegos inlets.

*Stratigraphical provenance.*—Santa Cruz Formation, late Burdigalian/early Langhian, Early-Middle Miocene (between 18 and 15 Myr.). Fossiliferous Level 6 of Tauber (1997a), late Burdigalian, ~17.5 Myr. (Fleagle et al. 2012).

*Description.*—Shell very fragmentary with more than 3 rounded whorls, of moderate growth, and irregular axial striae, umbilicus 30% of shell diameter.

*Measurements.*—MPM PI 3316: 3.8 × 3.4 mm, 3+ whorls.

*Comparative remarks.*—The only available specimen is broken and deformed, with its apex imbedded in the matrix. We tentatively assign the specimen to genus *Scolodonta* based on its small size, discoidal form of very low spire of few regularly convex whorls, with an open umbilicus, and the teleoconch possessing irregular axial growth striae. It differs from the Scolodontidae living in this area, i.e. *Happia ordinaria* (Smith, 1881), by its larger size and broader umbilicus (Hylton Scott, 1972). However, an accurate generic assignment, and a fuller description of this fossil species must await additional material available from new samplings.

Superfamily Punctoidea Morse, 1864  
Family Punctidae Morse, 1864  
Genus *Punctum* Morse, 1864

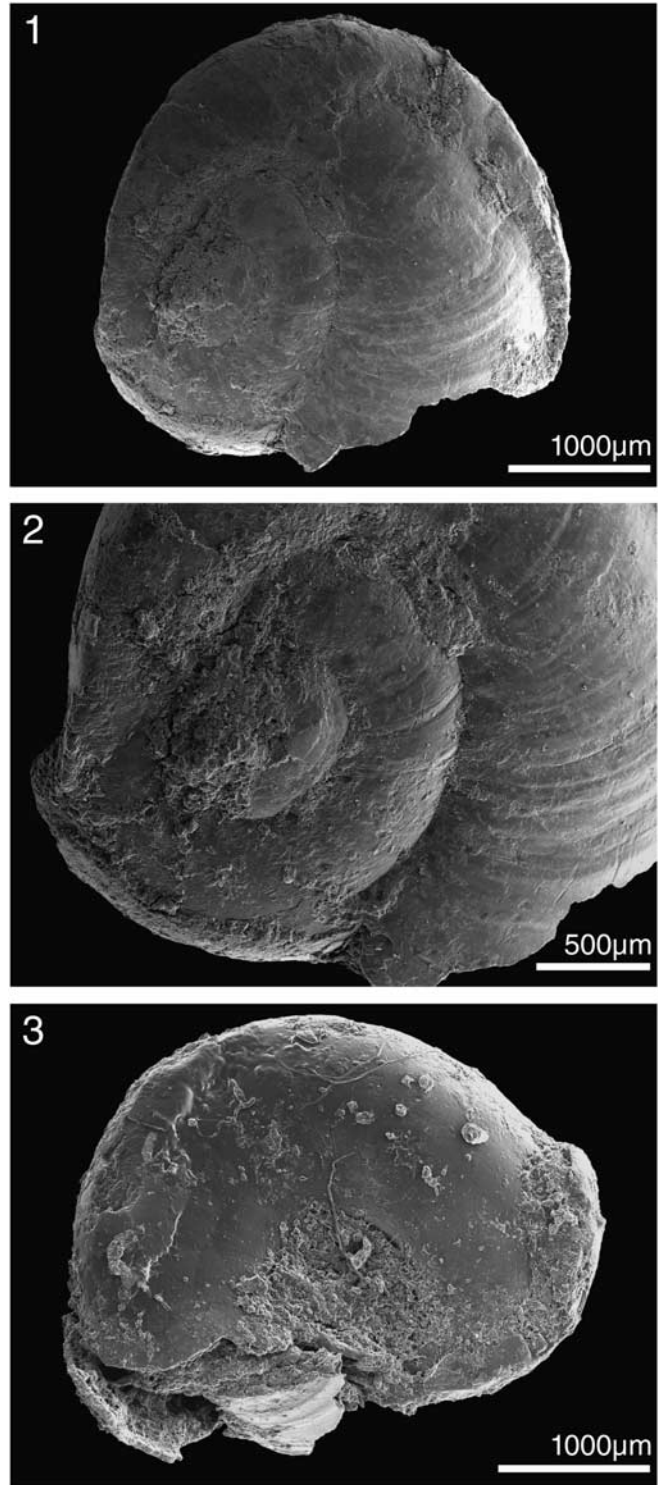


Figure 4. *Scolodonta* sp: (1–3) MPM PI 3316: (1) apical view; (2) detail of apex; (3) detail of umbilicus. Scale bars represent 1000 µm (1, 3) and 500 µm (2).

*Type species.*—*Helix minutissimum* Lea 1841, by original designation.

*Occurrence.*—Geographical and stratigraphical records of the genus include Europe, Africa, Australia, New Zealand, sub-antarctic islands and Juan Fernández Archipelago (Chile)

(Odhner, 1922; Zilch, 1959; Solem, 1983; Stuardo and Vega, 1985; Miquel and Araya, 2015). Oligocene–Recent (Zilch, 1959). Particularly in Argentina, this genus has not been found living. This is the first mention of the genus for continental South America; its record is Miocene–Recent.

*Punctum patagonicum* new species  
Figure 5.1–5.4

**Diagnosis.**—Shell with 3.5 convex whorls; protoconch with traces of axial costulae; teleoconch with strong axial ribs and three to eight axial costulae between two of them, and numerous spiral cords.

**Etymology.**—Neutral name. Refers to its record from the southernmost (austral) region of Argentina and Chile.

**Examined material.**—MPM PI 3317: Holotype. MPM PI 3318: Paratype.

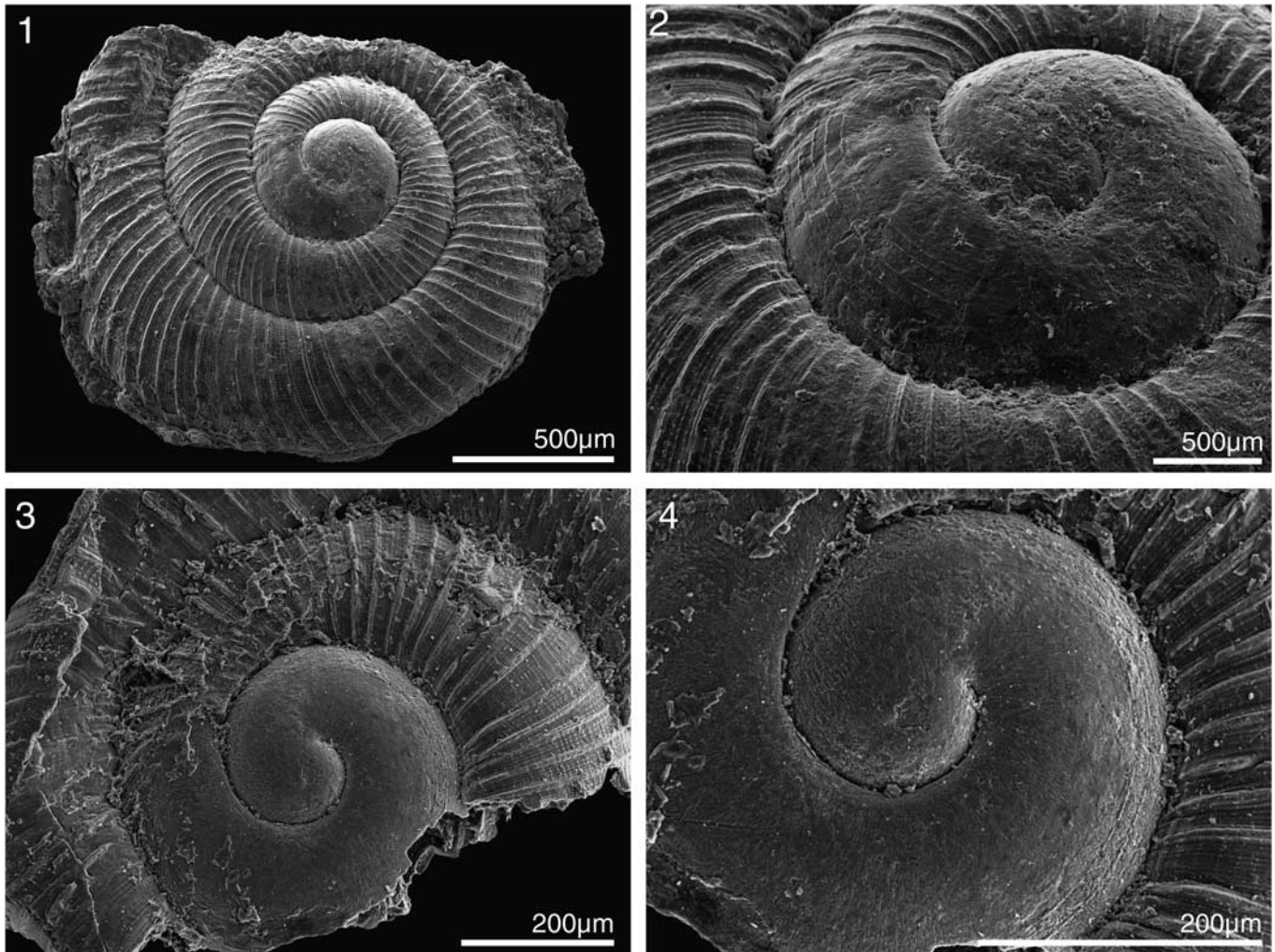
**Geographical provenance.**—‘Puesto de la Estancia La Costa’ (=Corrighuen Aike; 51° 12’ 8.2” S and 69° 03’ 35.6” W), between the Coyle and Gallegos Inlets.

**Stratigraphical provenance.**—Santa Cruz Formation, late Burdigalian/early Langhian, Early–Middle Miocene (between 18 and 15 Myr.). Fossiliferous Level 6 of Tauber (1997a), late Burdigalian, ~17.5 Myr. (Fleagle et al. 2012).

**Description.**—Shell fragmentary, lenticular, with nearly 3.5 convex whorls, apex protruding, suture deep, protoconch with more than 1.5 whorls, bearing traces of spiral costulae only; teleoconch with nearly 75 strong axial ribs, three to eight axial costulae between two of them, and numerous spiral cords.

**Measurements.**—Holotype: 1.7 × 1.45 mm, 3.5 whorls.

**Comparative remarks.**—The material is assigned to the genus *Punctum* because the shell is very minute, subdiscoidal and with few convex whorls, sculptured with delicate ribs, and bearing spiral costulae only on the protoconch. Species of *Punctum*



**Figure 5.** *Punctum patagonicum* n. sp.: (1) MPM PI 3317, holotype, apical view; (2) detail of the protoconch; (3) MPM PI 3318, paratype, apical view; (4) detail of the protoconch. Scale bar represents 500 μm (1, 2) and 200 μm (3, 4).



living in South America were described from Juan Fernández Archipelago, *P. conicum* Odhner 1922, and *P. depressum* Odhner 1922, whose identities are confirmed here through examination of new material. Although the only specimen of *P. patagonicum* n. sp. is fragmentary, its shell is different from *P. conicum* in size:  $1.95 \times 1.15$  and 4 whorls; *P. depressum* is different by the faster growth of the whorls and also by its size:  $1.05 \times 0.7$  mm and 3.75 whorls. Similar shells occur in charopid genera such as *Radiodiscus* Pilsbry and Ferriss 1906, and *Retidiscus* Fonseca and Thomé 1995, where a reticulated sculpture is based on axial costulae and marked spiral incisurae (Miquel and Cádiz Lorca, 2008).

*Other recent materials compared.*—*Punctum conicum* Odhner 1922: MACN-In 39491. Col. M. Ramírez, E. Soto and J. Pizarro, 20-II-2011. Two specimens. *P. depressum* Odhner 1922: MACN-In 39492. Col. M. Ramírez, E. Soto and J. Pizarro, 20-II-2011. Two specimens.

Family Charopidae Hutton, 1884  
Genus *Zilchogyra* Weyrauch, 1965

*Type species.*—*Helix costellata* Orbigny 1835, by original designation.

*Occurrence.*—The current range of this genus covers tropical areas of South America, including at least Peru, Brazil, Chile and Argentina (Fernández, 1973; Flórez Bustamante, 1968; Hylton Scott, 1970; Miquel et al. 2007; Miquel and Barker, 2009; Weyrauch, 1965). Middle Eocene–Recent (Miquel and Bellosi, 2010).

*Zilchogyra miocenica* new species  
Figure 6.1–6.3

*Diagnosis.*—Shell of low helicoid shape, with 4.5 very convex whorls; protoconch with 1.75 smooth whorls; teleoconch with marked irregularly axial ribs (approximately 90 on last whorl) and weak axial costulae.

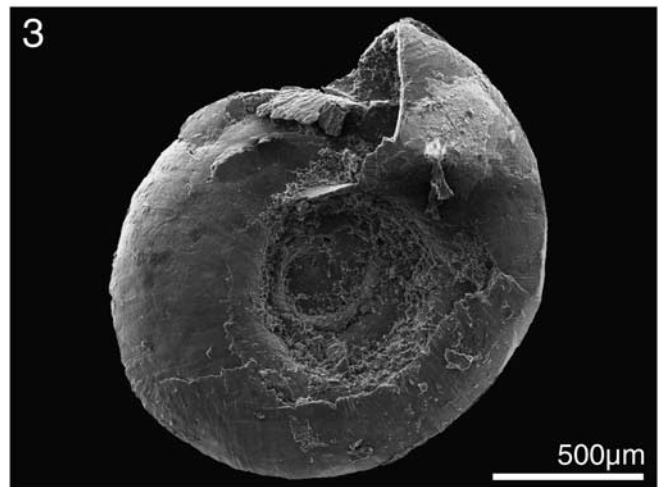
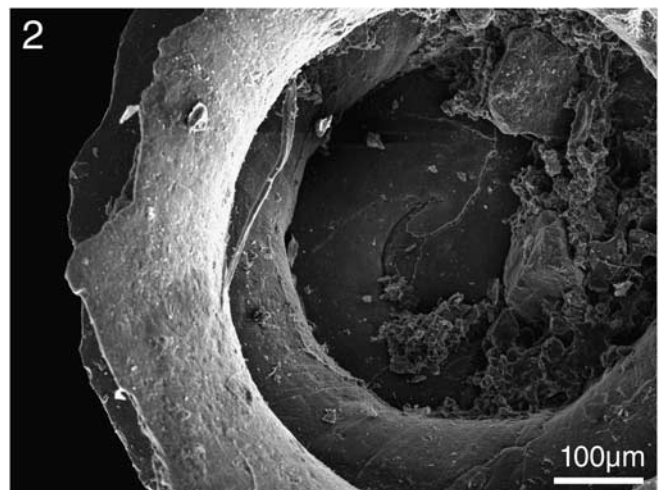
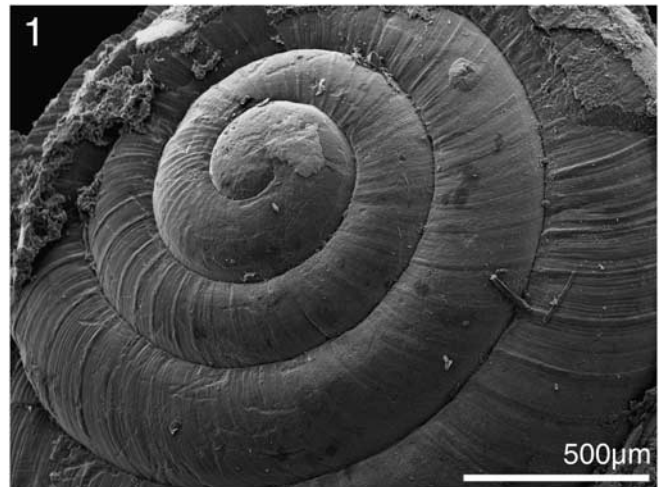
*Etymology.*—Feminine. Belonging to the Miocene.

*Examined material.*—MPM PI 3319: Holotype. MPM PI 3320: One Paratype (illustr.). MPM PI 3321–3335: Fifteen Paratypes.

*Geographical provenance.*—‘Puesto de la Estancia La Costa’ (=Corrighuen Aike;  $51^{\circ} 12' 8.2''$  S and  $69^{\circ} 03' 35.6''$  W), between the Coyle and Gallegos inlets.

*Stratigraphical provenance.*—Santa Cruz Formation, late Burdigalian/early Langhian, Early-Middle Miocene (between 18 and 15 Myr.). Fossiliferous Level 6 of Tauber (1997a), late Burdigalian, ~17.5 Myr. (Fleagle et al. 2012).

*Description.*—Shell discoidal of medium height, low helicoid, with 4.5 regular and convex whorls, suture deep; protoconch with 1.75 smooth whorls; teleoconch with very prominent, irregular axial ribs, approximately 50 on the first adult whorl,



**Figure 6.** *Zilchogyra miocenica* n. sp.: (1) MPM PI 3319, holotype, apical view; (2) MPM PI 3320, paratype, detail of umbilicus and protoconch; (3) MPM PI 3321, paratype, umbilical view. Scale bars represent 500  $\mu$ m (1, 3) and 100  $\mu$ m (2).

90 on last whorl, and delicate axial ribblets; umbilicus perspective (35% of major diameter), and aperture enlarged.

*Measurements.*—Holotype:  $2.5 \times 1.95$  mm, 4.5 whorls; Paratype:  $2.6 \times 2.5$  mm, 4.5 whorls.

*Comparative remarks.*—This species of Charopidae is assigned to *Zilchogyra* on the basis of the following conchological characters: shell discoidal, umbilicus perspective, regular convex whorls; nepionic whorls smooth; adult whorls with axial ribs and delicate ribbles and aperture enlarged (Miquel and Cádiz Lorca 2008). *Zilchogyra miocenica* n. sp. agrees with the type species, *Z. costellata* (Recent, living in Buenos Aires province), essentially by shell characters, but that species differs in size and sculpture, having a larger shell, with fewer axial ribs (52 to 60 in the last whorl) (Hylton Scott, 1964). *Z. matteriae* Hylton Scott 1972 (Recent, from Tierra del Fuego, Argentina) has a shell with a lower spire and a greater number of axial ribs (165 in the last whorl). *Patula michaelseni* Strebel 1907 (recent, from Chilean-Argentinean Patagonia) (possibly belonging to *Zilchogyra*, according to Hylton Scott, 1970), differs by the number of axial ribs (42 on the first teleconch whorl, 76 on the last whorl; Hylton Scott 1970). Fossils described from the Eocene at Gran Barranca (Chubut, Argentina) (Bellosi et al. 2002) are much larger (*Zilchogyra* sp. 1: 5.6 × 3.1 mm; *Zilchogyra* sp. 2: 5.3 × 2.7 mm), but they are too poorly preserved for detailed comparisons.

? *Punctoidea*  
? *Charopidae*

Genus *Patagocharopa* new genus

*Type species.*—*Patagocharopa enigmatica* n. sp., by monotypy.

*Diagnosis.*—Shell lenticular, with numerous semi-internal barriers, mostly in the periphery (angular, parietal, and basal walls) but others on the columellar area.

*Etymology.*—Feminine. Conjunction of the names ‘Patagonia’ and ‘Charopa,’ name of a typical genus for austral mollusks.

*Occurrence.*—Southern tip of America. Miocene.

*Description.*—Shell lenticular, very small, with both protoconch and teleoconch smooth; with numerous rounded semi-internal barriers: one angular, six parietal, one basal, three columellar, and one lamella and two additional teeth in the columellar wall.

*Remarks.*—Assignment of the new genus to *Punctoidea* and *Charopidae* is tentative, because of the fragmentary preservation of the only studied specimen. Internal or semi-internal barriers became visible due to the loss of the last part of the body whorl in the analyzed specimen (Fig. 7.1). Within *Punctoidea*, *Payenia* Rochebrune and Mabilie, 1891, and *Flammulina* Martens, 1873, have a smooth shell, ornamented with growth lines only, but both genera are different from *Patagocharopa* because they include larger species (5 and 6 mm, respectively), with less whorls (3.25 and 3 whorls), a very tight umbilicus, and lack apertural, semi-internal, or internal barriers. Only a few species of *Charopidae* (*Lilloiconcha* Weyrauch, 1965, and *Zilchogyra*) possess apertural and/or internal barriers, but they differ by their number and position within the shell (Weyrauch, 1965; Miquel et al. 2007; Miquel and Cádiz Lorca, 2008). This is the first time

that a specimen with the present features is described for South America.

*Patagocharopa enigmatica* new species  
Figure 7.1–7.3

*Diagnosis.*—Shell lenticular, with protoconch and teleoconch smooth, and with numerous rounded teeth, one angular, six parietal, one basal, three columellar and a lamella and two additional teeth in the columellar wall.

*Etymology.*—Feminine. Referring to its particular and amazing internal aperture structures (lamella and teeth).

*Examined material.*—MPM PI 3336: Holotype.

*Geographical provenance.*—‘Puesto de la Estancia La Costa’ (=Corrighuen Aike; 51° 12’ 8.2” S and 69° 03’ 35.6” W), between the Coyle and Gallegos Inlets.

*Stratigraphical provenance.*—Santa Cruz Formation, late Burdigalian/early Langhian, Early-Middle Miocene (between 18 and 15 Myr.). Fossiliferous Level 6 of Tauber (1997a), late Burdigalian, ~17.5 Myr (Fleagle et al. 2012).

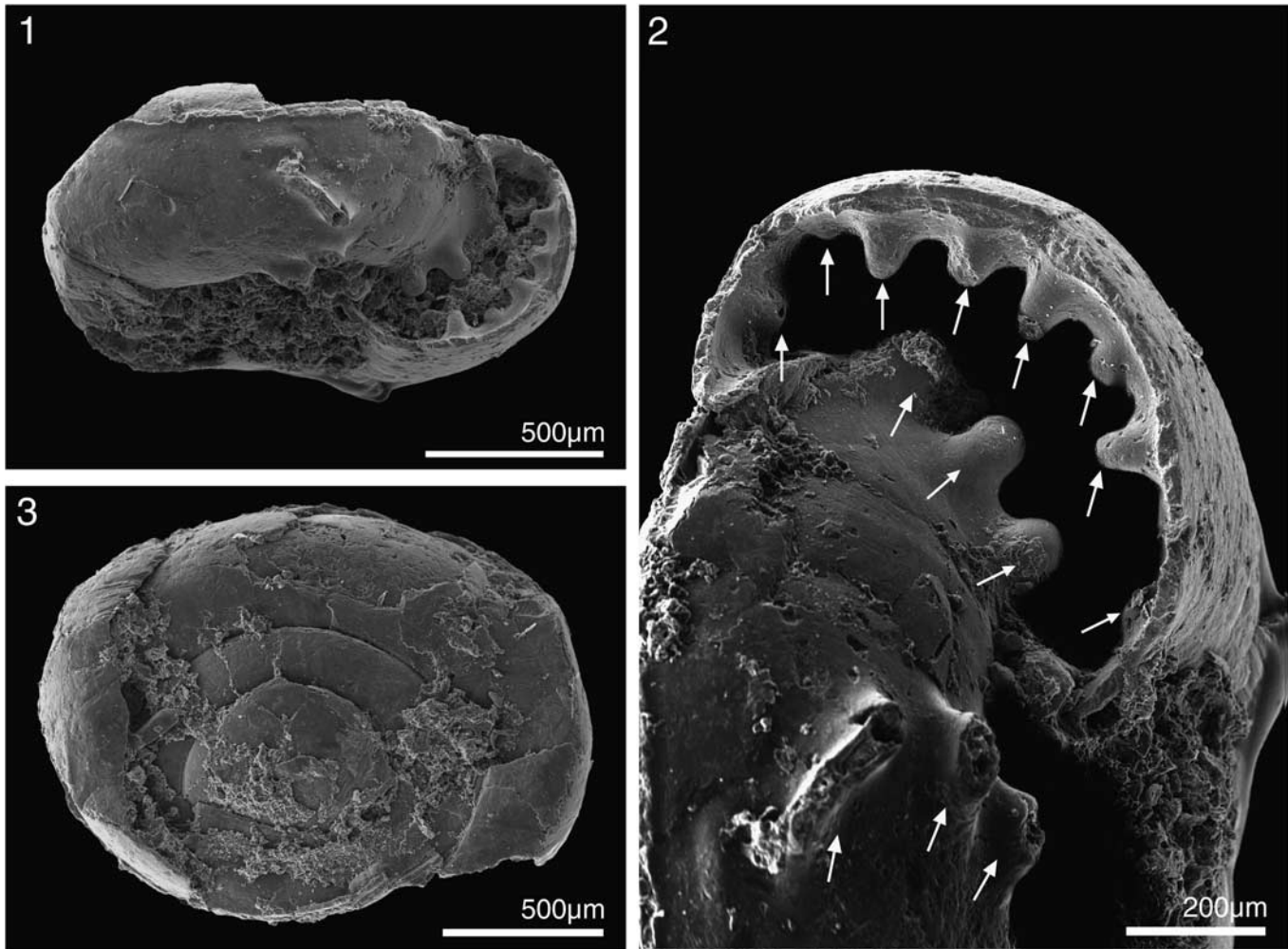
*Description.*—Fragment of shell lenticular, very small, with more than three whorls, with smooth protoconch and teleoconch; with numerous rounded semi-internal barriers—teeth and lamellae—on the inner surface of the whorl: one basal, six parietal and one angular lamellae, and on the columellar area lie an oblique lamella and two additional teeth; umbilicus covered by matrix.

*Measurements.*—Holotype: 1.6 × 0.7 mm, approx. four whorls.

## Discussion and paleoenvironmental interpretations

The examined specimens are very well preserved, retaining the shape, embryonic and adult whorls, and sculpture. In general terms, the fragmented shells seem to respond to taphonomic processes and can be attributed to sediment compaction; however, the fragmentary condition of the specimens can also be associated with our extraction procedures as evidence of abrasion and post-mortem transport is missing. The volcanic ashes containing the land snail fossil assemblage within Level 6 of the Santa Cruz Formation also contain vertebrate remains and coprolites, excellently preserved and showing concordant taphonomic signatures (Rodríguez P. E., unpublished data). Therefore, this land snail fossil assemblage can be attributed to demic, parautochthonous paleological entities and processes (Kidwell 1986), which preserved the shells and maintained them *in situ* (Fernández López, 1990: 75).

Geographic ranges of land snails are usually explained to a great extent by the prevailing relative environmental humidity. Other relevant factors such as atmospheric and soil temperature, leaf-litter depth, type of vegetation cover, and canopy closure affect the distribution of land snails. Extant representatives of the land snail families recognized in this fossil assemblage can



**Figure 7.** *Patagocharopa enigmatica* n. gen. n. sp.: (1–4) MPM PI 3336, holotype; (1) apertural view, arrows point the suture cicatrix; (2) detail of apertural teeth, arrows point the semi-internal barrier-teeth and lamellae; (3) apical view. Note: image (2) was digitally enhanced and modified to better visualize structures. Scale bars represent 500  $\mu\text{m}$  (1, 3) and 200  $\mu\text{m}$  (2).

be currently found in environments ranging from subtropical to cold, and from very humid to semiarid. The Vertiginids of the northern hemisphere inhabit a wide range of environments from coastal dunes, swamp forests or woody talus slopes of northern Europe and North America, to open deciduous forests, treeless marshlands, and wet meadows of warm lowland areas of central regions of the Holarctic continents (Vavrovà et al. 2009). However, some North American Vertiginidae are limited to xeric herbaceous-dominated prairies and shrublands (Nekola and Coles, 2001). In addition, South American records of *Gastrocopta nodosaria* occur in temperate and tropical regions of the country down to the northern area of Patagonia (Miquel and Aguirre, 2011). South American charopids are primarily mesic forest dwellers, but extend to dry and open scrublands of Andean-Patagonian forests in northwestern Patagonia (Miquel and Barker, 2009; Miquel and Bellosi, 2010). Punctidae species inhabit humus, and can be found on fallen leaves, under mesophytic bushes and trees (Pilsbry, 1948); particularly, in Juan Fernández Archipelago *Punctum* sp. dwells on the soil, among leaves and on ferns (Odhner, 1922). The species of Scolodontidae represent an important stock of the soil biota, mainly in

tropical rain forests, but they also can be found in dry forests, and a few in grasslands, being carnivorous (Ramírez, 1993). Thus, the families represented in the Santa Cruz Formation are not particularly informative about the paleoenvironmental conditions prevailing in the area during the Miocene, if the biology of the individual species is not considered.

The fossil site is located, phytogeographically, in the Patagonian Province (Cabrera, 1971), and zoogeographically it is located within the Patagonian Domain of the Andean-Patagonian Subregion (Ringuélet, 1961). Currently, the extensive xerophytic plateau of the Patagonian territory offers only few areas for the survival of land snails because of the dry and cold climate, with snowy winters, and strong winds and frosts during the whole year. This is reflected in the records of land snails from the region where collections mostly come from the mountain ranges and very few from the Patagonian plateau *sensu stricto* (Hylton Scott, 1963, 1968). The modern fauna is predominantly that of micromollusks of the family Charopidae with a much lower representation by species of Succineidae, Bulimulidae, Scolodontidae, Vertiginidae, and Macrocyclidae (Fernández, 1973).

To account for paleoenvironmental conditions prevailing in the area inhabited by the present fossil assemblage, a brief overview of the paleoclimatic progression and paleoenvironmental evolution that occurred throughout the Early Miocene is required.

According to Compagnucci (2011) changes in land surface represent one of the processes that affect climate in time scales from millions to hundreds of thousands of years, and the climatic conditions in the region of Patagonia were strongly affected by the uplift of the Andes. The Andean orogeny is the final consequence of the Andean structural cycle that developed throughout the past ~190 Myr (Early Jurassic to present), which results from the subduction of the eastern plates of the Pacific Ocean (Farallon and Nazca) and the Antarctic plate under Gondwanan basement (South American plate) at the west margin of South America (Armijo et al., 2015). As part of this Andean cycle, the uplift of the southern Patagonian Andes (approximately between 17 and 14 Myr) formed a large topographic barrier to atmospheric circulation in the Southern Hemisphere Westerlies and established a pronounced orographic rain shadow; such a barrier led to a strong aridification in the eastern foreland and increased precipitation rates on the windward western side of the mountains during the Miocene in Patagonia (Blisniuk et al., 2006, cited in Compagnucci, 2011).

Besides, ice had begun accumulating at the South Pole during the Late Eocene (approximately between 37.2 and 33.8 Myr) culminating in the Pleistocene ice age. Oligocene cooling occurred together with changes in continental distribution, plateau uplift and opening of oceanic gateways (Drake Passage and Tasmanian Gateway), implying the late Eocene establishment of the Antarctic Circumpolar Current and development of the Polar Frontal Zone, reducing poleward ocean heat transport and favoring glaciation over Antarctica. The Late Miocene Tortonian period (approximately between 11 and 7 Myr) was characterized by intensive Antarctic glaciations and the beginning of glaciations in the North Atlantic region (Compagnucci, 2011).

The Andes orogen interplayed with an increasingly drying climate driven by the global Cenozoic cooling, resulting in pronounced alterations of the paleoclimate conditions over Patagonia (Armijo et al., 2015). During the Miocene paleoclimate settings along southern Patagonia were fluctuating, but showed an overall downward trend in temperature and upward trend in aridity (Blisniuk et al., 2005, 2006; Kay et al. 2012a). Animal and plant communities changed according to these oscillations. Toward the end of the Paleogene and the beginning of the Neogene (Late Oligocene–Early Miocene) warm climates allowed the development of rainforest elements in the flora of extra-Andean Patagonia, with dominance of gallery forests to the east and a subtle emergence of xerophytic assemblages in coastal salt environments and pockets of inland areas. Even though drier conditions would have prevailed in lowland areas during the late Early Miocene (Late Aquitanian), the latest Early Miocene (Burdigalian) was characterized by a predominance of aquatic herbs and hydrophyte vegetation (Palazzesi et al., 2003; Barreda and Palazzesi, 2007, 2010), suggesting plentiful water availability.

Moreover, Palazzesi et al. (2003) suggested that the inferred paleofloristics is consistent with the paleovertebrate record,

as deduced from the work of Patterson and Pascual (1972) and Pascual et al. (2002), who highlighted that the greatest diversification of hypsodont-grazer mammals in Patagonia occurred during the Oligocene and Early Miocene; this supports a paleoenvironmental change toward an increasing predominance of grassy vegetation. Several works on fossil vertebrates have assessed the paleoenvironmental shift that occurred in southern Patagonia throughout the Miocene. Among others, these studies addressed a diverse group of mammals including arboreal porcupines (Echimyidae, Erethizontidae), microbiotheres similar to the extant “monito del monte” (Microbiotheriidae), and new world primates (Platyrrhini), all of which have been regarded as indicators of warm and humid climates and of forest environments (Pascual and Ortiz-Jaureguizar, 1990; Tauber, 1997b, 1999; Vizcaíno et al. 2006; Kay et al., 2012b). Patterson and Pascual (1972) and Pascual et al. (2002). In this regard, Tauber (1997b) also described a relative increase in the percentage of organisms with euhypsodont dentition—which are considered specialized grazers—against organisms with brachydont and brachydont-mesodont dentition toward the upper levels of Santa Cruz Formation. In addition, a general decrease in taxonomic and body size diversity of small-sized mammals and increasing taxonomic diversity and size of other mammals like glyptodonts and toxodonts was found. Overall, this points to a climate turnover throughout the Miocene from warm, moist, stable conditions to drier conditions with marked seasonality, and a shift from environments with predominant tree or shrubby vegetation to environments more open with predominantly grassy vegetation. Similar inferences resulting from analysis based on the diversity of the Santacrucian armadillos by Vizcaíno et al. (2006) reinforced the climate-turnover hypothesis.

In addition, analyses of sedimentological, paleopedological, and geomorphological evidence (Tauber, 1994, 1996), support the aforementioned Miocene paleoenvironment progression. Immature and mature paleosols, the latter with a high degree of animal and plant bioturbation, have been found in the lower beds of the Santa Cruz Formation, suggesting humid and stable environmental conditions; while toward the upper levels occurrence of evaporite crystals, geomorphological structures (interpreted as desiccation cracks) and inferred seasonal variations in rivers paleo-flux, indicate increasing seasonality and a drying trend.

However, paleoclimatic approximations based on analyses of community structure (cenograms), which allowed to infer variables such as rainfall and vegetation structure (Croft 2001), showed a less marked shift in paleoenvironmental conditions suggesting a slightly greater rainfall in the upper levels of Santa Cruz Formation that described in previous studies.

Following Kay et al. (2012a), the Early Miocene (17.4–17.5 Myr) Santacrucian-age fauna thrived in a mosaic of open temperate humid and semi-arid forests, with paleoclimatic reconstructions indicating annual rainfalls greater than 1000 mm and a mean annual temperature above 14°C in a period characterized by wet winters and dry summers, and a marked seasonality in the length of daylight. In addition to the presence of lakes, seasonal flooding led to the formation of marshlands dominated by herbaceous (both grass and forb) vegetation. To this extent, various elements of the vertebrate associations of the Santa Cruz Formation, other than mammals, suggest a mosaic of

closed canopy forest and open habitats during the late Early Miocene. Several studies have assessed groups of vertebrates such as frogs (Calyptocephalellidae and Leptodactylidae), teiids (*Tupinambis* sp.), colubrids, and iguanids, whose presence suggests warm and humid environmental conditions and the occurrence of permanent lowland lakes and quiet streams in forested areas (Fericola and Albino 2012). Other records such as birds like the falconid *Thegornis* (Noriega et al., 2011), and aquatic birds such as waterfowl, limpkins, spoonbills, and darters, indicated the presence of seasonally flooded open areas or permanent water bodies in more forested areas, whereas phorusrhacids and seriemids may have required open habitats because of their cursorial mode of locomotion (DeGrange et al., 2012).

Subsequently, the Late Miocene vegetation became similar to the modern pattern, with an expansion of steppe throughout extra-Andean Patagonia and withdrawal of forests to western areas where rainfall was still abundant (Barreda and Palazzesi, 2007).

Even though some degree of aridity occurred throughout the Early Miocene, paleoenvironmental conditions shifted into a more humid context toward the latest Early Miocene (Burdigalian), when Neotropical floral elements become predominant again (Barreda and Palazzesi, 2007, 2010). The environment during this time slice, known as the mid-Miocene Climatic Optimum (MMOC, 17 to 15 Myr; Zachos et al., 2001), can confidently be taken to be that which prevailed when the snail-bearing layer was deposited. According to Fleagle et al. (2012), this brief geological period can also be reliably correlated with warm-humid tropical conditions. Thus, the wide range of suitable habitat types suggested by the land snail paleocommunities, as indicated by the terrestrial molluscan taxa of our study, support and reinforce the pre-Late Miocene warm and humid tropical paleoenvironmental and paleoclimate settings proposed previously worldwide and for Patagonia.

In summary, the studied land snail assemblage includes the following specimens and their related current habitats: (a) *Gastrocopta patagonica* n. sp. (Vertiginidae), oldest record of the genus for Argentina and the southernmost record for South America, inhabits temperate and tropical regions; (b) *Scolodonta* sp. (Scolodontidae), inhabits from tropical rain forests, to dry forests and grasslands; (c) *Punctum patagonicum* n. sp. (Punctidae), first mention of the genus for continental South America, inhabits ferns, under mesophytic bushes and trees; (d) *Zilchogyra miocenica* n. sp. (Charopidae), first record of the genus from Miocene, inhabits tropical areas of South America from mesic forests to dry and open scrublands; and (e) *Patagocharopa enigmatica* n. gen and sp. (?Charopidae), first record for South America.

The studied assemblage comprises taxa in part typical of austral regions such as the punctoidean genera *Zilchogyra*, and *Punctum* (previously known in South America only from extant specimens recorded in Juan Fernández Archipelago), together with the much more widely distributed *Gastrocopta*. *Patagocharopa enigmatica* has no clear affinities to any fossil or recent South American continental molluscan faunas.

Being this the first record of this type of assemblage for South America, and considering the high significance of land and fresh-water snails for paleoenvironmental reconstructions (Rousseau et al., 1994; Rousseau and Puisségur, 1999; Rousseau and Wu, 1999; Del Río et al., 2007; Miquel and

Belosi, 2010), it is of major importance to emphasize the great potential of further studies of terrestrial mollusks from Patagonia to reveal other interesting elements of the assemblages and to enhance our full understanding of the Austral Miocene paleoenvironmental evolution.

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