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DÉBORA SABINA D'AMBROSIO[1]
ADRIANA GARCÍA[2]

1. Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Centro Científico Tecnológico-Consejo Nacional de Investigaciones Científicas y Técnicas (CCT-CONICET), Mendoza, Argentina.
2. School of Science, Faculty of Science, Medicine and Health (SMAH), University of Wollongong (UOW), New South Wales, Australia.

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Asociación Paleontológica Argentina
Maipú 645 1° piso, C1006ACG, Buenos Aires
República Argentina
Tel/Fax (54-11) 4326-7563
Web: www.apaleontologica.org.ar

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QUATERNARY *LIMNOCYTHERE* (LIMNOCYTHERIDAE) FROM ARGENTINA, SOUTH AMERICA: SPECIES DIVERSITY AND APPLICATION TO PALEOENVIRONMENTAL/BIOGEOGRAPHICAL RECONSTRUCTIONS

DÉBORA SABINA D'AMBROSIO[1], AND ADRIANA GARCÍA[2]

[1]Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Centro Científico Tecnológico-Consejo Nacional de Investigaciones Científicas y Técnicas (CCT-CONICET), Mendoza, Argentina. *sdambrosio@mendoza-conicet.gob.ar*

[2]School of Science, Faculty of Science, Medicine and Health (SMAH), University of Wollongong (UOW), New South Wales, Australia. *adrigarcia@outlook.com.au*

DSD: https://orcid.org/0000-0001-9446-1470; **AG:** https://orcid.org/0009-0005-3060-4731

Abstract. Non-marine ostracods are environmental proxies widely used in Quaternary environmental and climatic reconstructions. In South America (Neotropical Region), extant Limnocytheridae is the third most diverse family, with *Limnocythere* species typically inhabiting hyposaline to mesosaline waters. The South American Transitional Zone (SATZ), is defined across South America by arid-semiarid climate, holding the Argentinean section five endemic *Limnocythere* species, representing highest diversity of *Limnocythere* and the speciation role of this transitional area. This study analyses the diversity, paleoecological traits and distribution of Quaternary Argentinean *Limnocythere,* describing *Limnocythere perseverans* sp. nov. from Laguna Llancanelo basin, Salina del Bebedero and Laguna Runtuyoc (Argentinean SATZ), providing a dichotomous key for the 13 Quaternary species found in Argentina. The new species differs from *L. cusminskyae* (Neotropical Region, humid Chaco-Pampean) and *L. staplini* (Nearctic Region), in valve morphology (valve shape and hinge structure) and ecological requirements. *Limnocythere perseverans* sp. nov. prefers sodium-chloride, sulfate or chloride-sulfate waters, segregated from *L. cusminskyae* living in sodium, bicarbonate-rich waters, and *L. staplini* found in bicarbonate-depleted waters. These differences highlight its value to reconstruct changes in salinity and water chemistry. The morphological similarities among these three species open questions on biogeographical aspects of aquatic ecology. Further research is necessary to assess whether these species evolved from a shared ancestor or are an example of morphological convergence derived by the adaptation to similar ecological pressures within the Neotropical and Nearctic regions.

Key words. Non-marine ostracods. Paleosalinity. Paleohydrology. Saline lakes. Arid-semiarid diagonal. South American Transition Zone.

Resumen. *LIMNOCYTHERE* CUATERNARIOS (LIMNOCYTHERIDAE) DE ARGENTINA, AMÉRICA DEL SUR: DIVERSIDAD ESPECÍFICA Y APLICACIÓN PARA RECONSTRUCCIONES PALEOAMBIENTALES/BIOGEOGRÁFICAS. Los ostrácodos no-marinos son indicadores utilizados en reconstrucciones ambientales y climáticas del Cuaternario. En América del Sur (Región Neotropical), los Limnocytheridae actuales constituyen la tercera familia más diversa, con especies de *Limnocythere* que habitan aguas hiposalinas a mesosalinas. La Zona de Transición Sudamericana (ZTSA) definida a lo largo de América del Sur por un clima árido-semiárido, alberga en su sector argentino cinco especies endémicas de *Limnocythere*, representando la mayor diversidad del género y evidenciando el rol de especiación de esta zona. Este estudio analiza la diversidad, rasgos paleoecológicos y distribución del género *Limnocythere* del Cuaternario de Argentina, describiendo *Limnocythere perseverans* sp. nov. encontrada en Laguna Llancanelo, Salina del Bebedero y Laguna Runtuyoc (ZTSA Argentina), proporcionando una clave dicotómica para 13 especies cuaternarias registradas en Argentina. La nueva especie se diferencia de *Limnocythere cusminskyae* (Región Neotropical, Chaco-Pampeano húmedo) y *Limnocythere staplini* (Región Neártica) en la morfología de las valvas (contorno y estructura de la charnela) y en los requisitos ecológicos. *Limnocythere perseverans* sp. nov. prefiere aguas cloruradas-sódicas, sulfatadas o cloruradas-sulfatadas, diferenciándose de *L. cusminskyae*, que habita aguas ricas en sodio y bicarbonato, y *L. staplini* encontrada en aguas pobres en bicarbonatos. Estas diferencias resaltan su valor para reconstruir cambios en la salinidad y química del agua. Las similitudes morfológicas entre estas tres especies plantean interrogantes biogeográficos en ecología acuática. Futuras investigaciones permitirán evaluar si estas especies evolucionaron a partir de un ancestro común o si representan convergencia morfológica, producto de adaptaciones a presiones ecológicas similares en las Regiones Neotropical y Neártica.

Palabras clave. Ostrácodos no marinos. Paleosalinidad. Paleohidrología. Lagos salinos. Diagonal árida- semiárida. Zona de Transición Sudamericana.

INTRODUCTION

Ostracods (Class Ostracoda, Ordovician–Recent) are small aquatic crustaceans, with the non-marine lineage starting in the Carboniferous (360–299 Ma). Their soft body is protected by an external carapace formed by two valves dorsally articulated, composed of low-Mg calcite, which is the only part available for the study of fossil ostracods (taxonomy, paleoecology, biostratigraphy and paleoenvironmental reconstructions). The hinge, muscle patterns, ornamentation and overall shape of the valves are genetically dependent, are very valuable to differentiate ostracod genera and species (Sylvester-Bradley, 1956; Benson et al., 1961; Gutentag & Benson, 1962).

Limnocytheridae (Jurassic–Recent) is a non-marine family within the mostly marine lineage Cytheroidea (Ordovician–Recent), with *Limnocythere* (Jurassic–Recent) being the most diversified genus. Regarding extant taxa, Limnocytheridae is the third most diverse family of ostracods in South America (de Oliveira da Conceição et al., 2020).

Species of *Limnocythere* live in saline non-marine, coastal or inland permanent and ephemeral aquatic environments, in salinities ranging from hyposaline to mesosaline. *Limnocythere* species' preference of different water chemistry, makes them a tool as proxies for Quaternary hydrological reconstructions. Earlier studies from the Nearctic Region by Forester (1983, 1985) and Forester et al. (2005) demonstrated that *Limnocythere* species are adapted to waters with different, in some cases contrasting ionic composition, specifically *L. staplini* Gutentag and Benson, 1962, *L. sappaensis* Staplin, 1963, and *L. ceriotuberosa* Delorme, 1971. Equivalent results were found for *Limnocythere* species living in southern South America (Neotropical Region), such as *L. patagonica* Cusminsky and Whatley, 1996, and *L. rionegroensis* Cusminsky and Whatley, 1996, from Patagonia, and *L. cusminskyae* Ramón-Mercau et al., 2014, from the Chaco-Pampean area, described by Ramón-Mercau et al. (2014) and Pérez et al. (2025).

Biogeographic studies undertaken in the 1980s in Argentina, based on vegetation species' distribution and climate, defined an arid-semiarid belt named Arid Diagonal (AD), which extends from western Perú to western Argentina, along the N-S basin of Río Desaguadero-Salado, continuing towards the East along the Río Colorado basin up to the Atlantic Ocean (Bruniard, 1982). This AD is superimposed to the larger South American Transitional Zone (SATZ), Neotropic Region, defined by Morrone (2006), that extends north up to the high Andes of western Venezuela (Fig. 1). Previous studies on Argentinian Quaternary and extant non-marine ostracods, foraminifers and charophytes from the AD (González et al., 1981; García, 1999), identified this area as a transitional ecotone, or in the case of D'Ambrosio et al. (2024), as part of a larger Arid Basin. In this paper we used the term SATZ combining the concepts of the AD (Bruniard, 1982), and the SATZ (Morrone, 2006). This climatic zone represents a transitional area amongst two different climatic areas, thus explaining the speciation of aquatic taxa in Argentina (Fig. 1). Towards the north/north-east, the Atlantic monsoon produces subtropical summer rains (Chaco-Pampean humid area), while the Pacific westerlies affect the southwest-south of the SATZ (arid Patagonia, southern South America), with maxima precipitation in winter (Piovano et al., 2009). Due to the Quaternary ecological vulnerability to climate change and modern exacerbation due to human activities, a fluctuation of the SATZ role over time particularly in connection to Quaternary glacial/interglacial events is expected.

The objectives of this paper are to study the diversity of Quaternary *Limnocythere* species from Argentina, their use as paleoecological proxies and biogeographic connotations. This includes the description of a new species extensively distributed in core sediments from Laguna Llancanelo (Mendoza, SATZ), the revision of *Limnocythere* aff. *staplini,* from Salina del Bebedero, San Luis (Calvo Marcilese et al., 2019), and Laguna Runtuyoc, Jujuy (D'Ambrosio et al., 2020), both located in the SATZ; and a dichotomous key for the 13 Quaternary *Limnocythere* species found in Argentina.

MATERIALS AND METHODS

The ostracods used in this study were obtained from a 9 m long sediment core (LL3) from Laguna Llancanelo, Mendoza, Argentina, located 70 km east of the Andes (35° 00'–36° 30' S; 68° 30'–70° 00' W; 1,335 m above sea level); within the western-central section of the Argentinean SATZ (Fig. 1).

Preliminary research on core LL3, produced three radiocarbon ages from its base, middle and upper sediment layers, obtained from well-preserved, in situ gastropod shells of *Heleobia parchappi* (d'Orbigny, 1835) (Tab. 1). The samples for ^{14}C dating were processed at ANSTO (Australian Nuclear Science and Technology Organisation, Australia), by accelerator mass spectrometry (AMS). Additionally, ^{14}C ages from live specimens of *H. parchappi* from surface sediments, allowed the assessment of the reservoir effect on the samples. To calibrate the radiocarbon ages the SHCal20 (Southern Hemisphere calibration) (Hogg et al., 2020) and Calib 8.1 (Stuiver & Reimer, 1993) were used. All samples were analysed with a 2σ error.

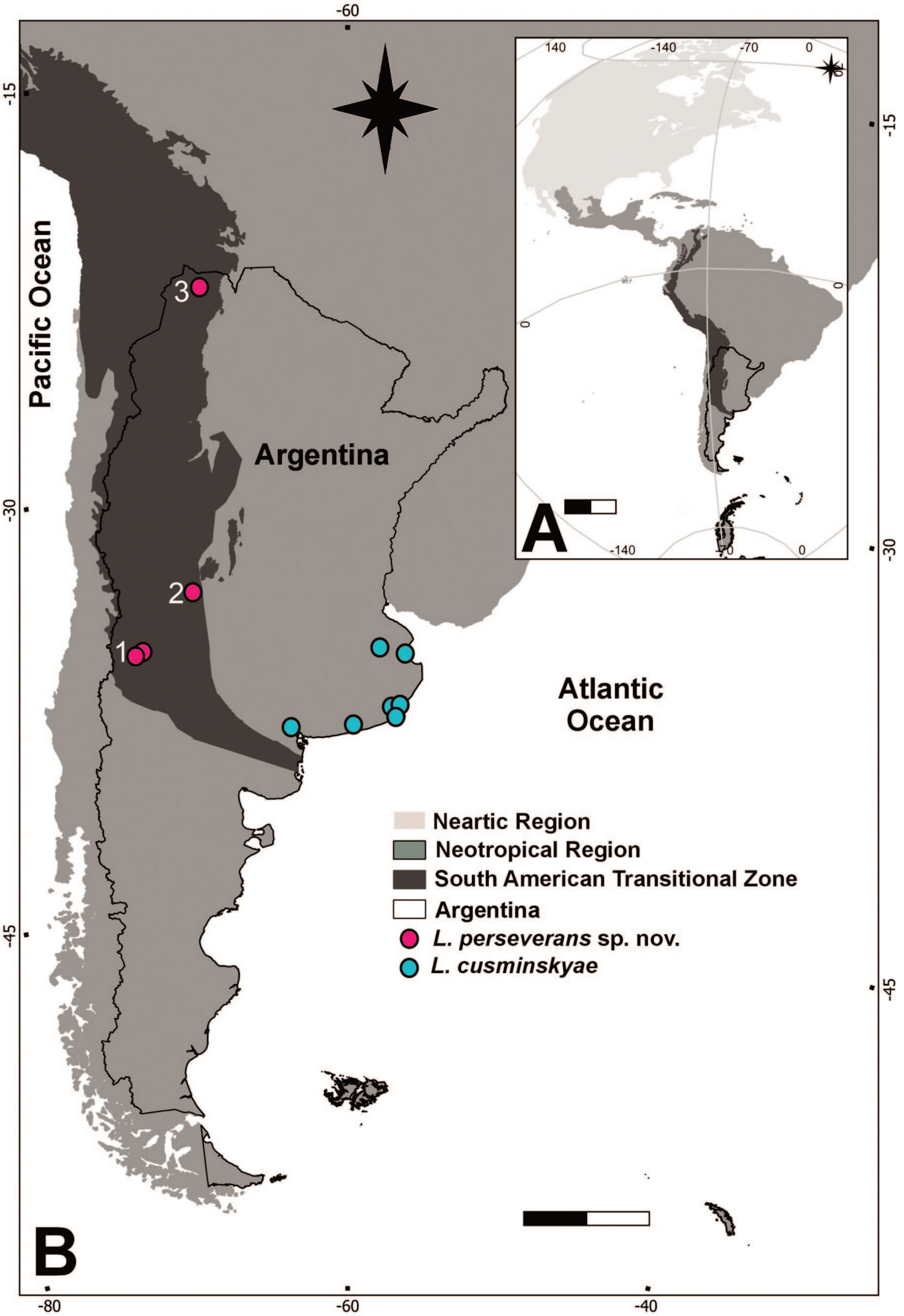

Figure 1. Localities of *Limnocythere perseverans* sp. nov. A, Map of the American continent including the SATZ (redrawn from Morrone et al., 2022); B, Map of Argentina, including the Argentinean SATZ, drew using data from this paper. Numbers indicate sampling sites: 1, Laguna Llancanelo; 2, Salina del Bebedero; 3, Laguna Runtuyoc. Scale= 100 km (A); 500 km (B).

TABLE 1. Radiocarbon (^{14}C) dates obtained from mollusk' shells (*Heleobia parchappi*, Laguna Llancanelo, core LL3, ~9 m long).

Sample	ANSTO Code	Depth (cm)	Conventional Radiocarbon AgeYears BP (interval 1-σ)	Calibrated Radiocarbon AgeWeighted average/cal.BP (interval 2-σ)
Modern	OZO637	0	Modern	-60
Core LL3	OZO297	28	2270 (± 45)	2229 (2125–2343)
	OZO300	370	14360 (± 80)	17464 (17129–17795)
	OZO303	857	27950 (± 180)	31876 (29369–30299)

Core sediment samples were sieved with a 63 µm mesh, dried, and stored in plastic bags. The fraction > 63 µm was revised and the ostracods (valves/carapaces) were picked using a stereomicroscope and kept in micropaleontological slides for identification and reference. The focus on the new species of *Limnocythere* is due to its great abundance along core LL3 (Laguna Llancanelo, Mendoza), and its previous record in two other Quaternary sites from the Argentinian SATZ. Previously left with open nomenclature as *Limnocythere* aff. *staplini* from Salina del Bebedero, San Luis (Calvo Marcilese et al., 2019) and from Laguna Runtuyoc, Jujuy (D'Ambrosio et al., 2020), the revised specimens from these sites are put in synonymy with *Limnocythere perseverans* sp. nov.

Higher taxonomy of Ostracoda follows the Treatise of Paleontology, Ostracoda (Benson et al., 1961), and Meisch et al. (2024) checklist for modern ostracods. For the genus *Limnocythere* specific diversification, research published by Gutentag and Benson (1962), Whatley and Cusminsky (1996), Cusminsky et al. (2011), Ramón-Mercau et al. (2014), Palacios-Fest et al. (2016), Ramos et al. (2016), and D'Ambrosio et al. (2020) were consulted. Scanning electron microscopy to obtain SEM images of the valves (JEOL JSM 6610 LV, IANIGLA, Argentina and JEOL JSM 6490 LA, University of Wollongong, Australia) were used, with all species measured by light microscopy. Values are expressed as the arithmetic mean ± the standard deviation (with the minimum and maximum values shown between brackets). Studied specimens are stored at the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza (Argentina) (IANIGLA-PI 3485–3502).

Abbreviations. Cp, carapace; **dv,** dorsal view; **ev,** external view; **H,** height of valve; **iv,** internal view; **L,** length of valve; **lv,** lateral view; **LV,** left valve; **n,** numbers of valves; **RV,** right valve; **W,** width of valve.

RESULTS

Sedimentology and dating

A succinct description of the core LL3 (Laguna Llancanelo) and preliminary dates obtained by AMS ^{14}C are presented in Figure 2. The core LL3, spanning the past ~35 ka is compared with the Holocene records from Salina del Bebedero (Calvo Marcilese et al., 2019) and Laguna Runtuyoc (D'Ambrosio et al., 2020) where the new species has been found (Fig. 2). Throughout the core LL3, the sediments show well-defined laminations. At the base (900–600 cm), an AMS ^{14}C of ~32 ka was obtained at 857 cm (Fig. 2, Tab. 1), sediments show an alternation of a distinct tephra-derived ash layer and fine sand/silty sands. Between 600 and 236 cm, the sequence consists of continuous lamination of organic-rich layers inter-bedded with silty clay and thin fine-sand layers (a date of 17,464 (± 333) cal. years BP at 370 cm depth was obtained, Fig. 2). The upper part of the profile (236–0 cm, surface dated at -60 years, Fig. 2), is characterized by alternating gypsum beds and silty clay with fine to medium sand layers (Fig. 2) (Connolly, 2011).

Sediment water content is highest at the top of the sequence (60%), decreasing progressively towards the base (12%). Most samples show water content above 20%.

Dating and Calibration

There was no reservoir effect as indicated after dating modern *Heleobia parchappi* shells. The age obtained from

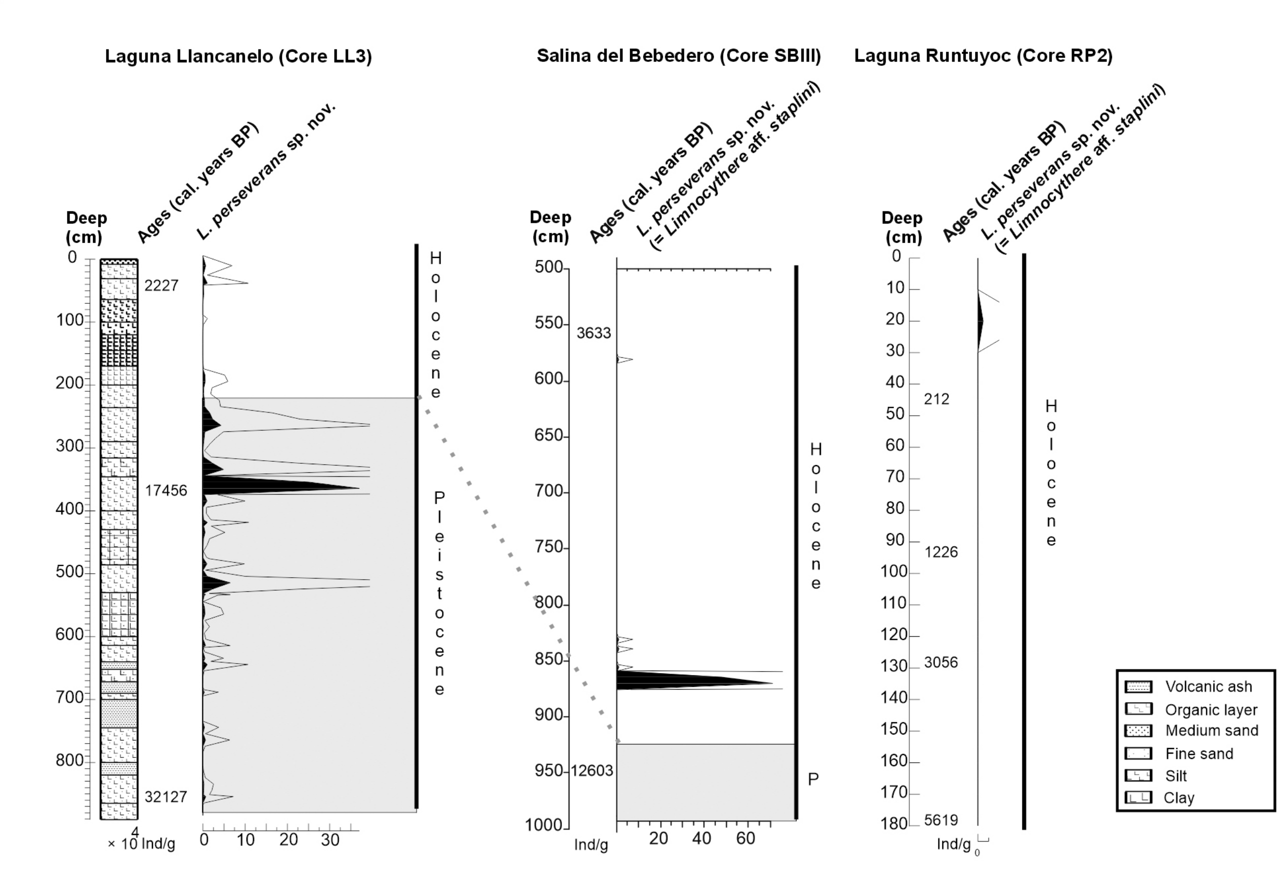

Figure 2. Stratigraphic diagram of sediment core from Laguna Llancanelo (core LL3), Salina del Bebedero (core SBIII) and Laguna Runtuyoc (core RP2), showing the lithological units in core LL3 and the calibrated ages at the corresponding depths in all cores. Core SBIII and Core RP2 images were modified from Calvo Marcilese et al. (2019) and D'Ambrosio et al. (2020), respectively. The temporal range corresponding to the Holocene and Pleistocene (in gray) in the cores was inferred in relation to the calibrated dates. Black-filled symbols and dashed lines indicate the presence of *Limnocythere perseverans* sp. nov.; dashed lines are shown with a ×10 exaggeration to improve visibility at low abundances. Abbreviations: Ind/g, individuals per gram.

surficial sediments was -60 (core taken in 2010). Calibrated ages (Fig. 2) were established using weighted-average probabilities in Calib 8.1 (Telford et al., 2004).

SYSTEMATIC PALEONTOLOGY

OSTRACODA Latreille, 1802
PODOCOPIDA Sars, 1866
CYTHEROIDEA Baird, 1850
LIMNOCYTHERIDAE Klie, 1938

Genus ***Limnocythere*** Brady, 1867

Type species. *Cythere inopinata* Baird, 1843. Recent, Great Britain.

Limnocythere perseverans sp. nov.
Figure 3

LSID urn:lsid:zoobank.org:act:AAF98FF9-6216-4C84-9359-F37F684FC425

2019 *Limnocythere* aff. *staplini* Calvo Marcilese et al. p. 149.
2020 *Limnocythere* aff. *staplini* D'Ambrosio et al., p. 4–5, fig. 3J.

Etymology. The epithet *perseverans* indicates a remarkable characteristic of the new species: 'persisting with determination through adversity'. The new species was found in areas of harsh climatic conditions, in waterbodies subjected to desiccation, highlighting the species' resilience through time, and adaptation to the fluctuating ecological conditions during the Late Pleistocene–Holocene.

Diagnosis. Sub-equal valves with strong sexual dimorphism.

In lateral view, the anterior margin is broadly rounded, and the posterior margin is sharply rounded. LV overlapping the RV in posterior margin. Male valve is reniform and female sub-reniform in lateral view. Female dorsal margin broadly arched, anterior and posterior cardinal angles both faintly discernible. Ventral margin slightly concave, convex towards the middle. Male dorsal margin straight, forming a soft angle when reaching the anterior and posterior regions. The ventral margin is straight in the middle of the valve. The hinge of both sexes is merodont modified, lophodont and

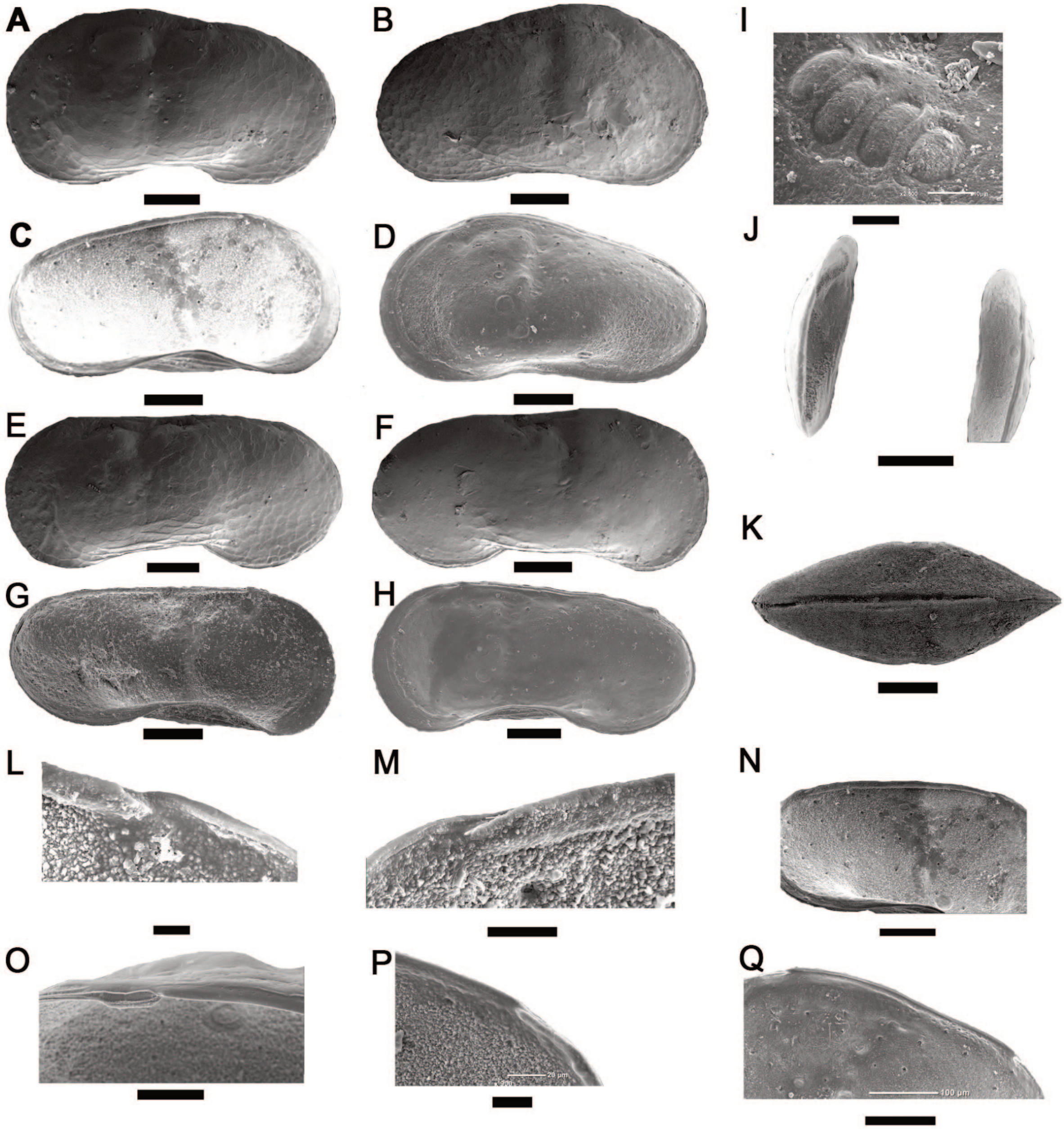

Figure 3. *Limnocythere perseverans* sp. nov. A, IANIGLA-PI 3493, ♀, LV, lv, ev; B, IANIGLA-PI 3494, ♀, RV, lv, ev; C, IANIGLA-PI 3495, ♀, LV, lv, iv; D, IANIGLA-PI 3496, ♀, RV, lv, iv; E, IANIGLA-PI 3497, ♂, LV, lv, ev; F, IANIGLA-PI 3498, ♂, RV, lv, ev; G, IANIGLA-PI 3499, ♂, LV, lv, iv; H, IANIGLA-PI 3500, ♂, RV, lv, iv; I, ♀, RV, lv, iv, muscle scar detail; J, IANIGLA-PI 3501, ♀, LV-RV, dv; K, IANIGLA-PI 3502, ♀, cp, dv; L–Q, hinge detail: L, IANIGLA-PI 3495, ♀, LV, iv, anterior tooth, detail; M, IANIGLA-PI 3495, ♀, LV, iv, posterior tooth, detail; N, IANIGLA-PI 3495, ♀, LV, iv, hinge detail, O, IANIGLA-PI 3496, ♀, RV, iv, anterior tooth detail; P, IANIGLA-PI 3496, ♀, RV, iv, posterior tooth detail; Q, IANIGLA-PI 3496, ♀, RV, iv, hinge detail. Abbreviations: cp, carapace; dv, dorsal view; ev, external view; iv, internal view; lv, lateral view; LV, left valve; RV, right valve. Scale= 10 µm (I, L); 20 µm (M, P); 50 µm (O); 100 µm (A–H, J, K, N, Q).

antimerodont, with a smooth groove and two smooth terminal teeth in the RV with a central smooth bar with an anterior and posterior smooth socket in the LV.

Type locality. Laguna Llancanelo, Mendoza Province, Argentina (35° 00'–36° 30' S; 68° 30'–70° 00' W).

Type material. Quaternary specimens at IANIGLA-PI 3485 at 3502 collections. Type material: Holotype, IANIGLA-PI 3485 ♂ RV, L = 582 µm, H = 288 µm; Allotype: IANIGLA-PI 3486 ♀ RV, L = 534 µm, H = 288 µm; IANIGLA-PI 3487 ♀ LV, L = 539 µm, H = 290 µm; Paratype: IANIGLA-PI 3488 ♂ LV, L = 539 µm, H = 269 µm; IANIGLA-PI 3489 ♂ RV, L = 562 µm, H = 252 µm; IANIGLA-PI 3490 ♂ LV, L = 592 µm, H = 239 µm; IANIGLA-PI 3491 ♀ RV, L = 544 µm, H = 288 µm; IANIGLA-PI 3492 ♀ LV, L = 529 µm, H = 260 µm; IANIGLA-PI 3493 ♀ LV, L = 441 µm, H= 248 µm; IANIGLA-PI 3494 ♀ RV, L = 558 µm, H= 270 µm; IANIGLA-PI 3495 ♀ LV, L = 553 µm, H= 239 µm; IANIGLA-PI 3496 ♀ RV, L = 548 µm, H= 240 µm; IANIGLA-PI 3497 ♂ LV, L = 649 µm, H= 281 µm; IANIGLA-PI 3498 ♂ RV, L = 575 µm, H= 253 µm; IANIGLA-PI 3499 ♂ LV, L = 539 µm, H= 241 µm; IANIGLA-PI 3500 ♂ LV, L = 603 µm, H= 274 µm; IANIGLA-PI 3501 ♀ Cp, L = 519 µm, W= 205 µm; IANIGLA-PI 3502 ♀ Cp (disarticulated valve LV–RV), L = 527 µm. Specimens IANIGLA-PI 3485 at 3492 were obtained from sediments at 370–371 cm deep from core LL3(~17500 cal. years BP). Specimen IANIGLA-PI 3493 was obtained from sediments at 650–651 cm deep from core LL3 with (~24100 cal. years BP), and IANIGLA-PI 3493 at 3502 from 28-29 cm (~2200 cal. years BP).

Referred Material. Specimens of *L. perseverans* sp. nov. analysed are 31,063 valves (female, male and juveniles) and 149 adult and juvenile carapaces collected from Laguna Llancanelo, Mendoza (core LL3), 22 valves from a Holocene core (core RP2) from Laguna Runtuyoc, Jujuy, and 320 valves from a Holocene sediment core (core SBIII) from Salina del Bebedero, San Luis.

Description of the valves

External view. *Limnocythere perseverans* sp. nov. is a medium sized *Limnocythere*, with a carapace reniform to sub-reniform shape in lateral view. Sub-equal valves with strong sexual dimorphism. Maximum height situated approximately at the anterior quarter of the valves. In lateral view, the anterior margin is broadly rounded while the posterior margin is sharply rounded. In dorsal view, the posterior section is depressed anteriorly and more globose towards the posterior margin. LV overlapping the RV in posterior margin.

The female valve is sub-reniform in lateral view. Dorsal margin broadly arched, in some cases with a small hump coinciding with maximum height in anterior dorsal margin, anterior and posterior cardinal angles both faintly discernible. Ventral margin slightly concave, convex towards the middle, with minimum height of valve about two thirds from anterior margin.

The male valve in lateral view is longer and reniform. Dorsal margin straight, forming a soft angle when reaching the anterior and posterior regions. The ventral margin is straight in the middle of the valve, sub-parallel to the dorsal margin, rounded towards the anterior and posterior regions.

Valve ornamentation is softly reticulated or, in some cases, completely absent, stronger in the proximity of the valve's edge. Four to five ribs (vertical) develop around the anterior margin, starting approximately at the dorso-anterior hump and continuing in the ventral part, while in the posterior margin they are visible just around the margin. One median-dorsal transversal sulcus and one or two smooth, very poorly developed tubercles occur approximately at the anterior third of the maximum length. Normal pores scattered on the surface. Central muscular scar is typical for the genus.

Internal view. Anterior and posterior margins rounded, ventral margin slightly curved inwards in the middle section more marked approximately two thirds from the anterior margin. Dorsal margin is straight in male and arched in female. Marginal zone well developed in the anterior, ventral and postero-ventral margins, but is two to three times larger in the anterior margin. Marginal pore canals undivided, straight.

The hinge is a modified merodont type, combining lophodont and antimerodont features. The RV has a smooth groove and two terminal medium-sized smooth teeth (one anterior and one posterior). The LV presents a central smooth bar with an anterior and posterior smooth socket. Muscle scars as in genus. Juveniles, male and female, have their valve contour like to the female adults, but a bit more rounded.

Measurements adults. Male: RV (n = 28), L = 597 ± 95 µm (552–647 µm); H = 274 ± 62 µm (238–300 µm); LV (n = 23), L = 591 ± 142 µm (515–657 µm); H = 271 ± 62 µm (241–303 µm). Female: RV (n = 69), L = 561 ± 144 µm (508–652 µm); H = 303 ± 114 µm (240–354 µm); LV (n = 72), L = 560 ± 246 µm (441–687 µm); H = 295 ± 118 µm (239–357 µm).

Remarks. Considering its general shape, *L. perseverans* sp. nov. is comparable to *L. cusminskyae* with distribution in Argentina, and *L. staplini* distributed in North America (see Tab. 2). The character that clearly differentiates *L. perseverans* sp. nov., *L. cusminskyae* and *L. staplini* is the hinge morphology. In *L. perseverans* sp. nov., the right valves' hinge is formed by a smooth dorsal depression ending in one anterior and one posterior smooth tooth, whereas in *L.*

TABLE 2. **Morphological, ecological and biogeographical comparison of *Lymnocythere staplini*, *L. cusminskyae* and *L. perseverans* sp. nov.**

L. staplini (Pliocene–Recent)	***L. cusminskyae*** (Late Pleistocene–Recent)	***L. perseverans* sp. nov.** (Late Pleistocene–Holocene)
Geographical distribution		
Nearctic Region	Neotropical Region (Humid Chaco-Pampean area)	Neotropical Region (Arid/Semiarid Argentinean SATZ)
Environmental characteristics		
Possibly in waterbodies subjected to evaporation.Water depleted of bicarbonates	Permanent waterbodies. Water enriched in bicarbonates	Waterbodies subjected to evaporation. Water depleted of bicarbonates
Valve morphology		
Hinge		
Merodont, Antimerodont	Merodont modified, Antimerodont	Lophodont, Antimerodont
Hinge RV ♀/♂		
Anterior tooth		
Crenulated	Small crenulated	Smooth
Posterior tooth		
Crenulated	Small smooth	Smooth
Central Depression		
Deep middorsal	Dorsal	Smooth dorsal
Hinge LV ♀/♂		
Anterior socket		
Crenulated	Crenulated	Medium-size and smooth
Posterior socket		
Crenulated	Smooth	Medium-size and smooth
Central Bar		
Dorsal curved	Smooth central	Central smooth
Anterior cardinal angle ♀/♂		
less pronounced	Prominent	absent or less pronounced
Maximum height and length of the female valves in lateral view		
Valves short and tall (low L/H ratio)	Valves long and low (high L/H ratio)	Valves long and low (high L/H ratio)

Abbreviations. **H,** height of valve; **L,** length of valve; **LV,** left valve; **RV,** right valve.

cusminskyae the teeth at each end of the dorsal depression are small, with the anterior smooth and the posterior crenulated. In *L. staplini* the two terminal teeth are crenulated developed at the end of a deep depression, in the middorsal part of the valve. The left valves of *L. perseverans* sp. nov. consists of a central smooth bar with smooth anterior and posterior medium-size sockets, in *L. cusminskyae* has a smooth central bar with two teeth sockets being the anterior smooth and the posterior crenulated, and *L. staplini*, has a dorsal curved bar, ending in one anterior and one posterior tooth sockets.

They also differ in the prominence of the anterior cardinal angle, which is absent or less pronounced in *L. perseverans* sp. nov. and prominent in *L. cusminskyae*. Regarding maximum height and length of the valves in lateral view, the female valves of *L. perseverans* sp. nov. and *L. cusminskyae* are longer compared to those of *L. staplini*.

Geographic and Stratigraphic Distribution. *Limnocythere perseverans* sp. nov. is found in the western section of the Argentinean SATZ (Central Andean area and in the Puna, NW Argentina). *Limnocythere perseverans* sp. nov. occurs through the core LL3 (0–64 cm; 100–121 cm; 170–681 cm; 690–695 cm; 750–781 cm; 820–891 cm) from Laguna Llancanelo, spanning the last ~35 ka; in sediments from Salina del Bebedero dated ~11.5 ka and ~4 ka, obtained from the mid-section of the sedimentary core (Calvo Marcilese et al., 2019); and in Laguna Runtuyoc (upper part of a sedimentary core) dated to ~300 cal. year BP (D'Ambrosio et al., 2020).

Environmental conditions. Laguna Llancanelo is a lentic mesosaline, shallow endorheic lake (max. 1–2 m depth, Total Dissolved Solids up to 42.3 g L^{-1}), fed by snowmelt water and subjected to evaporation. Previous ecological studies have characterized the lake water as chloride-sulfate, sodic or calcic rich (Ostera et al., 2004), relating this variation to the high evaporation rate; or as sodium chloride-sulfate type (Cátedras de Obras Hidráulicas e Ingeniería Ambiental, 2005), dry Salina del Bebedero is characterized by salt deposits predominantly composed of halite (ClNa), with areas that dried recently also containing gypsum (SO_4Ca and ClNa) (Beninato, 1999); Laguna Runtuyoc has higher levels of sulfates than chlorides, making it oligohaline (Seeligmann & Maidana, 2019).

Key to the Argentinian species of the genus *Limnocythere*, indicated for each species if is ♂, ♀, or both:

1a. Sub-quadrate valves, sub-rectangular, trapezoidal to sub-trapezoidal in lateral view 2
1b. Reniform valves, sub-reniform or elongated in lateral view........ 12
2a. Dorsal margin straight to slightly convex 3
2b. Dorsal margin slightly concave; trapezoidal valves in lateral view .... *L. titicaca* ♂
3a. Anterior margin produced into a distinct pointed hook .... *L. ruipunctifinalis* ♂♀
3b. Anterior valve margin rounded or truncate, not produced into a pointed hook 4
4a. Posterior margin truncated 5
4b. Posterior margin not truncated 6
5a. Sub-trapezoidal valves in lateral view and lanceolate in dorsal view........ *L. titicaca* ♀
5b. Sub-quadrate valves with obtuse cardinal angles .... *L. alexanderi* ♀
6a. Anterior margin broadly rounded and depressed........ 7
6b. Anterior margin broadly rounded but not depressed 9
7a. Antero-dorsal cardinal angle well-developed 8
7b. Antero-dorsal cardinal angle absent or weakly developed; ventral margin with strongly rounded anterior part, posterior part straight and keel like near oral incurvature .... *L. patagonica* ♀
8a. Postero-ventral arch rounded; hinge lophodont, antimerodont, RV with smooth groove with two terminals (one anterior, one posterior), medium sized smooth teeth. LV with a central smooth bar with and smooth anterior and posterior sockets .... *L. jujunensis* ♀
8b. Postero-ventral arch forming an obtuse angle; hinge adont; RV with central bar, LV with central groove........ *L. reticulata* (not specified)
9a. Posterior cardinal angle strongly developed 10
9b. Posterior cardinal angle absent 11
10a. Surface strongly punctate, particularly posteriorly where the undulations between puncta give a "wrinkled" appearance, abductor muscle scar slightly oblique........ *L. multiperforata* ♂♀

10b. Surface smooth to "wrinkled", but not strongly punctate; abductor muscle scar heart-shaped and less vertical .... *L. solum* ♂♀
11a. Antero-dorsal cardinal angle well-developed .... *L. alexanderi* ♂
11b. Antero-dorsal cardinal angle absent or weakly developed .... *L. rionegroensis* ♂
12a. Dorsal margin slightly to widely arched 13
12b. Dorsal margin straight 16
13a. Anterior and dorso-ventral margins compressed, giving valves a pointed appearance .... *L. foresteri* ♂♀
13b. Anterior and dorso-ventral margins not compressed 14
14a. Long and low valves (high L/H ratio) 15
14b. Short and tall valves (low L/H ratio); hinge merodont modified, lophodont .... *L. rionegroensis* ♀
15a. Anterior cardinal angle very marked; hinge merodont modified, antimerodont, RV with one small anterior smooth tooth, central groove, and one small posterior crenulated tooth; LV with central smooth bar .... *L. cusminskyae* ♀
15b. Anterior cardinal angle less marked or absent; hinge merodont modified, lophodont, antimerodont, RV with smooth groove and two terminal smooth teeth (one anterior, one posterior); LV with central smooth bar with anterior and posterior medium-size sockets .... *L. perseverans* sp. nov ♀
16a. Ventral margin strongly concave, valves bilobed in appearance .... *L. lysandrosi* ♀♂
16b. Ventral margin straight in the middle 17
17a. Anterior cardinal angle very marked; hinge merodont modified, antimerodont, RV with one anterior small, smooth tooth, a central groove and a small, crenulated posterior tooth, LV with smooth central bar........ *L. cusminskyae* ♂
17b. Anterior cardinal angle less marked or absent; hinge merodont modified, lophodont, antimerodont, RV with smooth groove with two terminal smooth teeth (anterior and posterior medium-size), LV with central smooth bar with smooth anterior and posterior sockets .... *L. perseverans* sp. nov. ♂

DISCUSSION AND CONCLUSION

Quaternary ostracods are important proxies to reconstruct paleolimnological conditions such as pH, salinity, depth, and water ionic composition, with the living representatives used as modern analogues to infer past environments and past climatic conditions (Delorme, 1989; Palacios-Fest et al., 1994; Mourguiart et al., 1998; Curry et al., 2012).

Non-marine limnocytherids are particularly good indicators of water chemistry and salinity, with *Limnocythere* species being selective of specific water ionic composition (Forester, 1983, 1986; Delorme, 1989; Smith, 1993). In the Neotropical Region, extant non-marine ostracods from Family Limnocytheridae are the third more diverse, with eighteen species described for genus *Limnocythere* (de Oliveira da Conceição et al., 2020; Meisch et al., 2024).

In Argentina, studies on Quaternary *Limnocythere* (see Tab. 3) started with Whatley and Cholich (1974) who propossed *Limnocythere multiperforata* and *L. solum* (as genus *Pampacythere*), with Zabert (1981) with the register of *L. reticulata*, all from the Chaco-Pampean area. Cusminsky and Whatley (1996) described *L. patagonica* and *L. rionegroensis* from Patagonia, and Ramón-Mercau et al. (2014), in their revision of Argentinean Quaternary *Limnocythere,* proposed *Limnocythere cusminskyae* based on new collections and specimens previously identified as *L. staplini* or *L.* aff. *staplini*, all from the Pampean region. Paleolimnological studies, particularly on Ostracoda, from the arid-semiarid Argentinean South American Transition Zone (SATZ) are fewer in comparison with published research from the Argentinean' Patagonia or Chaco-Pampean areas (Sabater et al., 2024). However, in recent years, Palacios-Fest et al. (2016) described the Quaternary species *Limnocythere alexanderi*, *L. foresteri*, *L. lysandrosi*, and *L. ruipunctifinalis* from the Puna area (NW Argentina), and D'Ambrosio et al. (2020) added the new Quaternary species *L. jujunensis* from Laguna Runtuyoc (NW Argentina, Puna area). With the addition in this paper of *L. perseverans* sp. nov. found in the central-west SATZ and NW SATZ, the number of Quaternary endemic species within the Argentinean SATZ are six; or seven when adding *L. titicaca* found in Quaternary Laguna Runtuyoc, Jujuy (D'Ambrosio et al., 2020), originally described based on extant specimens from Lago Titicaca (Bolivia, also located and endemic from the SATZ) (Lerner-Seggev, 1973). Thirteen Quaternary *Limnocythere* species have been described in Argentina to date. The published records are compiled in Table 3 (with references provided therein and in the reference list), providing the biogeographic framework for the new species described here.

TABLE 3. Quaternary *Limnocythere* species from Argentina: geographic distribution following climatic areas and aquatic ecology determined by the arid-semiarid Argentinean SATZ.

Limnocythere species	Site name	Coordinates		Publication paper	This paper
		Latitude	Longitude		
L. alexanderi Palacios-Fest et al., 2016	Laguna de los Pozuelos	-22.3680	-66.0044	Palacios-Fest et al. (2016) Mc Glue et al. (2017)	Arid/Semiarid Argentinian SATZ
	Laguna Rountuyoc	-22.6516	-65.6911	D'Ambrosio et al. (2020)	
L. cusminskyae Ramón-Mercau et al., 2014	Napostá Grande stream	-38.5716	-62.2667	Bertels & Martínez (1990) Bertels & Martínez (1997)	Humid Chaco-Pampean area
	Quequén Grande river*1	-38.5333	-58.7	Ferrero (1996)	
	Miembro Cerro de la Gloria*1	-35.9717	-57.4494	Bertels-Psotka & Laprida (1998)	
	Laguna Mar Chiquita	-37.7502	-57.4277	Ferrero (2009)	
	Las Brusquitas profile	-38.2333	-57.775	Márquez et al. (2016)	
	Laguna Chascomús*1	-35.5968	-58.0242	Laprida & Valero-Garcés (2009) Laprida et al. (2009)	
	Laguna La Brava	-37.8833	-57.9833	Laprida et al. (2014)	
L. foresteri Palacios-Fest et al., 2016	Laguna de los Pozuelos	-22.3680	-66.0044	Palacios-Fest et al. (2016) Mc Glue et al. (2017)	Arid/Semiarid Argentinian SATZ
L. jujunensis D'Ambrosio, 2020	Laguna Runtuyoc	-22.6516	-65.6911	D'Ambrosio et al. (2020)	Arid/Semiarid Argentinian SATZ
L. lysandrosi Palacios-Fest et al., 2016	Laguna de los Pozuelos	-22.3680	-66.0044	Palacios-Fest et al. (2016) Mc Glue et al. (2017)	Arid/Semiarid Argentinian SATZ
L. multiperforata (Whatley and Cholich, 1974) Laprida, 1998	Laguna Salada Grande	-36.8765	-56.9504	Whatley & Cholich (1974)	Humid Chaco-Pampean area
	Las Brusquitas profile	-38.2333	-57.775	Márquez et al. (2016)	
L. patagonica Cusminsky and Whatley, 1996	Laguna Los Juncos	-41.0505	-71.0086	Cusminsky & Whatley (1996)	Arid Patagonia
	Cari-Laufquen lake system	-41.5833	-69.4166	Whatley & Cusminsky (1999)	
	Cari-Laufquen lake system*1	-41.5833	-69.4166	Cusminsky et al. (2011)	
	Lago Cardiel	-48.8250	-71.2166	Markgraf et al. (2003) Ramos et al. (2019)	
	Temporary ponds in Southern Patagonia	-49 to -52	-69 to -73	Ramón-Mercau et al. (2012) Ramón-Mercau & Laprida (2016) Schwalb et al. (2002)	
	Laguna El Toro	-40.3166	-70.4166	Coviaga et al. (2018)	
L. perseverans sp. nov.	Laguna Llancanelo	-35.6485	-69.1609	This paper	Arid/Semiarid Argentinian SATZ
	Salina del Bebedero	-33.5380	-66.6336	Calvo Marcilese et al. (2019)	
	Laguna Rountuyoc	-22.6516	-65.6911	D'Ambrosio et al. (2020)	
L. reticulata Sharpe, 1897	Taco Pozo*1	-25.6221	-63.2643	Zabert (1981)	Humid Chaco-Pampean area
L. rionegroensis Cusminsky and Whatley, 1996	Lago La Salina	-41.2666	-69.5333	Cusminsky & Whatley (1996)	Arid Patagonia
	Cari-Laufquen lake system	-41.5833	-69.4166	Whatley & Cusminsky (1999)	
	Temporary ponds in Southern Patagonia	-49 to -52	-69 to -73	Ramón-Mercau et al. (2012) Ramón-Mercau & Laprida (2016) Schwalb et al. (2002)	
	Lago Cardiel	-48.8	-71.2	Markgraf et al. (2003) Ramos et al. (2019)	
	Laguna El Toro	-40.3166	-70.4166	Coviaga et al. (2018)	
	Napostá Grande stream	-38.5716	-62.2677	Bertels & Martínez (1990) Bertels & Martínez (1997)	Humid Chaco-Pampean area
L. ruipunctifinalis Palacios-Fest et al., 2016	Laguna de los Pozuelos	-22.3680	-66.0044	Palacios-Fest et al. (2016) Mc Glue et al. (2017)	Arid/Semiarid Argentinian SATZ
L. solum (Whatley and Cholich, 1974) Laprida, 1998	Laguna Salada Grande	-36.8765	-56.9504	Whatley & Cholich (1974)	Humid Chaco-Pampean area
	Laguna del Monte*1	-35.4626	-58.7930	Laprida et al. (2009)	
	Laguna Mar Chiquita*1	-37.7502	-57.4277	Ferrero (2009)	
	Las Brusquitas profile	-38.2333	-57.775	Márquez et al. (2016)	
L. titicaca Lerner-Seggev, 1973	Laguna de los Pozuelos	-22.3680	-66.0044	Palacios-Fest et al. (2016) Mc Glue et al. (2017)	Arid/Semiarid Argentinian SATZ
	Laguna Runtuyoc	-22.6516	-65.6911	D'Ambrosio et al. (2020)	

*1: Geographical coordinates searched from the web.

Ecologically, earlier studies on water chemistry and ostracod distribution from the Neartic Region undertook by Forester (1983, 1986) and Delorme (1989), showed that the Neartic species *L. staplini* and *L. sappaensis* are indicative of contrasting ionic water-composition. The former species prefers water bicarbonate-depleted, while the latter lives in bicarbonate-enriched waters. On the other hand, *L. ceriotuberosa* lives in bicarbonate-enriched waters dominated by chloride and characterized by low sulfate concentrations (Forester 1983, 1986; Delorme, 1989). Within Argentina, Cusminsky and Whatley (1996) described *L. patagonica* and *L. rionegroensis* from Patagonia, the former living in low salinity, bicarbonate-dominated waters while the latter thrives in mesosaline, sodium-dominated chloride-sulfate alkaline waters (Cusminsky & Whatley, 1996). In recent years, Ramón-Mercau et al. (2014) dealing with Chaco-Pampean limnocytherids remarked the different water preferences of *L. cusminskyae*, commonly found in permanent waterbodies close to the ocean, with hyposaline to mesosaline sodium-dominated alkaline waters, and *L. rionegroensis* living in saline (mesosaline) inland waterbodies, in sodium-dominated chloride-sulfate alkaline waters.

Geological and hydrological analyses from Laguna Llancanelo, Salina del Bebedero and Laguna Runtuyoc waterbodies, where *L. perseverans* sp. nov. was found, classified these waters as sodium-chloride, sulfate, or chloride-sulfate types (Beninato, 1999; Cátedras de Obras Hidráulicas e Ingeniería Ambiental, 2005; Ostera et al., 2004; Seeligmann & Maidana, 2019), that closely resemble water conditions preferred by *L. staplini* (Tab. 2, Delorme, 1989; Neartic Region). Therefore, the occurrence of *Limnocythere perseverans* sp. nov. in Quaternary sediments is indicative of ephemeral inland saline waterbodies characterized by sodium-dominated chloride or chloride-sulfate waters, subjected to desiccation under arid to semiarid climatic conditions. The new species is known only in sites within the Argentinean SATZ, but represents a valuable paleoenvironmental indicator for reconstructing past hydrological and hydrochemical conditions within the South American Transitional Zone.

The climatic character and ecological importance of the South American Transitional Zone are discussed in detail (see Introduction, Fig. 1), because this area holds the highest number of Quaternary *Limnocythere* species from Argentina. This transitional zone is characterized by arid-semiarid climate, having the eastern limit in Río Desaguadero-Salado Basin (the longest N–S river basin), which joins the Río Colorado Basin running W–E (from the Andes to the Atlantic Ocean), that becomes the southern border. This is consistent with the eastern and southern limits of the distinct ecotone identified by García (1999) (based on extant/Quaternary ostracods, charophytes and foraminifers from Salina del Bebedero, Río Desaguadero, and saline wetlands from dry southern La Pampa and south of Buenos Aires provinces), and with the boundaries determined by D'Ambrosio et al. (2024) based on extant ostracods. Towards the west, the Andes foothill is the western limit from Mendoza to the NW Puna, including the Payunia (~1400 m altitude), where Laguna Llancanelo is located. *Limnocythere perseverans* sp. nov. is found today in three disjunct Quaternary localities within this SATZ Laguna Llancanelo (Mendoza), Salina del Bebedero (San Luis) and Laguna Runtuyoc (Jujuy), though a more continuous presence of *L. perseverans* sp. nov. between Mendoza and Jujuy is expected. It is highly probable that the new species and closer taxa will be found in Quaternary sediments or alive along the SATZ from Argentina up to Venezuela in the arid-semiarid transitional zone, as described by Morrone (2006) (Fig. 1).

Limnocythere perseverans sp. nov. is found in Quaternary sediments from ephemeral saline inland waterbodies subjected to desiccation, located in the Argentinean SATZ (Neotropical Region). The new species is closely related to *L. cusminskyae*, described from sites located in the humid Chaco-Pampean area, Argentina (Neotropical Region), and *L. staplini* from North American ephemeral inland waterbodies (Neartic Region). They differ in stable, genetically controlled characters of the valves, such as valve's contour and hinge structure (Gutentag & Benson, 1962). The hinge morphology is distinctive and clearly separates these taxa: *L. perseverans* sp. nov. (RV) hinge has a smooth dorsal depression with one anterior and one posterior smooth tooth; *L. cusminskyae* (RV) hinge consists of a dorsal depression ending in an anterior smooth and the posterior crenulated tooth; and *L. staplini* (RV) hinge consists of two crenulated terminal teeth developed at the end of a deep depression.

The left valves have the complementary structure of bars and sockets to articulate with the depressions and teeth of the RV (see Remarks in the Systematic Paleontology section for more details, Tab. 2). Although is evident the process of speciation amongst *L. perseverans* sp. nov., *L. cusminskyae*, and *L. staplini*, general morphological similarities suggest the possible existence of a past common ancestor still unknown; or, otherwise, can indicate that these taxa with disjunct geographical distribution can be the product of convergent evolution, in response to similar environmental pressures (as occurred with Cypricercinae in South America; Ferreira et al., 2019). The presence of these close taxa, *L. perseverans* sp. nov., *L. cusminskyae*, and *L. staplini*, across the Neotropical and Nearctic regions raises biogeographical/paleoenvironmental questions concerning *Limnocythere* diversification, the connectivity of freshwater systems through time, their responses to climate and environmental changes, and the extent to which dispersal routes and biogeographic boundaries defined for terrestrial taxa can be relevant for aquatic organisms.

Extensive collection and research on fossil and extant ostracods from the Neotropic SATZ and the Neartic-Mexican Transition Zone, their ecology and distribution will allow to establish phylogenetic relationships and a better understanding of biogeographic patterns.

These biogeographic scenarios must be interpreted in the context of the major geological and climatic events that have shaped the American continent. The progressive Andean uplift (started ~200 Ma ago and intensified over the past 45 Ma), the completion of the land bridge connecting the separated masses of North and South America (~3 Ma ago), and the fluctuations associated with glacial/interglacial cycles during the past 2.6 Ma all played crucial roles in defining dispersal pathways, barriers, and the hydrological configuration of basins. These processes likely influenced not only terrestrial taxa but also the evolution and distribution of freshwater ostracods. Future research incorporating new Neogene to Recent records of *Limnocythere* species from both the Nearctic and Neotropical regions, complemented by morphological analyses and molecular approaches where possible, will be fundamental to resolving the evolutionary relationships among these species and understanding the historical biogeography of the genus across the Americas.

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