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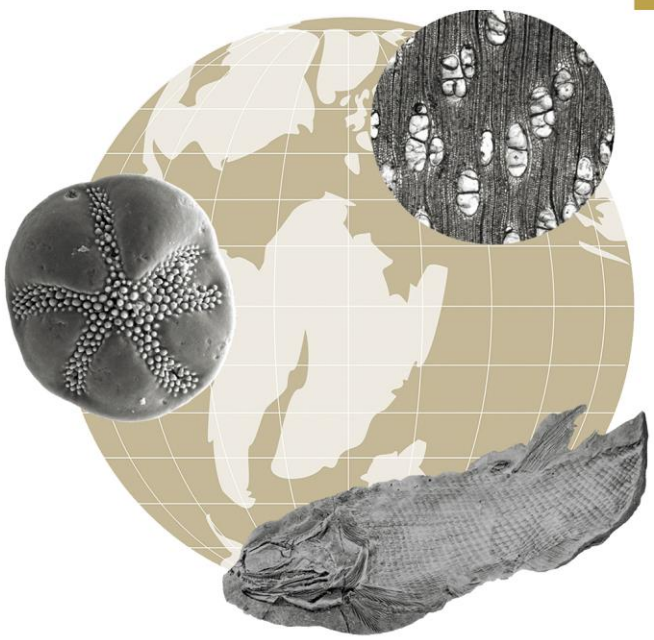

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FOSSIL GASTROPODS FROM RELICTIC PLEISTOCENE PALUSTRINE DEPOSITS OF TIOPUNCO, SANTA MARIA VALLEY, TUCUMÁN, ARGENTINA

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López-Isla et al.: Pleistocene gastropods, Santa María Valley.

This study refines the taxonomic composition of the Quaternary fossil assemblage from the Tiopunco area, based on stratigraphic sampling and updated conchological analyses.

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Abstract. This study documents a Pleistocene fossil gastropod assemblage from the Tiopunco area, Santa María Valley, Tucumán Province, northwestern Argentina. Fossil material was recovered from two discrete fossiliferous levels within the Divisadero Chico profile, developed in fine-grained palustrine deposits that rest unconformably on the Andalhuala Formation. The assemblage includes freshwater, amphibious and terrestrial gastropods, associated with scarce vertebrate remains represented by micromammals and possible birds. A detailed taxonomic revision refines previously reported identifications and allows recognition of *Galba viator*, *Biomphalaria* sp., *Radiodiscus* sp. aff. *R. compactus*, *Succinea* sp., *Scolodonta semperi*, and *Rotadiscus amancaezensis*, the latter two recorded for the first time at this locality. Gastropod shells are commonly preserved as complete or nearly complete specimens, with differential fragmentation related to shell size and thickness. Sedimentological and taphonomic evidence, including the absence of abrasion, the presence of in situ root structures, and pedogenic features, indicates low-energy depositional conditions and relatively rapid burial. Overall, the Tiopunco assemblage represents an autochthonous to parautochthonous record formed in shallow palustrine environments with episodic subaerial exposure, contributing new and chronologically constrained data to the Quaternary paleontological record of intermontane Andean valleys.

KEY WORDS. Fossil gastropods. Pleistocene. Santa María Valley. Northwestern Argentina

Resumen. GASTERÓPODOS FÓSILES DE DEPÓSITOS RELÍCTICOS PALUSTRES DEL PLEISTOCENO DE TIOPUNCO, VALLE DE SANTA MARÍA, TUCUMÁN, ARGENTINA. Este estudio documenta un conjunto fósil de gasterópodos del Pleistoceno procedente del área de Tiopunco, Valle de Santa María, provincia de Tucumán, noroeste de Argentina. El material fósil fue recuperado de dos niveles fosilíferos discretos dentro del perfil Divisadero Chico, desarrollados en depósitos palustres de grano fino que apoyan en discordancia sobre la Formación Andalhuala. El conjunto incluye gasterópodos de agua dulce,

anfibios y terrestres, asociados con escasos restos de vertebrados representados por micromamíferos y posibles aves.Una revisión taxonómica detallada permitió refinar las identificaciones previamente reportadas y reconocer *Galba viator*, *Biomphalaria* sp., *Radiodiscus* sp. aff. *R. compactus*, *Succinea* sp., *Scolodonta semperi* y *Rotadiscus amancaezensis*, siendo estas dos últimas registradas por primera vez en esta localidad. Las conchas de gasterópodos se preservan comúnmente como ejemplares completos o casi completos, con una fragmentación diferencial relacionada con el tamaño y el espesor de las conchas. La evidencia sedimentológica y tafonómica, incluyendo la ausencia de abrasión, la presencia de estructuras radiculares in situ y rasgos pedogenéticos, indica condiciones depositacionales de baja energía y un enterramiento relativamente rápido. En conjunto, el registro de Tiopunco representa una asociación autóctona a parautóctona formada en ambientes palustres someros con exposición subaérea episódica, aportando nuevos y cronológicamente bien restringidos datos al registro paleontológico cuaternario de los valles intermontanos andinos.

PALABRAS CLAVE. Gasterópodos fósiles. Pleistoceno. Valle de Santa María. Noroeste de Argentina.

INTRODUCTION

Due to their ubiquity in Quaternary intermontane paleoenvironmental settings, including fluvial, lacustrine, glaciolacustrine, and palustrine systems, molluscs constitute pivotal proxies for paleoecological reconstructions and biostratigraphic correlations. They are also widely used in studies addressing morphological variation and taxonomic diversity in response to environmental change. Within molluscs, gastropods represent a particularly informative group owing to their ecological sensitivity, high abundance, and good preservation potential in continental intermontane basins (De Francesco & Hassan, 2009; Neubauer, 2024).

The paleontological material analyzed in this study comes from a relict Pleistocene deposit located in the Tiopunco area, Santa María Valley, Tucumán Province, Argentina. Stratigraphically, the fossiliferous horizons are situated at the base of the deposit informally referred to as Divisadero Chico, where two distinct fossil-bearing levels have been identified. Previous reports from the study area documented the presence of *Biomphalaria* sp., *Lymnaea viatrix* (= *Galba viator*), *Succinea* aff. *S. meridionalis*, and *Radiodiscus* sp. aff. *R. compactus* (Gavriloff et al., 2017; López Isla, 2017; López Isla et al., 2018). These fossiliferous levels also yielded remains of scarce micromammals, including small rodent elements tentatively referred to the subfamily Sigmodontinae, possible avian remains, and a gastropod assemblage. Together, these findings represent one of the most significant Pleistocene paleontological records documented to date for this sector of the Santa María Valley.

The fossiliferous succession rests unconformably on the Andalhuala Formation and is predominantly composed of siltstone to sandy siltstone deposits. It reaches an approximate thickness of 5 m and displays well-developed pedogenic features, including abundant root traces, as well as planar to gently inclined stratification (López Isla, 2017).

Lithologically, the succession consists of interbedded massive siltstones and sandy siltstones arranged in decimeter-thick levels, together with very fine-grained sandstones locally

containing granules, organized into centimeter- to decimeter-scale packages. These deposits have been interpreted as a succession of palustrine and edaphic levels (López Isla, 2017), conditions particularly favorable for the preservation of fossil remains. The Divisadero Chico succession is constrained to the middle–late Pleistocene based on U–Th zircon dating (254 +150/–88 ka, 2σ; López-Isla et al., in press).

Quaternary lacustrine and palustrine deposits in the central region of the Calchaquí Valleys have been reported by several authors (Frenguelli, 1936; Vilela & García, 1978; Gallardo, 1996). During the Pleistocene, these valleys were predominantly characterized by arid climatic conditions, punctuated by wetter episodes associated with changes in precipitation regimes. These fluctuations favored the development of temporary water bodies and the accumulation of fine-grained sediments in topographically depressed sectors of the valley (Wayne, 1999; Bookhagen et al., 2001; Trauth & Strecker, 1999, Trauth et al., 2003; Alonso et al., 2006). Although previous paleontological studies established the presence of a diverse malacofauna in the Divisadero Chico succession, taxonomic resolution remained limited by sample size and preservation.

The present study builds upon these previous works by integrating detailed stratigraphic control with expanded sampling and updated conchological analyses, allowing a refined assessment of the taxonomic composition of the Quaternary gastropod assemblage from Tiopunco.

Institutional abbreviations. CIME. Integral Center of Electron Microscopy, San Miguel de Tucumán, Tucumán, Argentina. **IPI.** Instituto de Paleontología de Invertebrados, Fundación Miguel Lillo (FML), San Miguel de Tucumán, Tucumán, Argentina.

Anatomical abbreviations. ad, apertural diameter; ah, apertural height; Bwh, body whorl height; H, total shell height; Md, major diameter of the shell; md, minor diameter; sh, spire height.

MATERIAL AND METHODS

Study area

The Tiopunco sedimentary section is located in the eastern piedmont of the Santa María Valley, northwestern Argentina, approximately 12 km north of the town of Amaicha del Valle and 7 km east of the Río Santa María (Fig. 1). The area forms part of the northern sector of the Santa María Valley, an elongated intermontane depression characterized by Neogene continental sedimentation and later Quaternary reworking (Bossi & Palma, 1982; Bossi et al., 2001).

The Neogene stratigraphic record in the Tiopunco area is dominated by continental deposits of the Santa María Group, which include coarse- to fine-grained fluvial, alluvial, and lacustrine sediments accumulated during the Late Miocene–Early Pliocene (Georgieff, 1998; Bossi et al., 2001). These deposits record a progressive transition from proximal alluvial and fluvial environments to more distal fluvial–lacustrine settings, reflecting long-term variations in sediment supply and accommodation within the valley.

In the Tiopunco sector, the Neogene succession comprises, from base to top, the Las Arcas, Chiquimil, and Andalhuala formations (Bossi et al., 2001; Spagnuolo et al., 2015). These units are unconformably overlain by Pleistocene deposits, including fluvial, alluvial, lacustrine, and palustrine sediments. Near the Quebrada del Medio, ~9 m of palustrine deposits rest on the Neogene succession across a well-defined angular unconformity at the Divisadero Largo and Divisadero Chico outcrops, both located at approximately 1,850 m a.s.l. (Fig. 1A-B) (López Isla, 2017; López Isla et al., 2018). A simplified 5.4-m-thick stratigraphic section was logged at Divisadero Chico to provide basic sedimentological context (Fig. 1C). These palustrine levels constitute the focus of the present study.

Material

Fossil material was recovered from Divisadero Chico, where two distinct fossiliferous levels were identified at 80–200 cm and 280–380 cm above the base of the logged section. Gastropod shells occur in both levels, whereas micromammal remains, including identifiable rodent elements, and possible bird remains were recorded only in the upper level, the latter inferred from their hollow structure and morphology. Fossils are embedded within fine-grained sandy siltstones affected by pedogenetic processes and characterized by abundant root traces and calcrete features, which favored their preservation. Shell preservation ranges from complete to fragmented specimens, with no evidence of abrasion or preferred orientation. The confinement of fossils to these two stratigraphic horizons indicates discrete fossil-bearing intervals, reflecting specific environmental conditions suitable for both the life and burial of these organisms.

All recovered fossil gastropods are housed in the Invertebrate Paleontology Collection of the Fundación Miguel Lillo (FML), Instituto de Paleontología de Invertebrados (IPI), Tucumán, Argentina, under the following catalog numbers: FML-IPI 4815 (*Succinea* sp.; 97 individual shells and 4 shell fragments); FML-IPI 4816 (*Galba viator*; 2 specimens)); FML-IPI 4817 (*Radiodiscus* sp. aff. *R. compactus*; 7 specimens); FML-IPI 4818 (*Rotadiscus amancaezensis*; 9 specimens); FML-IPI 4819 (*Scolodonta semperi*; 4 specimens); and FML-IPI 4820 (*Biomphalaria* sp.).

GASTROPODS: Taxonomic Study

Seven standard gastropod shell measurements were taken using the ImageJ software (Schneider et al., 2012). The shell axis (columella) was aligned with the X-axis of the coordinate system, and the maximum shell breadth was measured in dorsal (plane) view. The selected measurements were: major diameter of the shell (Md); minor diameter (md); total shell height (H); body whorl height (HBw); spire height (sh); shell aperture height (ah); and shell aperture

diameter (ad) (Fig. 2). Measurements were obtained from a selected subset of adult and well-preserved specimens suitable for reliable measurement, excluding juvenile, incomplete, or strongly fragmented shells. The measured subset included 16 specimens: two specimens of *Galba viator* species complex, five of *Biomphalaria* sp., five of *Succinea* sp., one of *Scolodonta semperi*, one of *Rotadiscus amancaezensis*, and two adult specimens of *Radiodiscus* sp. aff. *R. compactus*. Juvenile and fragmented specimens were considered for qualitative taxonomic and taphonomic observations when informative. Measurements were used to support shell descriptions rather than to perform a formal statistical morphometric analysis Maxima, minima, mean, and standard deviation were for were reported for each measurements, all expressed in millimeters (mm). The counting of shell whorls followed the methodology described by Kerney & Cameron (1979). In some specimens, protoconch and teleoconch sculpture were examined and photographed with a JEOL JSM-35CF scanning electron microscope at the Centro de Microscopía Electrónica (CIME, San Miguel de Tucumán, Tucumán, Argentina).

RESULTS

TAXONOMIC DESCRIPTION OF FOSSIL GASTROPODS

Class Gastropoda Cuvier, 1795

Subclass Heterobranchia Burmeister, 1837

Infraclass Euthyneura Spengel, 1881

Superorder Hygrophila Férussac, 1822

Superfamily Lymnaeoidea Rafinesque, 1815

Family Lymnaeidae Rafinesque, 1815

Subfamily Lymnaeinae Rafinesque, 1815

Genus *Galba* Schrank, 1803

***Galba viator* (d'Orbigny, 1835)**

Type: *Buccinum truncatulum* Müller, 1774 accepted as *Galba truncatula* (Müller, 1774) (type by subsequent designation)

(Figures 3 A-B)

Lymnoeus viator d'Orbigny, 1835: 24

Galba viator—Lounnas et al., 2017: 65.

Type locality: oris Patagonensibus (*ventricosa*). provincia Limacensi (Republica Peruviana) (*elongata*).

Shell description. Shell dextral, small, thin, and ovate, consisting of four to five and a half convex whorls. It is uniformly pale brown, with a smooth protoconch and a high spire occupying about one third of the total shell length. The apex is obtuse, and the whorls increase regularly in diameter. The body whorl is convex, and the teleoconch exhibits shallow, oblique axial ribs. The suture is simple and deep. The aperture is elongated-ovate and tall, measuring about half the total shell length. The parietal space is wide, and the peristome is simple and sharp, with a slightly reflected palatal border. The shell is rimate.

Shell measurements (mm): H: 6.750-6.857 (6.80, 0.08); Bwh: 5.230-5.310 (5.27, 0.06); sh: 1.590-1.690 (1.64, 0.07); Md: 4.170-4.410 (4.29-0.17); ah: 3.490-3.550 (3.52-0.04); ad: 2.400-2.420 (2.41, 0.01).

Ecological requirements: Members of this family inhabit a diverse range of aquatic environments, including both flowing (lotic) and still (lentic) waters. Their habitats vary widely, from small, temporary ponds to large lakes. These snails are commonly found in unpolluted waters rich in calcium, typically with minimal current, low turbulence, muddy substrates, and abundant aquatic vegetation (Castellanos & Landoni, 1981; Cuezzo, 2009). *Galba viator* is an amphibious snail (it breathes atmospheric air) that prefers clean, still waters with silt and aquatic vegetation. Some populations inhabit lentic environments, such as shallow

waters and groundwater-fed springs emerging at the surface within palustrine wetlands. These snails can be found attached to rocks, aquatic vegetation, or floating on the water's surface. They thrive in waters with temperatures ranging from 13 to 23°C, preferring temperate conditions and slightly acidic pH values near neutrality. The snail can survive in shallow, slow-moving waters and can even tolerate dry periods by burying itself in sediment and secreting a mucous substance that closes the aperture (Landoni, 1992; De Francesco et al., 2007; Tomassi et al., 2019).

Remarks: According to Alda et al. (2021), under evolutionary concepts, *Galba viator* species complex included to *G. viator* d'Orbigny, 1835, *G. cubensis* (Pfeiffer, 1839) and *G. neotropica* (Bargues, Artigas, Mera y Sierra, Pointier & Mas-Coma, 2007). Because these species may show overlapping shell morphologies, the Tiopunco material is retained as *G. viator* on conchological grounds, but its paleoecological interpretation is framed within the broader *G. viator* species complex.

Family Planorbidae Rafinesque, 1815

Subfamily Planorbinae Rafinesque, 1815

Genus *Biomphalaria* Preston, 1910

Type species: *Biomphalaria smithi* Preston, 1910 (type by original designation)

***Biomphalaria* sp.**

(Figures 3 C-E)

Shell description. Shell planispiral, medium-sized, with five convex whorls that increase progressively in diameter, the last whorl being the largest. The shell is uniformly pale brown and glossy. The basal side is concave, with the initial whorls sunken; the apical side is flattened. The body whorl is convex and larger in both height and diameter than the preceding whorls.

The teleoconch presents fine radial growth striae. The suture is simple and deep, particularly on the apical side. The aperture is subrounded, and the peristome is simple and not expanded.

Shell measurements (mm): Bwh: 2.054-3.709 (2.69, 0.89); Md: 6.883-13.343 (9.22, 3.58); md: 6.180-11.744 (8.21, 3.07); ah: 2.728-5.43 (3.68, 1.52); ad: 1.896-3.380 (2.45, 0.81).

Ecological requirements: Planorbids are common freshwater snails found in both flowing (lotic) and still (lentic) water bodies. These snails inhabit a wide range of environments, including flooded areas, permanent lagoons, streams, rivers, drainage channels, marshes, and swamps. While they are typically found attached to aquatic vegetation or on the bottom substrate, they can also be seen moving freely in the water column (Pointier, 2008; Cuezzo, 2009; Ovando & Marchi, 2021).

Remarks. The Tiopunco specimens are assigned to *Biomphalaria* sp. because they show the typical planispiral shell morphology of Planorbidae, with convex whorls, a concave basal side, and a simple, non-expanded peristome. Species-level identification is avoided because diagnostic characters are insufficiently preserved and because several species of *Biomphalaria* show overlapping shell morphologies.

Superorder Eupulmonata Haszprunar & Huber, 1990

Order Stylommatophora Schmidt, 1855

Suborder Helicina Schileyko, 1979

Superfamily Succineoidea Beck, 1837

Family Succineidae Beck, 1837

Subfamily Succineinae Beck, 1837

Genus *Succinea* Draparnaud, 1801

Type species: *Helix putris* Linnaeus, 1758

***Succinea* sp.**

(Figures 3 F-H)

Shell description Shell dextral, elongate-oblong (higher than wide), composed of 3 ½ convex whorls. It is uniformly yellowish-white, with a smooth protoconch, short spire, and a tall, convex body whorl representing approximately three quarters of the total shell height. The teleoconch exhibits shallow axial ribs, and the suture is relatively deep. The aperture is large, oblong (taller than wide), occupying about two thirds of the shell height, with a simple, sharp, and thin peristome. The umbilicus is closed and sealed by a parietal callus.

Shell measurements (mm): H: 6.66-7.91 (7.37, 0.48); Bwh: 5.69-6.68 (6.37-0.37); sh: 0.90-1.31 (1.06, 0.19); Md: 4.09-4.94 (4.54, 0.29); ah: 3.90-4.83 (4.48-0.34); ad: 2.65-3.31 (3.04, 0.25).

Ecological requirements: *Succinea* is a genus of small, herbivorous, terrestrial snails. They exhibit a strong affinity for humid environments, particularly those associated with freshwater bodies. They are commonly found on riverbanks and streambeds, among marsh vegetation, in rain-flooded soils, under rocks at the margins of lotic and lentic water bodies, and even in brackish environments such as coastal marshes. Other *Succinea* species inhabit more strictly terrestrial areas, such as under shrubs, in leaf litter of shaded and humid areas, and on stream banks. Although *Succinea* is primarily associated with aquatic environments, its ecological distribution is broad, ranging from highly humid habitats to drier terrestrial zones (De Francesco et al., 2007; Miquel & Aguirre, 2011).

Remarks. Species-level assignment is avoided because shell characters alone are insufficient to distinguish several species of *Succinea*, particularly in fossil material lacking anatomical or molecular data. The Tiopunco specimens are therefore conservatively assigned to *Succinea* sp.

Suborder Scolodontina Hausdorf & Bouchet, 2017

Superfamily Scolodontoidea Baker, 1925

Family Scolodontidae Baker, 1925

Subfamily Scolodontinae Baker, 1925

Genus *Scolodonta* Döring, 1875

Type species: *Streptaxis (Scolodonta) semperi* Doering, 1875

***Scolodonta semperi* (("1874" [1875b]))**

(Figures 4 A-C)

Streptaxis (Scolodonta) semperi Doering, ("1874" [1875b]): 439

Scolodonta semperi Hylton Scott, 1948: 209

Scolodonta semperi Aguirre et al., 2011:13

Type locality: "Sierra de Córdoba, Río Primero valley; in the forests of Jesús María, among and beneath decomposing leaves; … near Villa Vicencio, Sierra de Mendoza" (("1874" [1875b])).

Shell description. Dextral, small, discoidal, and thin, comprising 3 1⁄2 to 4 1⁄2 slightly convex whorls. It is homogeneously whitish and glossy, with a smooth protoconch and a short spire. The body whorl is rounded and tall, accounting for approximately 90% of the total shell height. The teleoconch bears oblique growth striae, and the suture is simple and slightly deep. The aperture is semicircular, with a simple, sharp peristome. The umbilicus is wide and perspective, occupying about 30% of the shell's major diameter.

Shell measurements (mm): H: 1.209; Bwh: 1.112; sh: 0.094; Md: 2.051; md: 1.758; ah: 0.826; ad: 0.474.

Ecological requirements: *Scolodonta semperi* is a species of land snail, typically found in ground cover and shady locations. It exhibits carnivorous feeding habits. Species within the Scolodontidae family constitute a significant component of soil biota, especially in tropical rainforests. They are often encountered under decaying leaves and rotten logs in shady areas, but can also be found in dry forests and, less commonly, in grasslands (Aguirre et al., 2011;

Miquel & Aguirre, 2011). According to Miranda & Cuezzo (2010) and Miranda et al. (2022), it is very abundant in the Yungas rainforest.

Suborder Helicina Schileyko, 1979

Superfamily Punctoidea Morse, 1864

Family Charopidae Hutton, 1884

Genus *Rotadiscus* Pilsbry, 1926

Type species: *Helix hermanni* Pfeiffer, 1866.

***Rotadiscus amancaezensis* (Hidalgo, 1869)**

(Figures 4 D-F)

Helix amancaezensis Hidalgo, 1869: 411; —Hidalgo, 1870: 38; —Fischer-Piette, 1950: 74.

Rotadiscus amancaezensis— Miquel et al., 2004: 927.

Type locality: Amancaes, near the city of Lima, Republic of Peru (Paz) (Hidalgo, 1869).

Shell description. Shell dextral, small, discoidal, and thin, consisting of 5 to 5 1⁄2 slightly convex whorls. It is uniformly pale brown, with a smooth protoconch and a very low, slightly raised spire. The body whorl is rounded and tall, representing approximately 95% of the total shell height. The teleoconch displays well-marked oblique ribs, regularly spaced, with shallow secondary ribs in between. The suture is simple and slightly deep. The aperture is semicircular, with a simple, sharp peristome. The umbilicus is wide and perspective, occupying about 40–45% of the shell's major diameter.

Shell measurements (mm): H: 1.066; Bwh: 0.886; sh: 0.126; Md: 1.539; md: 1.503; ah: 0.874; ad: 0.461.

Ecological requirements: *R. amancaezensis* is a land snail that inhabits humus, leaf litter, and among small roots, in relatively humid and shaded areas under shrubs. It is primarily found in damp vegetated habitats rich in fungi, fallen leaves, and detritus, which serve as both its food

source and shelter (De Francesco et al., 2007; Miquel & Aguirre, 2011). It is a very abundant species in the Yungas rainforest (Miranda & Cuezzo, 2010; Miranda et al., 2022).

Subfamily Rotadiscinae Baker, 1927

Genus *Radiodiscus* Pilsbry, 1906

Type species: *Radiodiscus millecostatus* Pilsbry & Ferriss, 1906 (type by original designation)

***Radiodiscus* sp. aff. *R. compactus* (Suter, 1900)**

(Figures 4 G-I)

Pyramidula patagonica compacta— Suter, 1900: 334.

Radiodiscus compactus (Suter, 1900) -- Miquel, et al., 2007: 212

Type locality: Brazil, Rio Grande do Sul state (Salvador, 2020).

Shell description. Shell dextral, small, discoidal, and thin, consisting of 3 1⁄2 to 4 convex whorls. It is uniformly pale brown. The protoconch bears approximately 16 thin, shallow radial ribs. The spire is low, and the body whorl is tall, rounded, and slightly descending toward the aperture. The teleoconch displays well-defined axial ribs, with closely spaced axial microribs in between, intersected by fine spiral grooves. The suture is deep. The aperture is semicircular, and the peristome is simple and sharp. The umbilicus is wide and perspective, occupying about 25% of the shell's major diameter.

Shell measurements (adult specimen)**:** H: 0.775; Bwh: 0.61; sh: 0.078; Md: 1.753-2.3; md: 1.578-2.04; ah: 0.688; ad: 0.543.

Ecological requirements: *Radiodiscus* is a land snail, inhabits humus, leaf litter, and among small roots, in relatively humid environments. This species was cited by Miquel et al. (2007) for river ravines, among scrubland and in humid forests. Other authors are mentioned for the Lower Montane Forest of the Yungas ecoregion (Miranda & Cuezzo, 2010; Miranda et al.,

2022).

Remarks. The Tiopunco material is referred to *Radiodiscus* sp. aff. *R. compactus* because it shows closer conchological resemblance to *R. compactus* than to other *Radiodiscus* species recorded from Argentina. Among the regionally relevant taxa, *R. amoenus* and *R. golbachi* were considered the most appropriate for comparison based on available occurrence records and published descriptions. The original descriptions of these species were reviewed, together with comparative material of extant *R. amoenus*. The Tiopunco specimens differ from *R. amoenus* by their larger shell, lower spire, fewer whorls, and wide, perspective umbilicus. They also differ from *R. golbachi* by their smaller shell, lower spire, and wider umbilicus. The available optical and SEM images allow comparison of protoconch and teleoconch sculpture, which are relevant characters in this genus. However, because the available material is limited and includes nine juveniles and only one adult specimen, the identification is maintained at affinity level.

FOSSIL VERTEBRATES

The material consists of dark brown, highly fragmented elements isolated through picking under a stereomicroscope. Most fragments correspond to a very small rodent, including cranial and postcranial bones. Among the identifiable elements are a partially preserved incisor and a section of a radius (Fig. 5A–F). The morphology and dimensions of the incisor suggest an attribution to the subfamily Sigmodontinae, possibly Calomys or Eligmodontia, although specific identification remains uncertain.

In addition, a few long, hollow, and fragile bones (Fig. 5A–F) may correspond to a bird, based on their thin cortex and pneumatic internal structure. However, given the limited number of elements and the absence of diagnostic features, this attribution remains tentative.

DISCUSSION

The fossil record of Tiopunco comprises six freshwater, amphibious, and terrestrial gastropod taxa belonging to five families that are still extant today. The gastropod assemblages documented at Tiopunco provide new, stratigraphically constrained data on the Pleistocene malacofauna of the Santa María Valley, northwestern Argentina, and enable direct comparison with other well-documented Quaternary assemblages from the region.

Previous studies have demonstrated that mixed assemblages of freshwater, amphibious, and terrestrial gastropods are not uncommon in late Pleistocene palustrine and marginal lacustrine settings, particularly where low-energy depositional conditions favor the preservation of small and fragile shells (De Francesco et al., 2020). In the Andean piedmont of Mendoza, De Francesco et al. (2007) described a late Pleistocene gastropod assemblage from the La Bomba section (Arroyo La Estacada, Tunuyán River basin), dated between ca. 35,000 and 31,000 yr BP. This assemblage includes *Galba viator* and *Biomphalaria peregrina* as dominant freshwater and amphibious taxa, associated with terrestrial gastropods such as *Succinea meridionalis*, *Rotadiscus amancaezensis*, and *Radiodiscus* sp. aff. *R. quillajicola*. A similar taxonomic composition was later discussed by De Francesco & Hassan (2009), who emphasized the dominance of *G. viator* and *Biomphalaria* in specific stratigraphic levels and interpreted these associations as indicative of shallow, vegetated water bodies surrounded by humid terrestrial habitats.

The Tiopunco assemblage closely resembles these Mendoza records in the coexistence of freshwater (*Galba viator*, here discussed within the *Galba viator* species complex sensu Alda et al. (2021),, *Biomphalaria* sp.), amphibious (*Succinea* sp.), and terrestrial taxa (*Rotadiscus amancaezensis*, *Radiodiscus* sp. aff. *R. compactus*). This taxonomic treatment is adopted because Alda et al. (2021) showed that several *Galba* species with elongated shells, including *G. viator*, *G. cubensis*, and *G. neotropica*, form part of a cryptic group in which shell

morphology alone is insufficient for reliable species-level delimitation. Therefore, although the Tiopunco material is retained as *G. viator* on conchological grounds, its paleoecological interpretation is framed within the broader *G. viator* species complex. Although the *Radiodiscus* material from Tiopunco is referred to as R. sp. aff. *R. compactus*, whereas Mendoza records are commonly assigned to *R.* sp. aff. *quillajicola*, both cases highlight the recurrent presence of microdiscoidal charopids in Pleistocene palustrine and marginal lacustrine deposits of western Argentina. These differences at the species-affinity level likely reflect regional biogeographic variation and/or unresolved taxonomic issues related to shell miniaturization and morphological convergence.

The terrestrial gastropod *Scolodonta semperi*, absent from the La Bomba assemblage, is nevertheless well documented in the Argentine Pleistocene. Miquel & Aguirre (2011) reported this species from several localities spanning the Bonaerense and Lujanense, including Miramar (Buenos Aires Province), Santa María (Córdoba Province), Tafí Viejo (Tucumán Province), and late Pleistocene deposits of Mendoza. Its presence at Tiopunco therefore fits well within the known Quaternary distribution of the species and represents an additional record from an intermontane valley of northwestern Argentina.

The genus *Succinea* deserves particular attention, as it provides a direct regional link between the Tiopunco assemblage and previous Pleistocene records from Tucumán. *Succinea* sp. has been documented from Pleistocene deposits at Tafí Viejo (Cuezzo, 1990; Miquel & Aguirre, 2011), while *Succinea meridionalis* shows a continuous fossil record from the Ensenadense through the Holocene in several regions of Argentina. The occurrence of *Succinea* at Tiopunco reinforces the interpretation of persistent humid microhabitats associated with water bodies in the Santa María Valley during the Pleistocene.

Beyond taxonomic composition and regional comparisons, the taphonomic characteristics of the Tiopunco assemblage provide additional constraints on its depositional setting and post-

depositional history. Gastropod shells are preserved within yellowish-gray sandy siltstone levels displaying parallel to slightly inclined stratification and are closely associated with carbonate nodules, rhizoconcretions, and in situ root traces. Robust shells, including those of *Succinea* sp., *Galba viator* species complex, and *Biomphalaria* sp., are commonly preserved as complete or nearly complete specimens, retaining diagnostic morphological features such as protoconch sculpture and aperture shape. However, in the case of *Galba*, these conchological features support assignment to *G. viator* but do not resolve species-level limits within the *G. viator* species complex In contrast, smaller and thinner shells assigned to *Radiodiscus* sp., *Rotadiscus amancaezensis*, and *Scolodonta semperi* exhibit a higher degree of fragmentation, reflecting differential resistance to post-depositional processes such as mechanical compaction, trampling at the sediment–water interface, and early diagenetic alteration.

The absence of abrasion, reworking, or sedimentary evidence of significant transport, together with the close association of the assemblage with pedogenetic features and root structures, supports an autochthonous to parautochthonous origin. These attributes are consistent with accumulation under low-energy depositional conditions in shallow palustrine environments, characterized by fluctuating water tables, episodic subaerial exposure, and sustained substrate saturation.

In addition to gastropods, the same fossiliferous levels yielded scarce micromammal remains, including isolated incisor teeth and fragmented bones tentatively attributed to Sigmodontinae. Although their low abundance precludes a detailed taxonomic or paleoecological analysis, their occurrence is compatible with the inferred marginal lacustrine to palustrine setting, although their low abundance and fragmentary preservation preclude detailed palaeocological interpretation and highlights the potential of the Tiopunco deposits as a starting point for future studies focused on Quaternary fossil micromammals.

Overall, the Tiopunco gastropod assemblage integrates elements previously documented in both the Andean piedmont of Mendoza and northwestern Argentina, but within a stratigraphically well-defined palustrine context. This record expands the geographic coverage of Pleistocene gastropod assemblages in Argentina and underscores the importance of intermontane valleys as archives of Quaternary biodiversity, complementing the better-known lowland and piedmont records.

CONCLUSION

This study documents a Pleistocene fossil gastropod assemblage from the Tiopunco area, Santa María Valley, northwestern Argentina, recovered from two discrete fossiliferous levels within the Divisadero Chico profile. U–Th zircon data constrain the succession to the middle–late Pleistocene, providing a robust chronological framework for the assemblage.

Conchological analyses allowed the identification of *Galba viator*, *Biomphalaria* sp., *Radiodiscus* sp. aff. *R. compactus*, *Succinea* sp., *Scolodonta semperi*, and *Rotadiscus amancaezensis*, with *Scolodonta semperi* and *Rotadiscus amancaezensis* recorded for the first time at Tiopunco. These records refine the Quaternary paleobiogeographic distribution of gastropod taxa in northwestern Argentina and improve the characterization of the local malacofauna.

The taxonomic composition, preservation patterns, and stratigraphic context of the assemblage are consistent with low-energy palustrine to marginal freshwater environments and primarily reflect local paleoenvironmental conditions. Overall, the Tiopunco assemblage represents a well-preserved and chronologically constrained contribution to the Quaternary gastropod record of intermontane Andean valleys, highlighting their significance as archives of regional biodiversity during the Pleistocene.

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FIGURE CAPTIONS

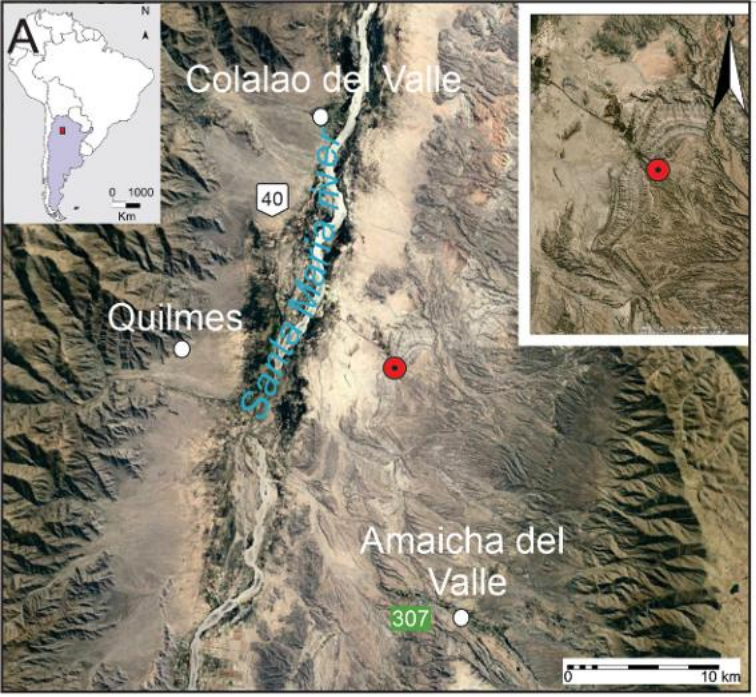
Figure 1. Location of the Tiopunco study area and stratigraphic context of the Pleistocene palustrine deposits (Santa María Valley, northwestern Argentina). A, Regional view of the Santa María Valley showing the location of the Tiopunco area and main access routes. B, Satellite image of the study area, indicating the palustrine outcrop (red box) and the fossil-bearing sector with the position of the logged section (red star) (scale bar: 150 m). C, Simplified stratigraphic log of the Divisadero Chico section, showing lithologies, sedimentary structures, and fossil-bearing levels.

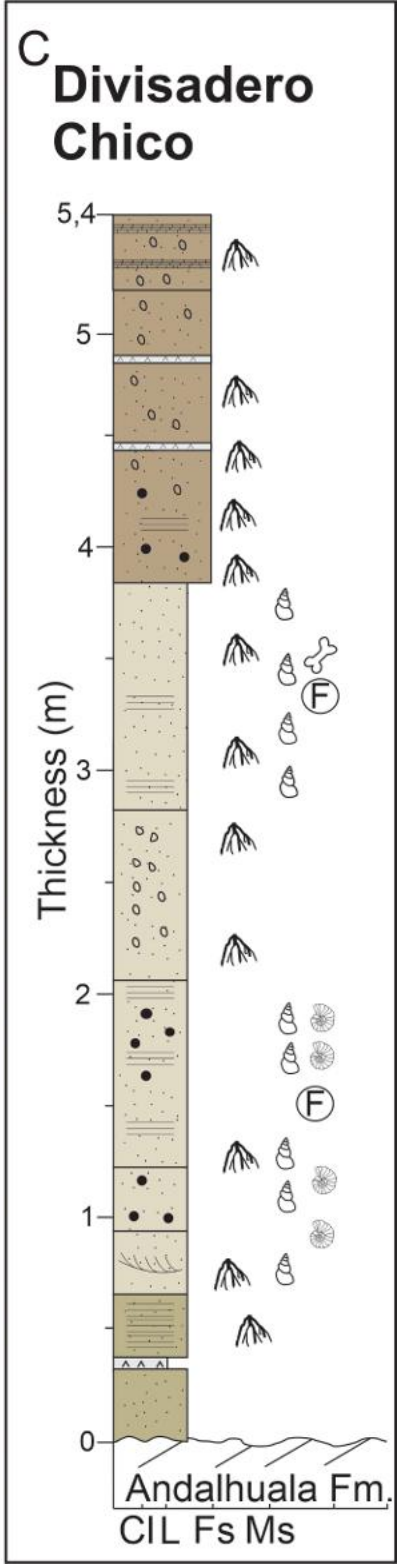
Figure 2. Linear measurements used for morphometric analysis: major shell diameter (Md), minor diameter (md), total shell height (H), body whorl height (HBw), spire height (sh), aperture height (ah), and aperture diameter (ad).

Figure 3. Gastropod assemblage from Tiopunco. A-B, Shell of *Galba viator* (d'Orbigny, 1835), discussed within the *G. viator* species complex sensu Alda et al. (2021). A, ventral view; B, lateral view; C-E, Shell of *Biomphalaria* sp., C, basal view; D, apical view; E, apertural view F-H; Shell of *Succinea* sp., F, shell in ventral view; G, lateral view; H, dorsal view, D-E, F-H, Scale bars: 3 mm.

Figure 4. Gastropod assemblage from Tiopunco. A-C, Shell of *Scolodonta semperi* (("1874" [1875b])), A, dorsal view; B, ventral view; C, detail of smooth protoconch; D-F, Shell of *Rotadiscus amancaezensis* (Hidalgo, 1869), D, apertural view; E, ventral view; F, dorsal view, detail of protoconch without sculpture, G-I, Shell of *Radiodiscus* sp. aff. *R. compactus* (Suter, 1900) (SEM images), G, apertural view showing prominent radial costulae; H, ventral view close-up of the central umbilical region highlighting the incremental costulae; I, dorsal view, detail of protoconch sculpture. Scale bars: A-B, D-E, 1 mm; G-H, 100 μm; I, 20 μm

Figure 5. SEM images of vertebrate microfossils from the upper fossiliferous level of Tiopunco. A–D, Cranial and postcranial remains of a small rodent. A, Partial incisor; B–C, Shaft fragments of long bones, one with preserved epiphyseal region; D, Complete rod-like bone interpreted as a radius; E–F, Hollow, fragile bone fragments tentatively attributed to a bird, based on their thin cortex and internal pneumatic structure.





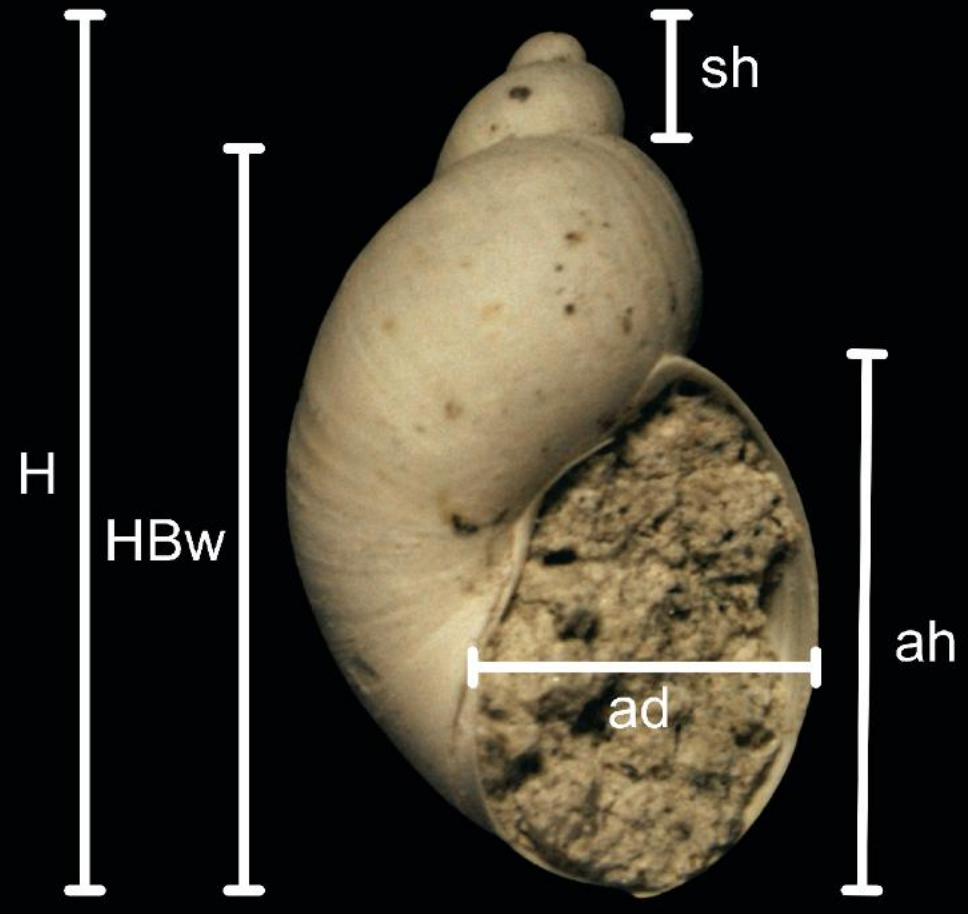
References

- Tiopunco area
- Divisadero Chico
- National Route 40
- 307 Provincial Route 307

Legend

Cl-Clay
L-Silt
Fs-Fine sand
Ms-Medium sand

- Parallel lamination
- Cross lamination
- Roots
- Calcretes
- Fossil gastropods
- Granules
- Ⓕ Fossil sample
- Tuffaceous level
- Vertebrate remains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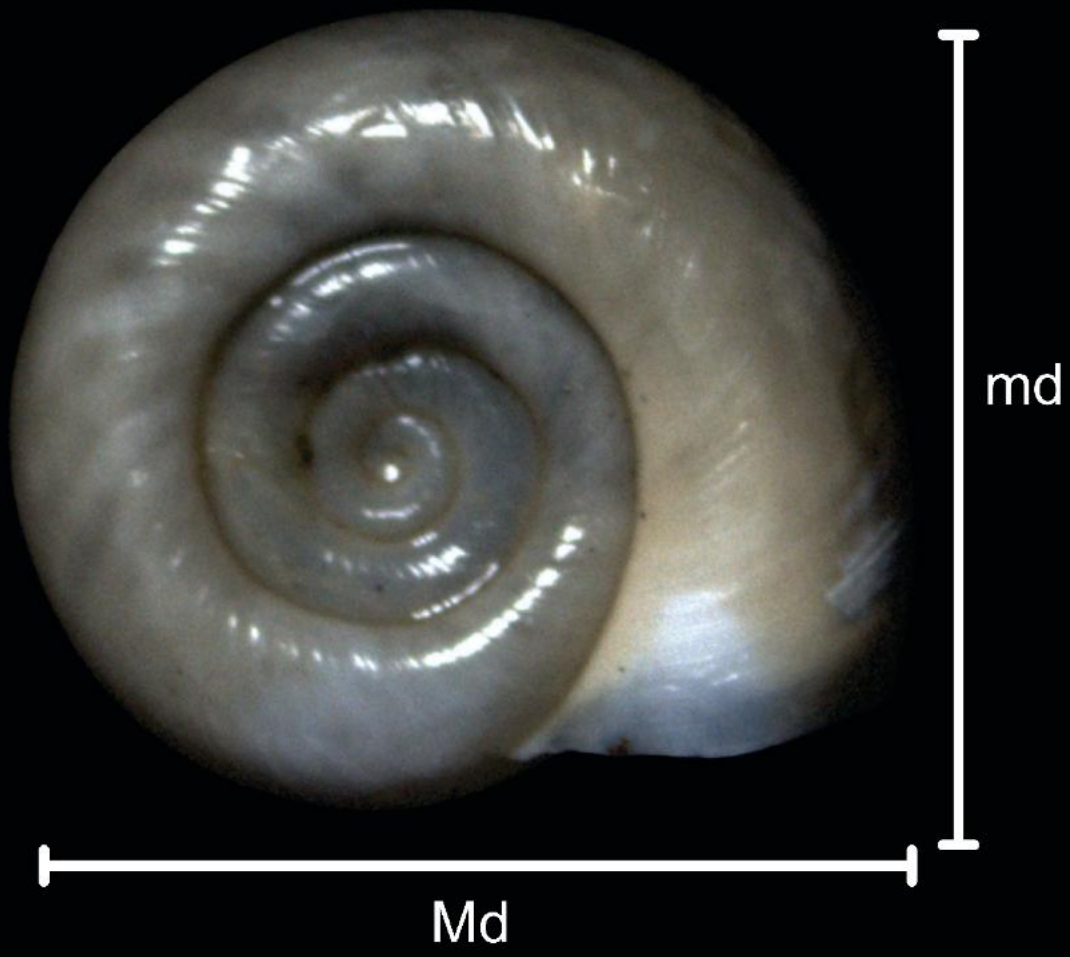
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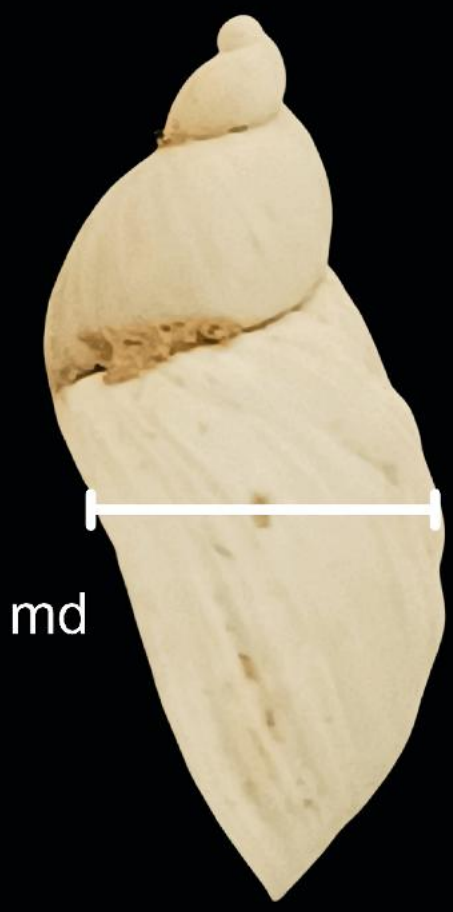
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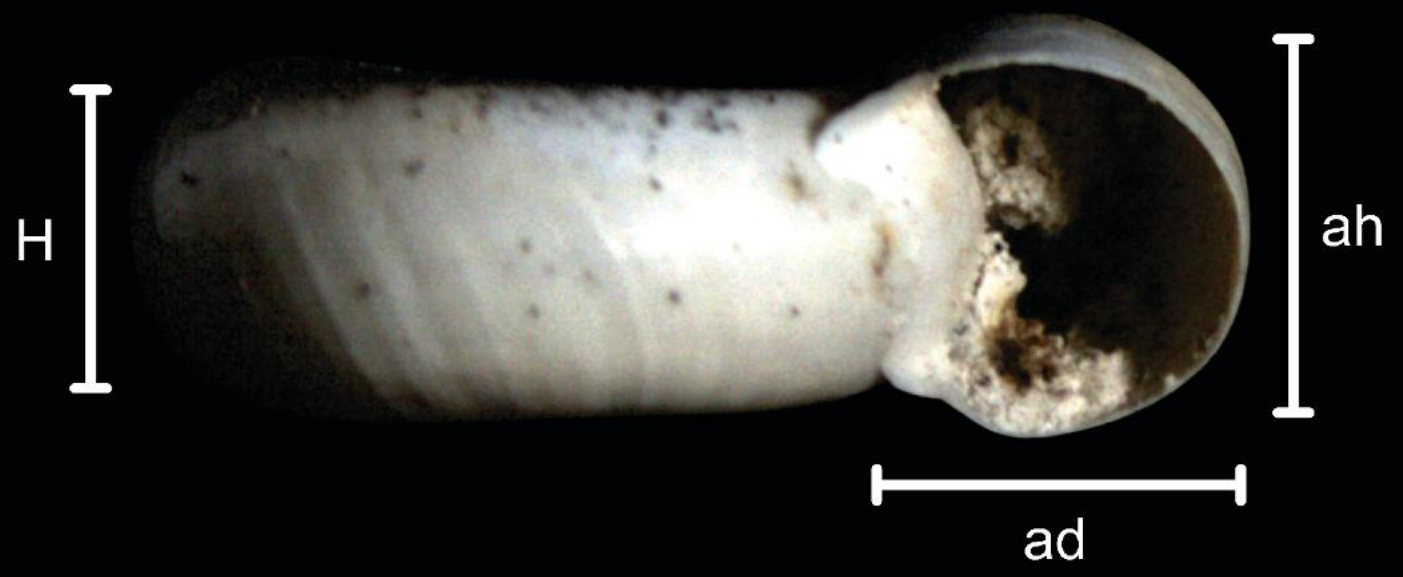
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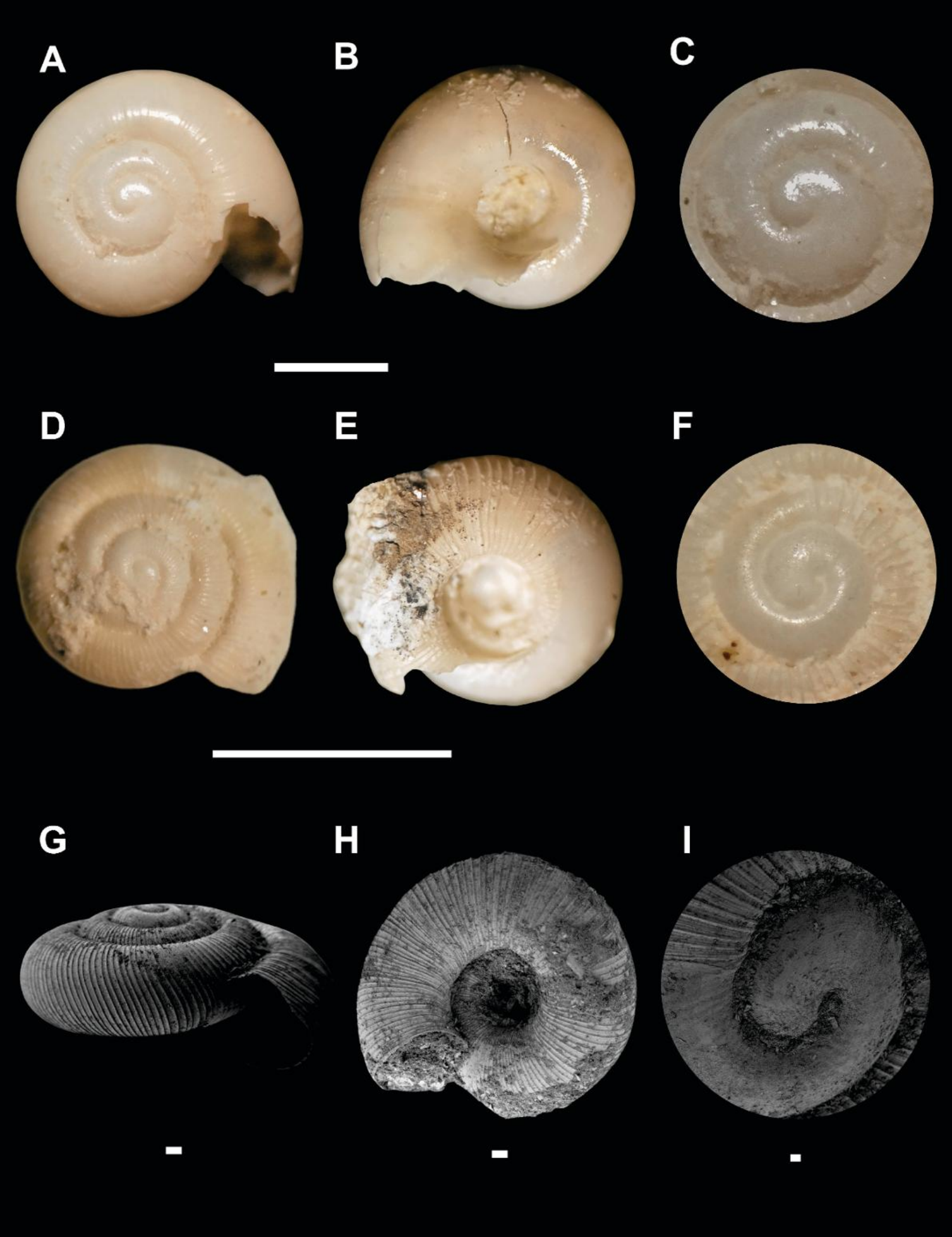
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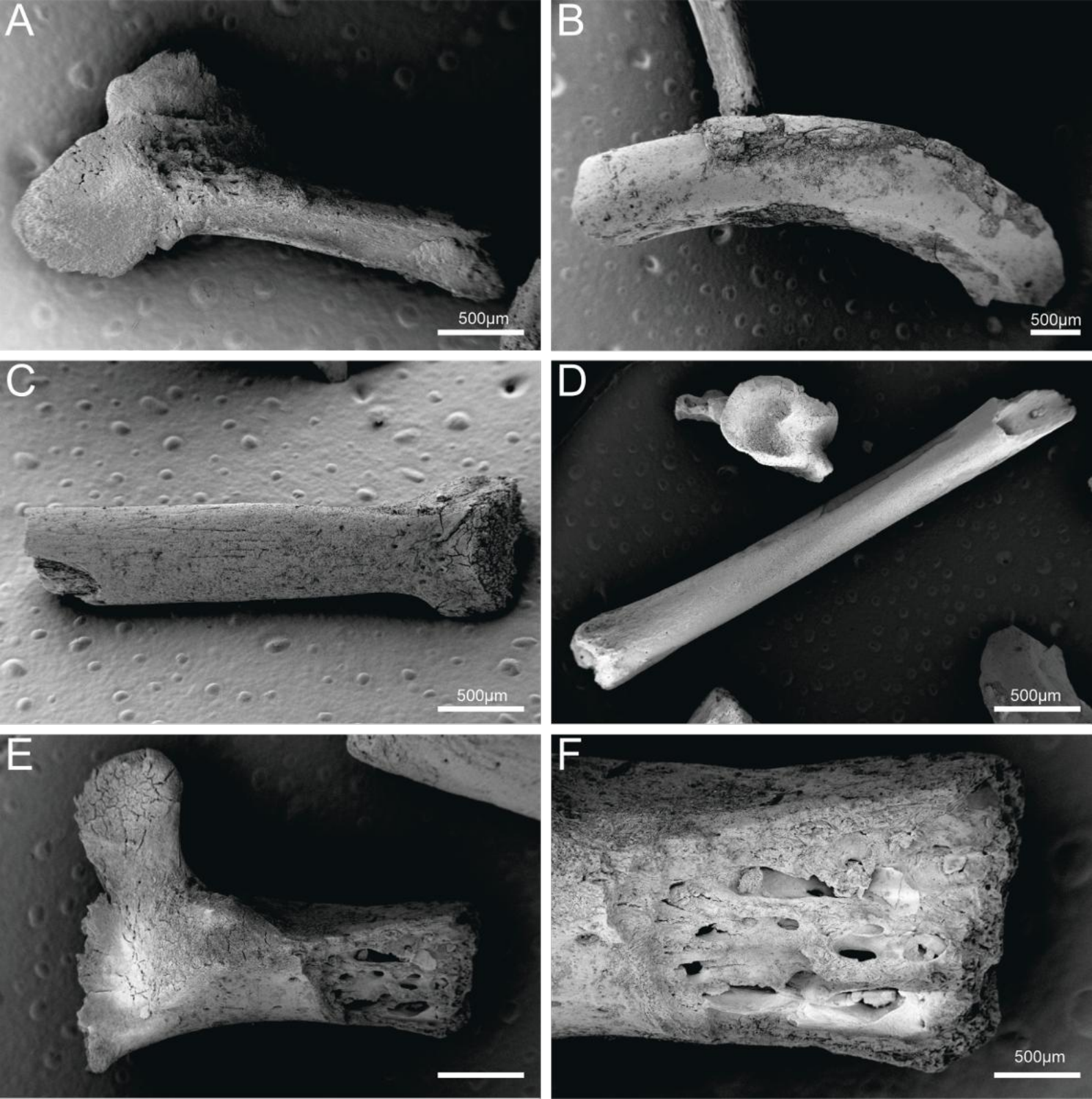
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