



Taphonomic analysis of fish in rift lacustrine systems: Environmental indicators and implications for fish speciation

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ABSTRACT

Two rift-basin lacustrine successions (Cacheuta and Los Rastros Formations) in the Middle Triassic of Argentina were studied to test two different hypotheses: 1) fish taphonomy is useful as an indicator of environmental conditions for these two paleolakes; and 2) fish taphonomy is useful for understanding environmental effects on speciation. The fish fossils are found, in two lacustrine deposits, as isolated and disarticulated scales and cranial bones, clumps and stringers of scales, articulated body segments, and complete specimens. Four taphofacies are defined for Cacheuta specimens (Ca-A to Ca-D), and three taphofacies are defined for Los Rastros fish assemblages (LR-A to LR-C). A Principal Components Analysis was performed, with the taphonomic features supporting the seven taphofacies defined.

A taphonomic model is proposed that characterizes a lacustrine-deltaic environment developed in the rift basin and identifies three sub-environments, each one with its particular fossil assemblages. The fish assemblages in the Los Rastros Formation suggest that the fishes preserved in delta-front and turbidity-current deposits (LR-B and LR-C taphofacies) were allochthonous to the lake and probably inhabited the delta plains and affluent fluvial system. In contrast, the isolated fish remains, preserved in open-lake deposits (LR-A taphofacies), likely represent both autochthonous and/or allochthonous specimens. In the Cacheuta Formation, articulated and isolated fish remains preserved in open lake deposits (Ca-A and Ca-D tafafacies), might represent autochthonous lacustrine specimens, based on the good preservation of the material. The fish remains preserved in underflow and turbidity current deposits (Ca-B and Ca-C taphofacies) were allochthonous to the lake and probably inhabited the delta plain and affluent fluvial system.

The fish taphonomic study of two different rift-basin lacustrine successions allows test of the two proposed hypotheses. Fish taphonomy was useful as an indicator of environmental conditions because the differences in fish preservation allowed differentiation of the sub-environments and reconstruction of the environmental conditions and dynamics of the rift lake basins. Also, fish taphonomy was useful for understanding environmental effects on speciation by characterizing the environments and dynamics that promote the development of new fish species, recognizing fish-inhabited environments, and identifying the generalist and specialist species.

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1. Introduction

The preservational modes of fishes can be sensitive environmental indicators of conditions that characterize sub-environments and depositional processes in lacustrine systems. Environmental characteristics (e.g., water depth, temperature, and oxygenation) of a paleolake can be reconstructed by studying the taphonomy of fish remains, including species composition, size of specimens, disarticulation of skeletons, etc. (e.g., McCune, 1990; Ferber and Wells, 1995; Barton and Wilson, 2005; Whiteside et al., 2011). Some earlier studies (e.g., Wilson, 1980, 1988; McCune, 1987; Elder and Smith, 1988) laid the groundwork for applying principles of lacustrine fish taphonomy to reconstruction of

paleoenvironments. As a result, several recent studies have used fish taphonomy, among other data, to help characterize lacustrine paleoenvironments (e.g., Wilson, 1996; Wilson and Barton, 1996; Chen, 2000; Mancuso, 2003; Fürsich et al., 2007; Stigall et al., 2008).

In addition, fish taphonomy helps us to understand environmental effects on speciation in the lacustrine systems. In particular, rift lakes seem especially conducive to speciation of fishes, perhaps because in deep lakes the habitats may be continually renewed (e.g., Smith, 1987; McCune, 2004). Although the environment is thought to play a major role in determining diversification rates, little is known about the relationship between ecological conditions and the extent of divergence (e.g., McCune, 1996, 2004; Landry et al., 2007; Day et al., 2008; Whiteside et al., 2011). Fish taphonomic analysis could be useful for recognizing the environment inhabited by fish (e.g., Gore, 1988; Mancuso, 2003) and for characterizing the environment conditions that are

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conductive to generating new fish species. Moreover, this kind of analysis could also allow discrimination between generalist and specialist species.

This paper presents a fish taphonomic study of two rift-basin lacustrine successions in the Middle Triassic of Argentina. The study seeks to test two different hypotheses: 1) that fish taphonomy is useful as an indicator of environmental conditions for these two paleolakes; and 2) that fish taphonomy is useful for understanding environmental effects on speciation.

2. Geological setting

Triassic non-marine sedimentation of Argentina occurred in extensional basins associated with the breakup of Pangea that was initiated during the earliest Triassic (Uliana and Biddle, 1988). Two of the largest basins were developed with NNW–SSE trends along the

southwestern margin of Gondwana (Fig. 1), related to a strong basement fabric control (Martínez et al., 2006). The basins were filled by thick, entirely non-marine successions of predominantly fluvial and lacustrine sediments that record almost the whole Triassic (Fig. 2).

The Cacheuta Formation, in the Cuyana Basin of Mendoza and San Juan provinces, is a deep lacustrine succession dominated by black shales and siltstones (Fig. 3A, B). The thickness of the formation ranges from 30 to 80 m, depending on location in the hemi-graben. It is exposed in the Cerro Cacheuta, Potrerillos, Divisadero Largo, and Cerro Bayo areas, where outcrops share similar depositional characteristics that are summarized in Table 1 (Bellosi et al., 2001; Mancuso et al., 2004).

The Los Rastros Formation, in the Ischigualasto–Villa Unión Basin of San Juan and La Rioja provinces, is a lacustrine-deltaic succession that consists of several coarsening-upward cycles of black shales, siltstones, and sandstones (Fig. 3C, D). The thickness of this unit ranges from 160

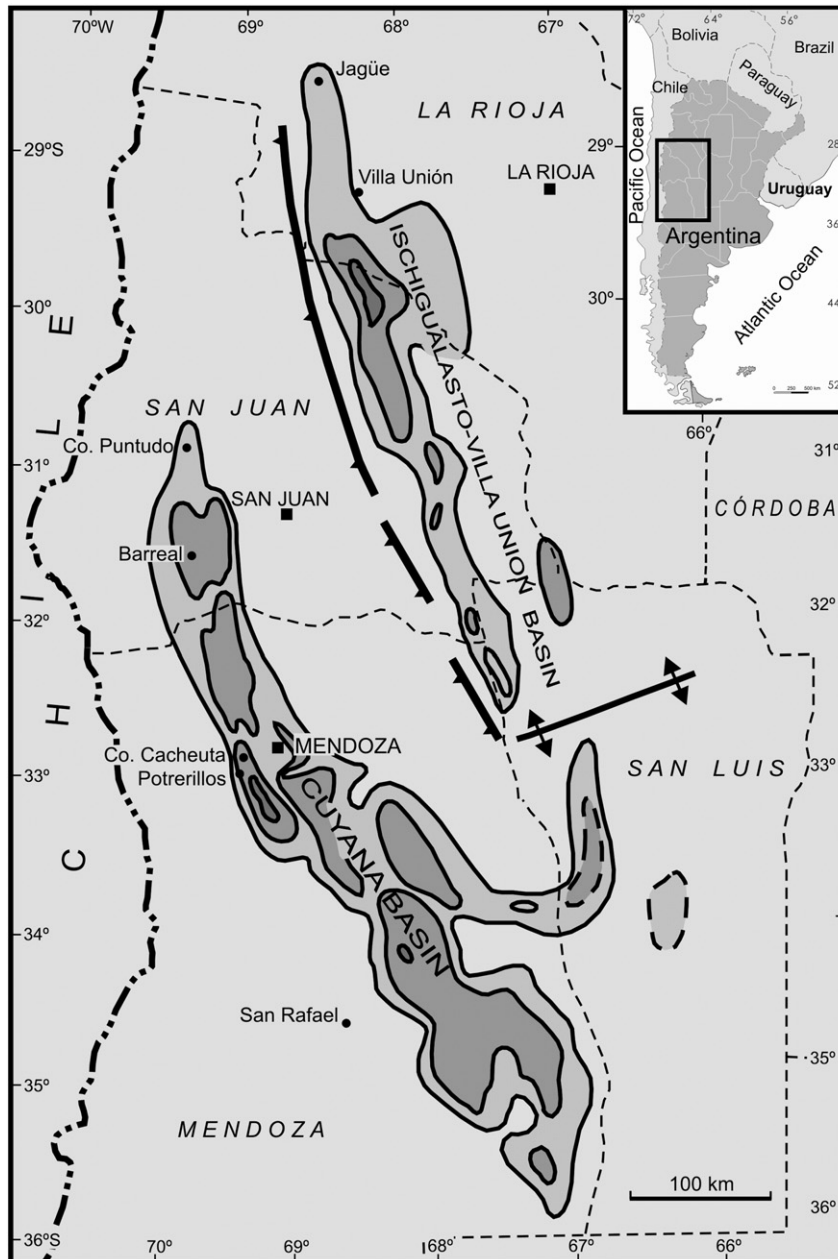


Fig. 1. Location map of the Cuyana and Ischigualasto–Villa Unión basins. The darker shades of gray represent the deeper areas of the basins. Modified from Stipanovic and Marsicano (2002).

Cuyana Basin					Ischigualsto-Villa Unión Basin			
DEPOSITIONAL SYSTEMS	TECTONIC PHASE	LOGGED SECTION	FORMATION	AGE	FORMATION	LOGGED SECTION	TECTONIC PHASE	DEPOSITIONAL SYSTEMS
FLUVIAL DELTAIC	Sag		RÍO BLANCO	Rhaetian	LOS COLORADOS		Sag	FLUVIAL
LACUSTRINE	Synrift II		CACHEUTA	Norian	ISCHIGUALASTO		Synrift III	FLUVIAL
DELTAIC			POTRERILLOS	Carnian	LOS RASTROS	Synrift II	DELTAIC LACUSTRINE	
FLUVIAL			CERRO DE LAS CABRAS	Ladinian	CHAÑARES		FLUVIAL	
LACUSTRINE FLUVIAL ALLUVIAL FAN	Synrift I		RÍO MENDOZA	Anisian	TARJADOS	Synrift I	FLUVIAL PLAYA LAKE FLUVIAL PLAYA LAKE	
			BASEMENT	Olenekian Induan	TALAMPAYA		FLUVIAL ALLUVIAL FAN	
			Paleozoic	BASEMENT				

Fig. 2. Generalized logs of the Cuyana and Ischigualsto-Villa Unión basins, showing a lithostratigraphic section, units, depositional characteristics, and tectonic phases. The star marks indicate radiometric ages in M.a. (Ávila et al., 2006; Spalletti et al., 2008; Martínez et al., 2011). Modified from Kokogian et al. (1993).

to 600 m, depending on location in the hemi-graben. It is exposed in the Cerro Bola, Ischigualsto Provincial Park, and Talampaya National Park areas. These outcrops display similar depositional characteristics, which are summarized in Table 2, but differ in the number of cycles depending on location (Mancuso and Marsicano, 2008; Mancuso and Caselli, in press).

3. Fish taphonomy

3.1. Fish material

The studied material includes fish remains that were systematically collected throughout the sections at different localities for both units, and material previously collected that is housed in museums and for which the original location in the sections is certainly known. In this way, 72 fossil assemblages were obtained, each one from an individual layer.

The fish fossils of the Cacheuta Formation are found as isolated and disarticulated scales and cranial bones, clumps and stringers of scales, articulated body segments, and complete specimens (Fig. 4). Identified specimens include five taxa (Table 3): *Amblypterus lujanensis* (Holotype MCNAM-PV 2767), *Challaia cacheutensis* (Holotype MCNAM-PV 768), *Challaia magna* (Holotype MCNAM-PV 2790), *Challaia multidentata* (Holotype MCNAM-PV 2792), and *Neochallaia tellecheai* (Holotype MCNAM-PV 2702) (López-Arbarello et al., 2010). The studied material is housed in the Museo de Ciencias Naturales y Antropológicas “Juan Cornelio Moyano” Mendoza, Argentina (MCNAM).

The fish specimens of the Los Rastros Formation are found as isolated and disarticulated scales and cranial bones (fragmentary and/or complete), clumps of scales, articulated body segments, and complete specimens (Fig. 5), and are assigned to four taxa (Table 3): *Gualolepis*

carinaesquamosa (Holotype PULR 106, 107), *Rastrolepis riojaensis* (Holotype PULR 103A,B), *Rastrolepis latipinnata* (Holotype PULR 105A, B, C), and *Challaia elongata* (Holotype MLP 44-VII-16-3) (López-Arbarello et al., 2006). The studied material is housed in the Museo de La Plata, La Plata, Argentina (MLP) and the paleontological collections of the Universidad Nacional de La Rioja, La Rioja, Argentina (PULR).

3.2. Data analysis

To identify the taphonomic processes responsible for each fish assemblage, and to define taphofacies, several taphonomic attributes of the fish fossils were studied. These attributes include taxa represented, number of individuals, relative abundance, degree of articulation, biofabric (packing, sorting, density), post-mortem modifications (compaction, abrasion, cracking, breakage, oxidation, recrystallization), spatial arrangement (orientation, cross-cutting), and host sediment, among others. The compilation of these parameters was conducted according to currently accepted methodologies (e.g., Eberth et al., 2007). Taphofacies were defined based on the combination of recurring taphonomic and sedimentological parameters that are easily recognizable in the field, have different states, and characterize the fossil assemblages. These taphofacies summarize the variable preservation of fossils both within and between facies, and reflect their post-mortem history (Brett and Baird, 1986; Speyer and Brett, 1986).

Principal Components Analysis was performed on these data to verify the division into and definition of the taphofacies. The analyses were performed using the fossil assemblages as OTUs (Operational Taxonomic Units). The attributes were standardized as proportions and normalized into the 0–1 range (e.g., proportion of fish/total of all kinds of fossils in the assemblage, preservation of hard part/total number of fish on surface, plan-view orientation/total number of

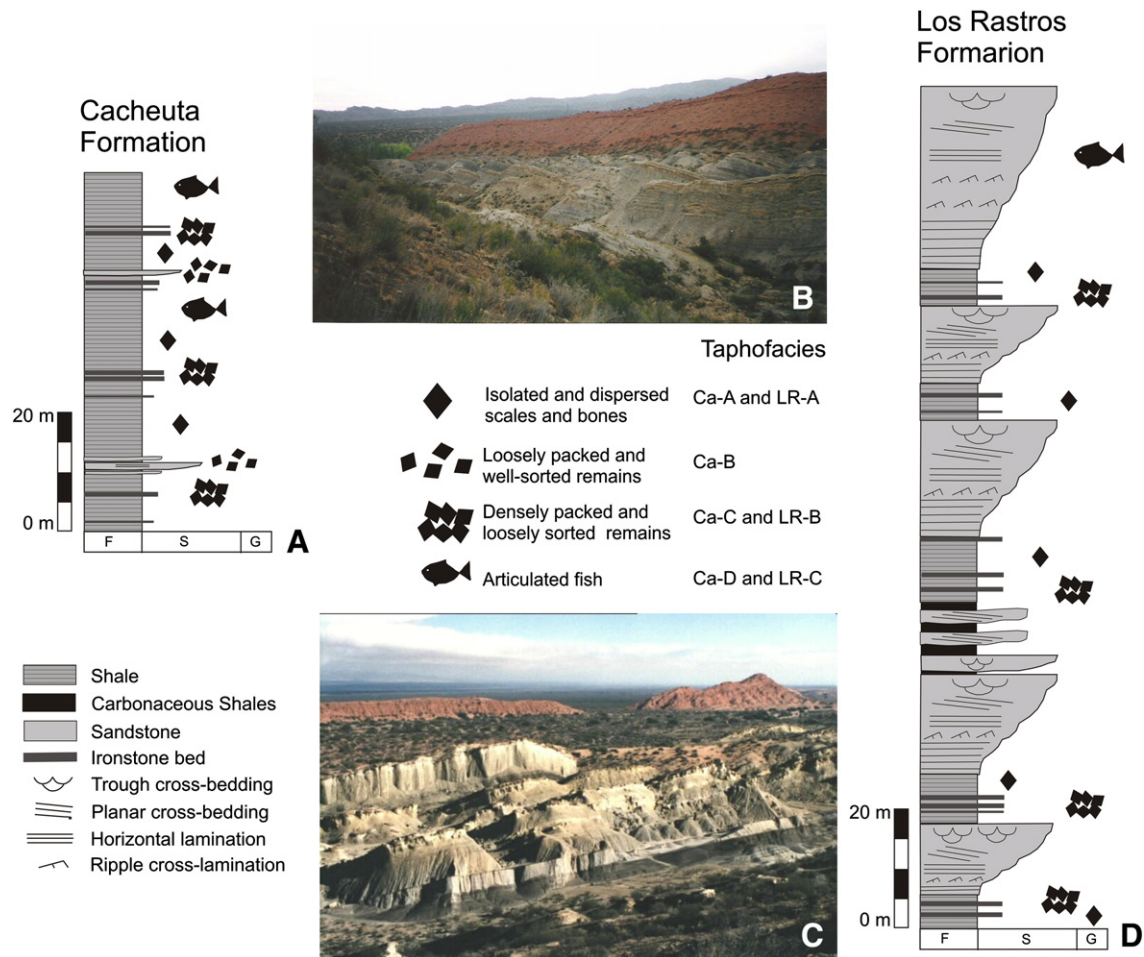


Fig. 3. A. Sedimentological section of the Cacheuta Formation in the Potrerillos area. B. Exposures of the Cacheuta Formation in the Potrerillos area. C. Exposures of the Los Rastros Formation in Talampaya National Park area. D. Sedimentological section of the Los Rastros Formation in the Talampaya National Park area. F, S, G represent mudrock, sandstone, and gravel respectively.

fish, cracking/total number of fish), according to Wilson (1980) and Mancuso and Marsicano (2008); the analyses compared 72 fossil assemblages (58 assemblages from Cacheuta and 14 assemblages from Los Rastros) across 15 variables (Table 4).

3.3. Description of fish taphofacies

Four taphofacies are defined for Cacheuta specimens (Ca-A to Ca-D) (Figs. 3, 4, and 6), and three taphofacies are defined for Los Rastros

fish assemblages (LR-A to LR-C) (Figs. 3, 5, and 6). The name of each taphofacies includes an abbreviation of the formation name (Ca: Cacheuta; LR: Los Rastros).

The Ca-A taphofacies is characterized by well-sorted, isolated and dispersed scales and bones in dark shale facies (Fm, FI of Ca-A facies association) (Figs. 4A–B and 6). Taphofacies Ca-B is dominated by disarticulated and associated scales and bones forming clumps and stringers, concordant to stratification in a gray siltstone facies (FSm, FSI of Ca-A facies association). The elements are typically loosely packed

Table 1
Summary of Cacheuta facies associations.

Facies and interpretation	Lithology	Structures	Bedding	Fossil content	Lateral and vertical relationships
Ca-A offshore lacustrine and prodelta deposits	Dark gray, black carbonaceous claystone and fine-grained siltstone (Fm, FI)	Horizontally laminated to massive	Units are tabular, 1–8 m thick, and laterally persistent for several hundreds of meters. Individual massive beds are 1–5 cm thick	Palynomorph and algae, locally abundant plants, insects, conchostracans, coprolites, fish and temnospondil amphibians	FI and Fm facies commonly overlie the Potrerillos Fm. and are overlain by the Rio Blanco Fm
	Gray siltstone to fine-grained sandstone (FSm, FSI)	Massive, occasionally horizontal laminated	Individual beds are tabular, 0.05–0.2 m thick, laterally persistent for hundreds of meters, and have abrupt upper and lower contacts	Locally abundant plants, conchostracans, insects and fish	FSm and FSI facies are interbedded with FI and Fm facies, and pass laterally into FI and Fm facies
	Very dusky purple iron mudstone to very fine-grained sandstone (SFm, SFI, SFr)	Massive, horizontal- and ripple-laminated	Individual beds are tabular, 0.03–0.1 m thick, laterally persistent for hundreds of meters, have abrupt upper and lower contacts, and exhibiting rare erosional bases	Locally fossiliferous (common plants, abundant conchostracans and fish)	SFm, SFI, and SFr facies are interbedded with FI and Fm facies, and pass laterally into FI and Fm facies

Table 2
Summary of Los Rastros facies associations.

Facies and interpretation	Lithology	Structures	Bedding	Fossil content	Lateral and vertical relationships
LR-A <i>offshore lacustrine and prodelta deposits</i>	Dark gray, black carbonaceous claystone and fine-grained siltstone (Fl)	Thinly horizontally laminated, locally fissile or massive. Very rare mudcracks	Units are tabular, 0.4–2 m thick, laterally persistent for several hundreds of meters. Individual massive beds are 1–5 cm thick	Abundant palynomorphs and algae, locally abundant plants, bivalves, insects, conchostracans, and fish.	Fl facies commonly overlies CH-B and CH-C (Chañares Fm.) and is overlain by Wm facies, Sl facies, Fm, Sh, Sp, St facies (LR-D), Sp, St facies (LR-E).
	Very dusky purple iron mudstone to very fine-grained sandstone (SFm)	Massive, horizontal laminated. Occasionally silty and sandy beds are normally graded.	Individual beds are tabular, 0.01–0.3 m thick, laterally persistent for hundreds of meters, and have abrupt upper and lower contacts, exhibiting rare erosional bases.	Locally fossiliferous (common plants, abundant conchostracans and fish, and sporadically fish locomotion traces).	SFm facies is interbedded with Fl facies, and pass laterally into Fl facies.
LR-B <i>marginal palustrine along the shoreline of the lake</i>	Pale yellowish orange wackestone and locally packstone (Wm)	Massive to mottled, microbrecciated, desiccation cracks	Individual beds are tabular, 0.1–0.3 m thick, persist laterally for hundreds of meters (500 m approximately), and have abrupt upper and lower contacts.	Roots traces, tetrapod tracks.	Wm facies is interbedded with Fl facies (LR-A), and pass laterally into Fl facies (LR-A) and LR-D.
LR-C <i>Siliciclastic wave-dominated coastline</i>	Gray and green moderate to well sorted fine to medium-grained sandstone (Sl)	Subhorizontal to low-angle cross-stratification, planar or ripple and relic wave-ripple lamination, with probable wrinkle structures.	Units are tabular, 2–5 m thick, persist laterally for tens of meters, and have abrupt non-erosional boundaries. Cross-lamination forms sets 0.1–0.4 m in thickness.		Sl facies overlies Fl facies (LR-A), and passes laterally into LR-A and LR-D facies, and vertically into LR-A facies.
LR-D <i>deltaic front with progradation of the mouth bar</i>	Green siltstones and gray claystone (Fm)	Internally massive, alternation siltstone and claystone from a rhythmic deposit	Units are tabular, 5–20 m thick and laterally persist for several tens to hundreds of meters. Individual beds are tabular, 0.1 m thick and have non-erosional boundaries.	Plants	Fm facies overlies Fl facies (LR-A) and passes laterally into LR-A and sandstone facies (LR-D), and vertically into sandstone facies (LR-D).
	Grayish orange moderate to well sorted, fine-to medium-grained sandstone (Sr, Sh) Grayish orange to grayish olive, moderately to well sorted medium-to coarse-grained sandstone, rare sandy conglomerates (Sh, Sp, St)	Ripple cross-lamination, horizontal lamination, small-scale hummocky cross-stratification Horizontal lamination, planar to trough cross-bedded	Beds are tabular to plane-convex, 0.05–0.6 m thick, extend laterally for tens to hundreds of meters, and have non-erosional boundaries. Beds are tabular to plane-convex, 0.5–3 m thick, extend laterally for several tens to hundreds of meters, and have non-erosional boundaries and sporadically slightly erosional basal boundaries.	Commonly dispersed and locally abundant plants, fish, and rare invertebrate and tetrapod traces Commonly dispersed and locally abundant plants, sporadically invertebrate traces.	Sr, Sh facies overlie Fm facies (LR-D) and rarely Fl facies (LR-A), and pass laterally into Fm and Sh, Sp, St facies (LR-D) and vertically into Sh, Sp, St facies (LR-D) Sh, Sp, St facies overlie Sr, Sh and Fm facies (LR-D) and pass laterally and vertically into Fl facies (LR-A) and Sr, Sh, and Fm facies (LR-D), and are overlain by LR-E.
LR-E <i>deltaic plain deposit with distributary fluvial system and delta swamps within the deltaic plain</i>	Grayish orange, yellowish gray moderate to well sorted medium- to coarse-grained sandstone (Sp, St)	Planar to trough cross-stratification, locally ripple cross-lamination at the top of beds, lags of mud intraclasts	Individual beds are lenticular to tabular 0.1–3 m thick, extend laterally for several to tens of meters, have erosional basal boundaries and planar upper boundaries. Co-sets are 0.3–0.6 m thick	Commonly woody plants, tetrapod and invertebrate traces, and rare amphibian remains.	Sp, St facies overlie LR-D and occasionally Fl facies (LR-A), and pass laterally into LR-D and LR-A, and vertically into Fl facies (LR-A), and are overlain by the Ischigualasto Formation
	Black, dusky brown mudstone to very fine-grained sandstone, and coal layers. (FCS)	Massive, horizontal and ripple cross-lamination.	Individual beds are tabular, 0.2–0.5 m thick, laterally persist for several to tens of meters, and have non-erosional boundaries.	Very abundant carbonized plants and plant debries.	FCS facies is interbedded with Sp, St facies (LR-E), and pass laterally to Sp, St facies (LR-E).

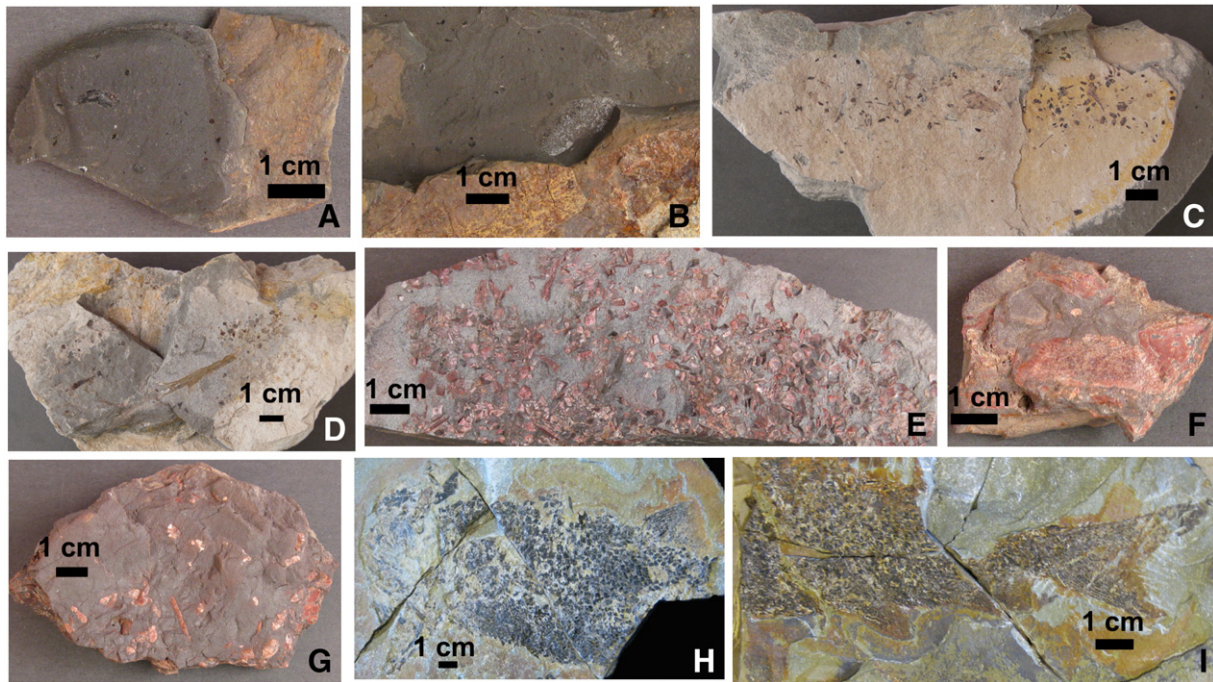


Fig. 4. Fish fossils of the Cacheuta Formation. A–B. Taphofacies Ca-A. C–E. Taphofacies Ca-B. F–G. Taphofacies Ca-C. H–I. Taphofacies Ca-D.

and well sorted (Figs. 4C–E and 6). Taphofacies Ca-C is characterized by disarticulated and associated scales and bones forming clumps, with bioclasts cutting across stratification. The remains are densely packed, loosely sorted, and are found in iron mudstone facies (SFm, SFI, SFr of Ca-A facies association) (Figs. 4F–G and 6). Taphofacies Ca-D is dominated by dispersed and poorly sorted articulated fish, concordant to stratification, preserved in dark shale facies (Fm, FI of Ca-A facies association) (Figs. 4H–I and 6).

Taphofacies LR-A is characterized by well-sorted disarticulated scales and bones that are either dispersed and isolated or in small clumps, and are found in dark shale facies (FI of LR-A facies association) (Figs. 5A–B and 6). Taphofacies LR-B is characterized by densely packed, poorly sorted, partially disarticulated remains found in iron mudstone facies (SFm of LR-A facies association) (Figs. 5C–F and 6). Taphofacies LR-C is characterized by partially to totally articulated remains, which are densely to loosely packed and poorly sorted, and found in sandstone facies (Sh of LR-D facies association) (Figs. 5G–I and 6). The Los Rastros taphofacies presented here are the same as those defined for Los Rastros Formation fishes by Mancuso (2003) and Mancuso and Marsicano (2008).

Principal Components Analysis (PCA) was used to evaluate these taphofacies groupings statistically (Fig. 7), based on 15 different variables (Table 4). The PCA analysis supports the seven taphofacies

defined. The fossil fish assemblages are arranged in five groups based on the first two principal components, which describe 54.20% of the variation in the dataset. The first principal component is dominated by biofabric, spatial arrangement of fish fossils, and recrystallization variables, whereas the second principal component is dominated by relative abundance, degree of articulation, and compaction. The analysis groups the Ca-A and LR-A taphofacies together, as well as the Ca-C and LR-B taphofacies, because the fish remains included in these taphofacies have similar taphonomic characteristics. The single sample of LR-C taphofacies includes articulated fishes in sandstone facies that makes it different from other taphofacies. However, its proximity in the PCA analysis to the Ca-D taphofacies is supported by the similar taphonomic attributes of the fish included in these two taphofacies.

3.4. Interpretation of fish taphofacies

The features that characterize each taphofacies allow understanding of the post-mortem histories of these fish fossils. For example, disarticulation can be caused by scavenging, flotation decay, or turbulence, each of which leaves a characteristic signature in the fossil record (e.g., Elder and Smith, 1988; Ferber and Wells, 1995; Barton and Wilson, 2005).

In the Cacheuta succession, the isolated and dispersed fish remains (Ca-A taphofacies) are found in dark shale facies (FI, Fm). The disarticulation of the fish carcasses is interpreted, based on their dispersion pattern and biofabric, as a result of flotation-decay. Therefore, the remains arrived at the bottom of the lake completely disarticulated. The articulated fish of taphofacies Ca-D, also found in dark shale facies (FI, Fm), clearly arrived at the bottom intact without suffering flotation-decay, predation, or scavenging. Only four specimens of *Neochallaia tellechei* record a randomized dispersal pattern of abdominal elements that supports scavenging. The disarticulated and associated scales and bones (taphofacies Ca-B) found in gray siltstone facies (FSm, FSI) are interpreted to result from flotation-decay, turbulence, and/or scavengers in a river or delta plain, followed by reworking by laminar flow (i.e., remains are concordant to stratification) and burial in a prodelta setting. The disarticulated and associated scales and bones (taphofacies Ca-C) found in iron mudstone facies

Table 3
Abundance of fish taxa in the Cacheuta and Los Rastros formations.

Taxon	No. of specimens
Cacheuta Formation	
<i>Amblypterus lujanensis</i>	2
<i>Challaia cacheutensis</i>	1
<i>Challaia magna</i>	1
<i>Challaia multidentata</i>	1
<i>Neochallaia tellechei</i>	28
Los Rastros Formation	
<i>Gualolepis carinaesquamosa</i>	2
<i>Rastrolepis riojaensis</i>	1
<i>Rastrolepis latipinnata</i>	1
<i>Challaia elongata</i>	2

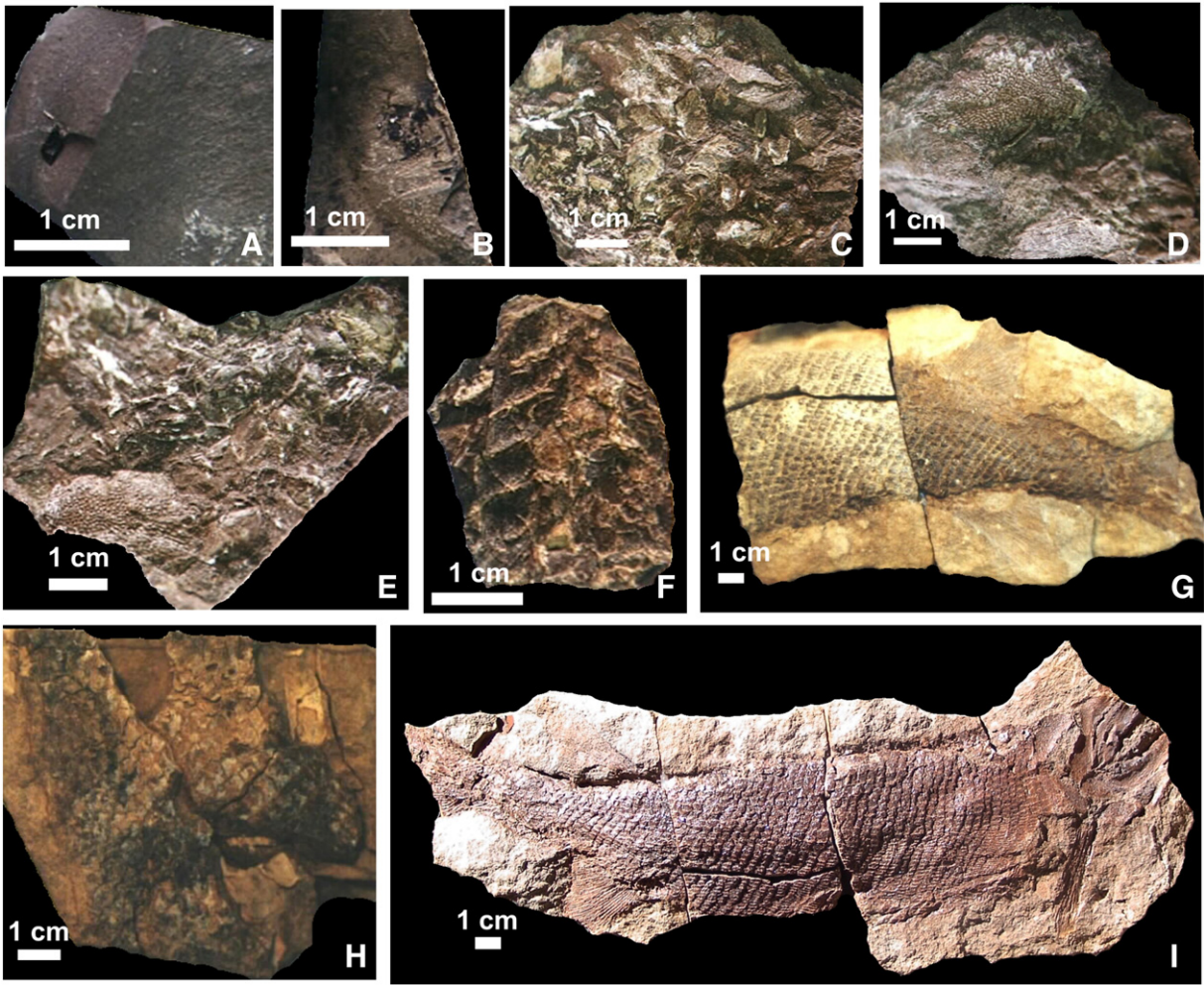


Fig. 5. Fish fossils of the Los Rastros Formation. A–B. Taphofacies LR-A. C–F. Taphofacies LR-B. G–I. Taphofacies LR-C.

(SFm, SFI), are interpreted to result from flotation-decay, turbulence, and/or scavengers in a river or delta plain, followed by reworking by turbulent flow (i.e., remains are cutting across the stratification) and deposited in a prodelta setting.

In the Los Rastros succession, the isolated and dispersed remains (taphofacies LR-A) are found in dark shale facies (FI), and show a similar post-mortem history as Ca-A remains. Therefore, it can infer that they arrived at the lake bottom after suffering flotation decay. The

disarticulated and associated scales and bones (taphofacies LR-B), are found in iron mudstone facies (SFm), and are evidence for the same post-mortem history as Ca-C remains. It is inferred that they

Table 4

List of taphonomic attributes, as variables, that were collected and analyzed for this study.

Variable	Description
P1	Proportion of fish/total fossils in the assemblage
P2	Preservation of hard parts/total fish on surface
P3	Degree of articulation
P4	Orientation in plane/total fish
P5	Cross-cutting stratification/total fish
P6	Packing
P7	Sorting
P8	Density (#fish/cm ²)
P9	Compaction/total fish
P10	Abrasion total fish
P11	Breakage/total fish
P12	Cracking total fish
P13	Oxidation/total fish
P14	Recrystallization/total fish
P15	Host sediment

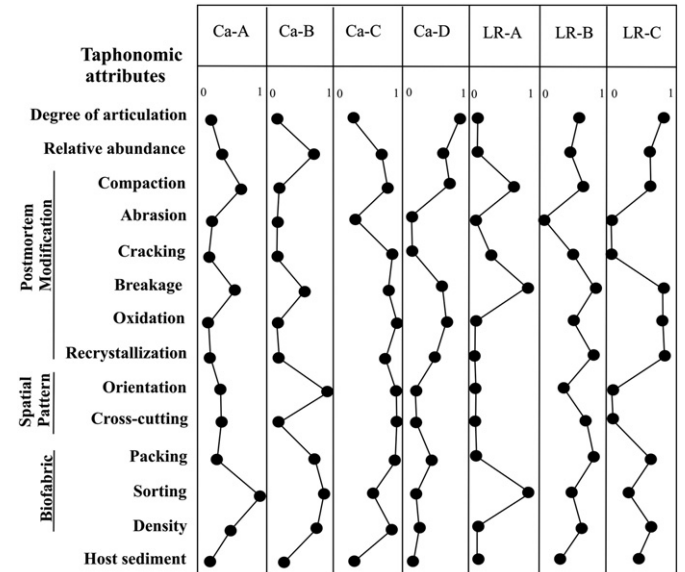


Fig. 6. Taphonomic attributes of fish taphofacies recorded from the Cacheuta and Los Rastros successions. The range (0–1) indicates the state of the taphonomic attribute from 0 to 100%.

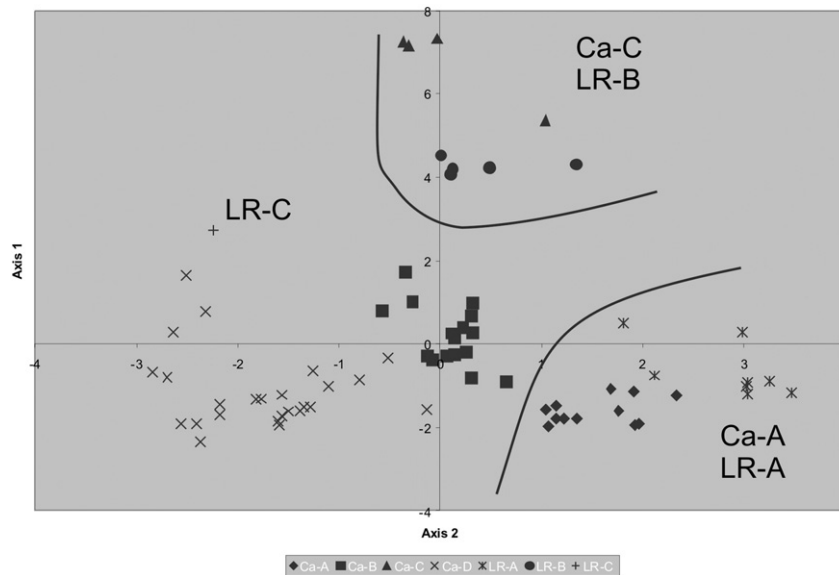


Fig. 7. Principal Components Analysis. The fish assemblages form five groups by the first two components, and support the seven taphofacies. Taphofacies Ca-A and LR-A form a group as do taphofacies Ca-C and LR-B, as these taphofacies have similar taphonomic histories.

were deposited at the lake bottom after suffering flotation decay, turbulence, and/or scavengers in a river or delta plain, followed by reworking by turbulent flow. Finally, the articulated remains of taphofacies LR-C, found in sandstone facies (Sh), arrived intact at the delta front from the delta plain and/or an affluent stream, without suffering flotation decay, predation, or scavenging.

4. Discussion

4.1. Fish taphonomy as an indicator of environmental conditions

The pattern of disarticulation of fish carcasses, which can be caused by scavenging, flotation decay, or turbulence, is useful as an indicator of conditions such as water temperature and oxygenation (Barton and Wilson, 2005). Specimens disarticulated by scavenging at the lake bottom display a dispersion of elements for short distances in several directions from carcasses. Scavenging suggests, at least, a sufficient level of oxygen at the sediment–water interface, and this oxygen level could have fluctuated over time (e.g., Elder and Smith, 1988; Ferber and Wells, 1995; Wilson and Barton, 1996; Barton and Wilson, 2005).

The disarticulation pattern recorded for Los Rastros and Cacheuta fishes (Figs. 4–6) suggests that the scavenging was, in general, absent in both lakes because the remains do not show the short dispersion expected for scavenging disarticulation. Absence of scavenging is probably due to anoxic bottom water, as is supported by the preservation of these specimens in the microlaminated black shale, lacking bioturbation and flow structures. This suggests that during these intervals of deposition, the lake was meromictic (permanent stratified). Only four specimens from the Cacheuta Formation (taphofacies Ca-D, specimens MCNAM-PV 2720, 2725, 2727, and 2802 of *Neochallaia tellecheai*) show evidence of scavenging, with scales and cranial bones disarticulated and slightly randomly dispersed (Fig. 4H). This evidence suggests that, at least a few times, the Cacheuta paleolake had sufficient oxygen levels at the sediment–water interface to support scavengers.

Flotation of carcasses is a result of bacterial decay mediated by temperature and pressure of the water. When water temperature remains low enough so that decay gas concentrations are not enough to float the carcasses, fish carcasses are undisturbed. When the water

temperature is high enough, decay accelerates and gas concentrations can be enough to lift the carcasses (full flotation). Individual elements sporadically fall to the bottom as they disarticulate from the floating carcass, and the fish remains are found as disarticulated and isolated elements (beginning often with bones of the skull). With intermediate water temperatures, gas concentrations are only enough to lift the fish abdomen partially from the bottom (partial flotation) and the fish remains remain partially articulated but with dispersed abdominal elements (Elder and Smith, 1988; Ferber and Wells, 1995; Wilson and Barton, 1996; Barton and Wilson, 2005). The abundance of disarticulated remains, both isolated and associated (taphofacies Ca-A and LR-A), is evidence for full flotation of fish carcasses found in open-lake facies of the Los Rastros and Cacheuta Formations. In contrast, the articulated fish (taphofacies Ca-D) found in the Cacheuta open-lake facies are evidence for no or only partial flotation.

An intact skeleton with disturbed or missing fin elements is evidence of turbulence or currents in a water body. In general, unidirectional scatter is associated with currents (e.g., Elder and Smith, 1988; Wilson and Barton, 1996; Barton and Wilson, 2005). Lack of disturbance of fin elements in articulated fishes of the Cacheuta Formation, and lack of unidirectional scatter of fish remains preserved in open-lake facies in both lakes, are indicators of quiet, deep water. In contrast, the fish remains found in underflow and turbidity facies often show unidirectional scatter, suggesting that these deposits are associated with currents.

However, the disarticulated and associated fish remains found in turbidity and underflow facies could have suffered flotation decay, scavenging and/or turbulence in a river or delta plain. Thus, the taphonomic attributes preserved (i.e., remains cutting the stratification or remains concordant to stratification) allow discrimination between these two deposit types.

In both lakes, the flotation-decay process is the main contributor to fish disarticulation. This evidence supports the interpretation of the Los Rastros paleolake as being warm with an anoxic bottom and lack of turbulence in the bottom of the open lake, with oxygenated and turbulent margins and deltas. The articulated fish remains found in the Los Rastros delta-front facies suggest rapid burial by the sediment that prevented flotation-decay, scavenging, and action of turbulence. The Cacheuta paleolake preserves evidence of fluctuation in temperature that allowed times of full, partial, and no flotation of fish carcasses.

The evidence supports the interpretation of the Cacheuta paleolake as having an anoxic bottom and lack of turbulence, but with some times of mixing allowing oxygenation of the water–sediment interface, temporarily supporting scavengers.

4.2. Taphonomic model

In the Cacheuta and Los Rastros successions, the fish remains are found in five different settings. Fish remains from open-lake facies are isolated and dispersed remains or articulated specimens; in underflow facies they are preserved as disarticulated and associated scales and bones; in distal turbidity-current facies they are preserved as disarticulated and associated scales and bones; and in delta-front facies the fish specimens are articulated (Fig. 8).

A taphonomic model for the Cacheuta and Los Rastros successions based on these defined taphofacies is proposed. The model is more comprehensive than the Los Rastros model presented by Mancuso (2003) and Mancuso and Marsicano (2008) and characterizes a lacustrine-deltaic environment developed in the rift basin with three sub-environments, each one with its particular fossil assemblages. The sub-environments are the offshore lacustrine facies (facies association Ca-A and LR-A), the prodelta facies (facies association Ca-A and LR-A), and the deltaic front facies (facies association LR-D) (Fig. 8).

The remains recorded in the offshore lacustrine sub-environment display two different post-mortem histories, depending on the water conditions. The isolated and dispersed fish remains (taphofacies Ca-A and LR-A) were disarticulated during flotation decay in the lake or in the trunk stream and stayed in suspension for varying periods according to their floating potential. The articulated fishes (taphofacies Ca-D) were quickly deposited on the bottom without suffering flotation decay, scavenging, or turbulence. Only some specimens suffered scavenging when the oxygen levels at the water–sediment interface were sufficiently high to support scavengers.

In the prodelta sub-environment, the remains arrived in the lake within underflow or turbidity currents. The disarticulated and associated fish remains (taphofacies Ca-B, Ca-C, and LR-B) were sorted and transported from trunk streams and delta-fronts and buried in the prodelta. The difference between the kind of flow (laminar or turbulent) is evidenced by the spatial arrangement and biofabric of the deposits. The underflow deposits show loosely packed and well-sorted bioclasts forming stringers concordant to stratification, whereas the turbidity currents show densely packed and loosely sorted bioclasts cutting the stratification.

The delta-front sub-environment includes articulated fishes (taphofacies LR-C). They were floating in the trunk stream and deposited quickly in the delta-front facies according to their hydraulic potential.

4.3. Fish taphonomy as an indicator of environment effects on speciation

The taphonomic analysis of fish can be an indicator of environment effects on speciation. Particularly, the taphonomic studies allow characterization of the condition and dynamics of the rift lake system where the fishes were more likely to generate new species. They, also, allow recognition of the environment where the fish lived, and identify generalist species vs. specialist species.

The taphonomic and faunal differences reported between the Cacheuta and Los Rastros paleolakes are mainly related to differing environmental conditions. On the one hand, the Los Rastros paleolake was a large, warm lake with a permanent anoxic bottom that enhanced the full flotation of autochthonous dead fish, and it was developed during initial and climax rifting (Mancuso et al., 2004; Mancuso, 2005; Mancuso and Caselli, in press). The tectonic stage explains the continuous generation of space and renewal of different sub-environments and resources provided by rejuvenation of uplift areas and possibly leading to relaxed selection. This is a significant difference from the known examples of the Newark Supergroup, where the semionotids showed a rapid diversification (up to 20 species) related to the development of cyclic formation and evaporation of the relatively ephemeral lakes (McCune, 2004).

On the other hand, the Cacheuta paleolake possessed a fluctuating temperature with an anoxic bottom, and occasional mixing that enhanced some periods of full flotation of the autochthonous dead fish and some periods of only partial or no flotation that allowed preservation of the autochthonous fish fauna. The paleolake was developed during late rift climax and initial post-rift time (Kokogian et al., 1993). Thus, the fluctuating lake conditions probably were associated with these tectonic stages, additionally modulated by climate fluctuation. However, the speciation pattern was, in the Cacheuta case, similar to the Los Rastros but with more diversification than in the Los Rastros fish fauna probably associated with fluctuating conditions that enhanced original and loss of the habitats.

The differences in abundance between the Cacheuta and Los Rastros fish records is associated with an unfavorable water chemistry during Los Rastros deposition that depressed the autochthonous vertebrate fauna (Mancuso, 2003; Ottone et al., 2005; Mancuso and

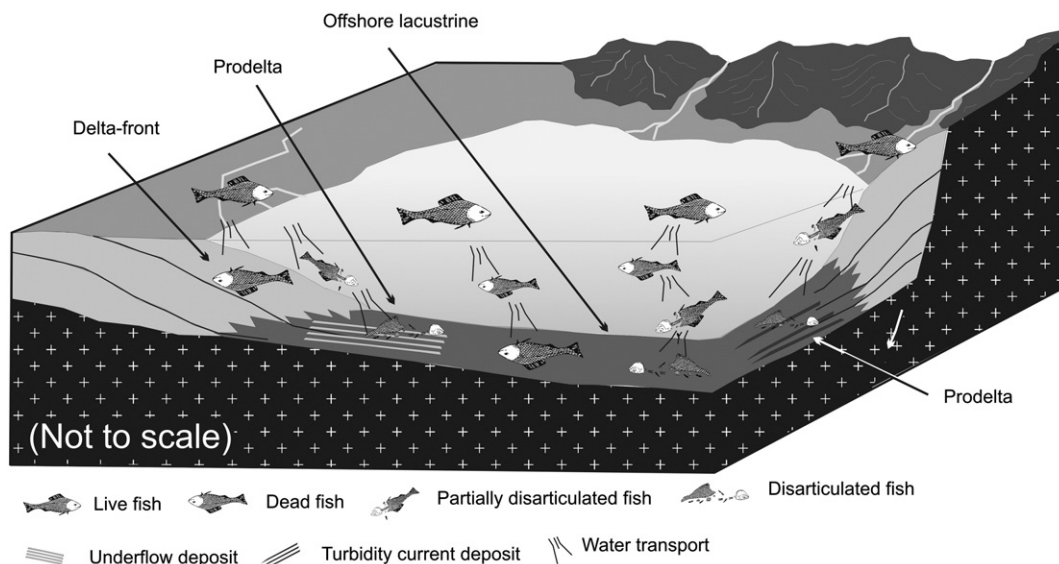


Fig. 8. Taphonomic model of the fish fossil occurrences in the rift lakes.

Marsicano, 2008), and abundant articulated and disarticulated fish remains and tetrapod body fossils during Cacheuta deposition (Marsicano et al., 2001; López-Arbarelo et al., 2010).

Finally, the evidence presented here allows to characterize the conditions and dynamics of the environment that were more likely to generate new species. Loss of habitats plays an important role in the generation of species, so conditions, mainly during quiet tectonic stages, of climate modulated fluctuation recorded in Cacheuta Formation, as in the Newark Supergroup, may be conducive to rapid diversification of fishes.

Gore (1988) suggested that the well-preserved and articulated fish remains in the deltaic facies are evidence that they were allochthonous to the lacustrine environment and were transported by river currents into the lake. Accordingly, Mancuso (2003) and Mancuso and Marsicano (2008) proposed that the fishes of the Los Rastros Formation preserved in delta-front and turbidity current deposits (taphofacies LR-B and LR-C) were allochthonous to the lake and probably inhabited the delta plain and affluent fluvial system. In contrast, the isolated fish remains preserved in open-lake deposits (taphofacies LR-A), might represent both autochthonous and/or allochthonous specimens. The fishes of the Cacheuta Formation preserved in open-lake deposits (taphofacies Ca-A and Ca-D), both articulated and isolated remains, might represent autochthonous lacustrine specimens, based on the well-preserved material, whereas the fish remains preserved in underflow and turbidity current deposits (taphofacies Ca-B and Ca-C) were allochthonous to the lake and probably inhabited the delta plain and affluent fluvial system.

Freshwater fishes can live in rivers and lakes, or can be restricted to either (McCune, 1987). The Cacheuta and Los Rastros successions preserved fish species that lived in both rivers and lakes. Some of them probably could frequent both environments, and other species were restricted to one or the other. To determine this for specific features would require species-level identification, which is currently only possible for articulated fish specimens from the open-lake and delta-front facies. Only a few articulated specimens were identified as different species of some multi-species genera (*Challaia* and *Rastrolepis*, see Table 3), because until now only the more complete specimens can be systematically determined. Therefore, current sample size of fossil is inadequate to determine which species were exclusive to the lake as opposed to which lived both in the trunk streams and lake. Based on information available now, only the genus *Challaia* was probably a taxon with species that lived in both environments.

Deep rift lakes, in general, develop important endemic lacustrine faunas because they are discontinuous water islands in a sea of land, have persisted for a long time, and are buffered from climatic change by great depth (McCune, 1987, 2004; Cohen, 2003; Whiteside et al., 2011). The Cacheuta fish assemblages include five species, three of them belonging to the same genus (*Challaia*) (Table 3), and represent a lacustrine fish fauna. In contrast, the Los Rastros fish assemblages include four species, two of them belonging to the same genus (*Rastrolepis*) (Table 3), and represents a predominantly fluvial fish fauna. *Challaia* is the only taxon common to both the Cacheuta and Los Rastros assemblages; moreover it is also present in the fluvial-deltaic Potrerillos Formation (Cuyana Basin). Therefore, it is proposed here that *Challaia* represents a lineage able to move freely between lotic and lentic habitats. Furthermore, the temporal extension of the record of this taxon (Fig. 2) and its occurrence in two separate rift basins (Cuyana and Ischigualasto-Villa Unión basins) indicates some kind of transient watershed connection between the basins and suggests the ability of this species to adapt to different environments and conditions. Accordingly, of the taxa presently known, *Challaia* is probably the only non-endemic element in these lacustrine basins. It was probably a colonist taxon in the Cacheuta paleolake that led to rapid speciation in endemic species flock enhanced by relatively rapid colonization of recently formed habitats, as occurred, for example, with the semionotids of the Newark Supergroup (e.g., McCune, 2004).

The genus *Challaia* is an unusual taxon whose species were possibly able to live in both lotic and lentic habitats. The rest of the identified taxa of these two fish faunas were endemic to each lake and are consistent with allopatric speciation recorded in other rift lakes (e.g., Smith, 1987; Cohen, 2003; Day et al., 2008; Whiteside et al., 2011). The presence of more than one species each of *Challaia* and *Rastrolepis* (see Table 3) is suggestive of sympatric speciation (e.g., Smith, 1987; Cohen, 2003; Day et al., 2008), perhaps facilitated by the diversity of environments and conditions in both lakes. McCune (1987, 1990, 1996, 2004) documented that the semionotids in the Newark Supergroup displayed rapid diversification related to relatively ephemeral lacustrine environments. In contrast, the Triassic basins in Argentina include relatively stable deep lakes that may have allowed for relaxed selection and did not promote rapid speciation.

Finally, the fish taphonomic study performed in the Cacheuta and Los Rastros paleolakes permits recognition of the environment where the fish lived, revealing if the fish were autochthonous or allochthonous to the lake. Also, the study allows identification of generalist species vs. specialist species, suggesting for the endemic species their preferences for life in lotic, lentic, or both kinds of habitats.

5. Conclusions

This fish taphonomic study of two different rift-basin lacustrine successions allowed testing of two proposed hypotheses. In the cases reported in this contribution, fish taphonomy was useful as an indicator of environmental conditions, as the fish remains associated with offshore, underflow, turbidity, and deltaic deposits allow characterization and differentiation of the deposits. The Cacheuta paleolake fluctuated in temperature, with an anoxic bottom and lack of turbulence, but with some times of mixing allowing oxygenation of the sediment–water interface. The Los Rastros paleolake was warm with an anoxic bottom and a lack of turbulence in the open lake, but with oxygenated and turbulent margins and deltas.

Fish taphonomy was also useful for understanding environmental effects on speciation. The fluctuating Cacheuta paleolake conditions associated with the tectonic stages of late rift climax and initial post-rift time, additionally modulated by climate fluctuation and enhanced by loss of habitat, promoted fish diversification. The Los Rastros tectonic stages of initial and climax rifting accompanied by the continuous generation of space and renewal of different sub-environments and resources provided by rejuvenation of uplift areas, led to relaxed fish selection. Thus, the differences in the tectonic stage that resulted in differences of environmental conditions and dynamics recognized with the help of the taphonomic study allowed identification of conditions either less conducive or more conducive to the generation of new species. The taphonomic analysis also gave evidence for identification of endemic species and their preferences for life in lotic, lentic, or both kinds of habitats. The results suggested that the Cacheuta fish assemblages represent mainly a lacustrine fish fauna, whereas the Los Rastros fish assemblages represent a predominantly fluvial fish fauna. The genus *Challaia* is an unusual taxon, common to both basins, that was possibly able to live in both lotic and lentic habitats. The endemic elements of these two fish faunas are consistent with allopatric speciation as recorded in other rift lakes, whereas the presence of more than one species of a single genus is suggestive of sympatric speciation.

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