

## Diversity of Cretaceous continental actinopterygians from Argentina, South America

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**Abstract** - South America holds a significant number of continental fish-bearing deposits of Cretaceous age. The principal purpose of the current article is to illustrate the diversity of continental actinopterygian assemblages of the main Cretaceous localities from Argentina, southern South America, providing an updated review and a discussion about their particular history. Various aspects of the knowledge concerning Cretaceous continental actinopterygian faunas from Argentina have been improved in last years, especially those related to morphology and alpha taxonomy. However, other issues such as phylogeny and biogeography, are unknown or on its beginning.

**Keywords:** Actinopterygii, intracontinental, Early Cretaceous, Gondwana, endemism

### 1. Introduction

South America holds a significant number of continental fish-bearing deposits of Cretaceous age. Among the most magnificent and well-known are the Lower Cretaceous basins from northeast Brazil which were developed during the break out of Gondwana in the Aptian-Albian (Brito and Yabumoto, 2011; Lindoso *et al.*, 2016).

The opening of the South Atlantic Ocean proceeded from south to north (Arai, 2014), and while by the Late Aptian this ocean was well-developed at southern latitudes, northern South America was still connected with Africa (San Martín and Ronquist, 2004). In this geological framework, especial attention has been dedicated to Brazilian localities being them used, sometimes, even as a western Gondwana synonymous (e.g., Maisey, 2000).

Continental actinopterygian-bearing localities of Southern South America are rare, overall during the the Cretaceous (Arratia and Cione, 1996; López-Arbarello, 2004). Thereby, the main relevant deposits are concentrated in the Early Cretaceous. They are different from sites of the same age from Brazil—which have a marine component from the Tethys—presenting a particular and a unique history. However, few aspects concerning their diversity and their general features have been documented.

Fossiliferous sites from southern South America, as well as other Early Cretaceous localities of western Gondwana, correspond to rift basins directly affected by tectonism (Maisey, 2000). In Uruguay, the Tacuarembó Formation outcrops in the Paraná Basin with records of some scales and holostean remains; however, this unit has a putative Lower Cretaceous age (Perea *et al.*, 2009; 2014). In Argentina, the El Gigante Group was deposited in the

Western Sierras Pampeanas rift system (Arcucci *et al.*, 2015), which is the focus of the present study.

The principal purpose of the current article is to illustrate the diversity of continental actinopterygian assemblages of the main Cretaceous localities from Argentina, southern South America, providing an updated review and a discussion about their particular history.

### 2. Geological Setting

The Lower Cretaceous rift system of Western Sierras Pampeanas (Fig. 1 a), in central Argentina, was developed during the open of the South Atlantic in the Aptian-Albian (Flores, 1969; Rivarola and Spalletti, 2006). This system was composed by several extensional, intracontinental and discrete basins which correspond to the reactivation of antique Triassic rifts during the Early Cretaceous (Benedetto, 2010). The El Gigante Group (Fig. 1 b) outcrops on the Western Sierras Pampeanas in San Luis Province and is mainly constituted by siliciclastic fluvial and lacustrine sediments besides eolian deposits (Castillo-Elías *et al.*, 2017).

### 3. Formations and localities

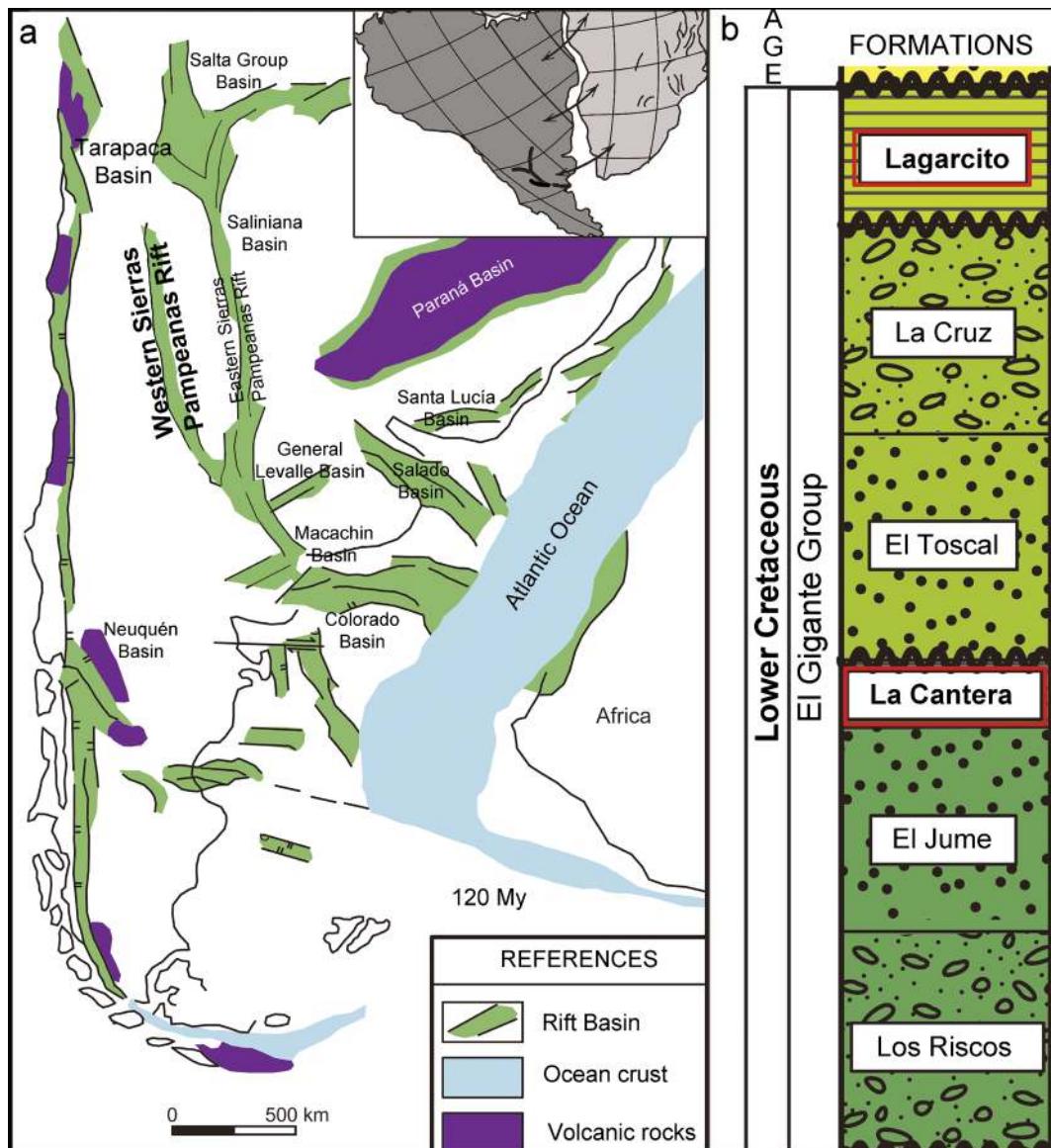
The La Cantera and Lagarcito Formations are the only fish-bearing units of the El Gigante Group.

#### 3.1 La Cantera Formation (Fig. 2)

Based on its lithological characteristics and on its freshwater biota, the La Cantera Formation (Fig. 2 a-b) has been interpreted as a lacustrine-delta environment (Arcucci *et al.*, 2015; Castillo-Elías *et al.*, 2016 a). It is composed by papery, laminated green-grey mudstones interbedded with siliciclastic siltstones (Criado-Roque *et*

al., 1981). According to current interpretations, the fluvial system had an ephemeral behavior and under certain conditions, numerous fluvial streams fed the lake increasing the level of the water. In addition, the lake was supposed to have had a restricted outlet, being hydrologically closed (Castillo-Elías *et al.*, 2016 a). Among biota, the freshwater algae constituted the dominant microphytoplankton assemblage (Prámparo, 1999). The palynomorph assemblage found in the La Cantera Formation places this unit in the late Aptian (Prámparo, 1994, Prámparo *et al.*, 2007). Fossil fishes come from *La Cantera de Gutierrez*, which is the type locality and the companion biota is composed by different aquatic freshwater insects, ostracods, and

macro- and micro- plant remains including mainly angiosperms, and sphenophytes, bryophytes, pteridophytes and gnetophytes (Arcucci *et al.*, 2015). Fossils are very well preserved, for instance, fishes present fully articulated skeletons, chondral elements (e.g., haemal arches), scales with their microstructure (see Giordano *et al.*, 2016), and body outlines (Fig. 2 c-e). Among plants, delicate remains of briophyte (see Puebla *et al.*, 2012), leaves, flowers, seeds and cones are preserved. This excellent preservation has been explained due to the presence of biofilms, which allow to preserve delicate organic and sedimentary structures (Castillo-Elías *et al.*, 2016b).



**Figure 1.** (a) Location of the intracontinental Albian-Aptian Western Sierras Pampeanas Rift System. Modified from Gabriela Castillo-Elías *et al.* (2017). (b) El Gigante Group, San Luis, Argentina.

### 3.2 Lagarcito Formation (Fig. 3)

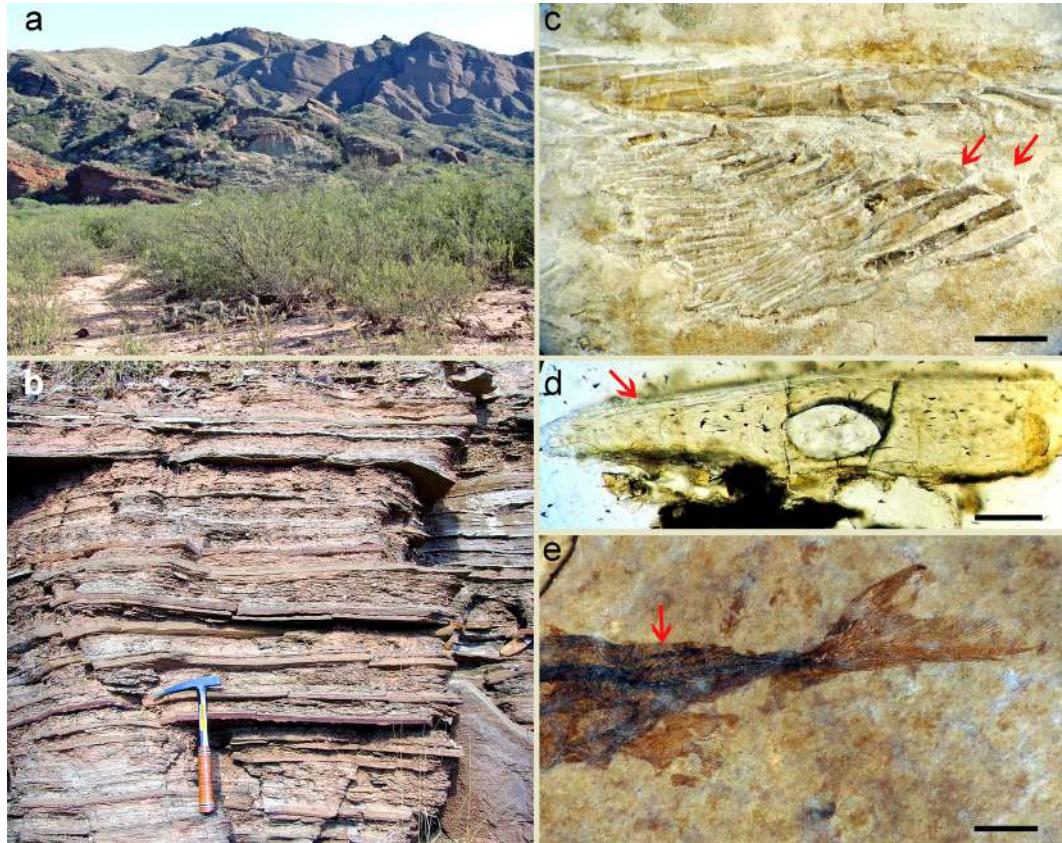
The fossil-bearing facies of the Largacito Formation have been interpreted as a perennial lake which was occasionally filled by endorheic ephemeral fluvial system (Chiappe *et al.*, 1998a), controlled by climate as well as

tectonism (Rivarola and Spalletti, 2006).

Based on its fossil association as well as on its stratigraphic relationships, The Lagarcito Formation has been dated of Albian age (Chiappe *et al.*, 1998a, b). Additional palynological data positions the formation between the

Aptian-Albian (Prámparo *et al.*, 2005; Narváez *et al.*, 2013; Mego and Prámparo, 2013). Moreover, K-Ar datation indicates 107.4-109.4 My for basalts of the La Cruz Formation, which underlies the Lagarcito Formation (Yrigoyen, 1975).

The type locality where fishes come from is called *Loma del Pterodaustro* and is located in the Sierra de las Quijadas National Park, San Luis, Argentina (Fig. 3). The associated biota is composed by some fossil traces, plant remains, conchostracans and several remains of the well-known pterosaur *Pterodaustro guinazui* (Chiappe *et al.*, 1998a, b; Arcucci *et al.*, 2015).



**Figure 2.** La Cantera Formation (a) Outcrops overall view. (b) Stratigraphic section in the type locality. (c) Caudal fin of a basal Actinopterygii (MIC-V562a); red arrows show haemal arches (chondral elements preserved). Scale bar = 2 mm. (d) Lepisosteoid-type scale (MIC-V523); red arrow shows ganoine layers (microstructure preserved). Scale bar = 0.5 mm. (e) Postcranial portion of a basal actinopterygian (MIC-V666); red arrow indicates body outline preserved. Scale bar = 5 mm.



**Figure 3.** Lagarcito Formation (a) Stratigraphic section in the type locality. Courtesy of Federico Gianechini. (b) Photograph of the *Loma del Pterodaustro* quarry during one of the field works in 1994. Courtesy of David Rivarola.

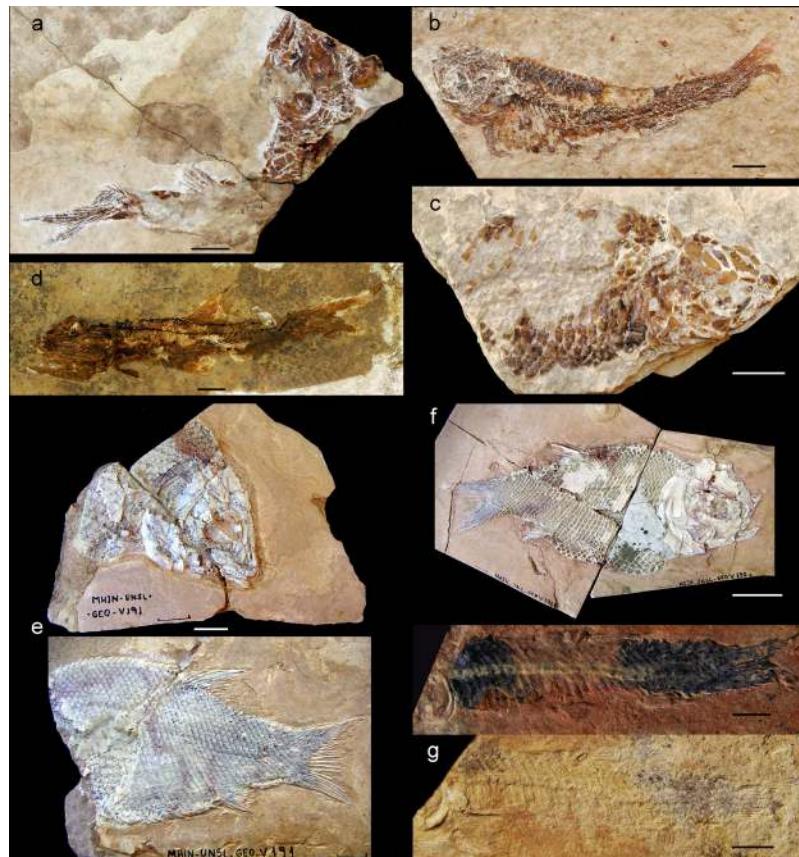
#### 4. Actinopterygian diversity

##### 4.1 La Cantera Formation (Fig. 4 a-d)

A curious pattern of this fish fauna and the associated biota is the small maximum size reached by all taxa of the assemblage. Each fish species, for instance, does not exceed 10 cm of total length. Two large sets of Actinopterygii have been identified, constituting one of them a group of ganoid neopterygians and the other, a basal actinopterygian group. Ganoid neopterygians (Fig. 4 a-c) were previously identified as “Pholidophoriformes” (Flores, 1969; López-Arbarello, 2004). However, detailed morphological and comparative studies, including phylogenetic analyses, were recently made (Giordano, 2015; Giordano *et al.*, 2016), showing that this group constitutes a new family of Teleosteomorpha *sensu* Arratia (2001). This new taxon shares numerous

cranial and postcranial characters with other teleosteomorphs, although its position among Teleosteomorpha is uncertain. In order to clarify this issue, new and more extensive comparisons are being carried out. It is important to remark that this new family, correspond to an endemic taxon of southern South America.

Despite being the less studied fish group of the locality, basal actinopterygians are the most frequent, being approximately 70% of the total fish assemblage (Fig. 4 d). They were occasionally revised and preliminary interpreted to have affinities with coccolepisids (Spinuzza, 1986; López-Arbarello, 2004). However, their position among chondrostean is not clear (pers. obser.). Thereby, detailed studies regarding the morphology, taxonomy and systematic of this group are currently in process.



**Figure 4.** Actinopterygii diversity held in Museo Interactivo de Ciencias (MIC), UNSL: La Cantera Formation (a-d) and Lagarcito Formation (e-g). (a) MIC-V659a: Teleosteomorpha nov. fam nov. gen et sp [A] (unpublished results). Scale bar = 5 mm. (b) MIC-V701a: Teleosteomorpha nov. fam nov. gen et sp [A] (unpublished results). Scale bar = 5 mm. (c) MIC-V705: Teleosteomorpha nov. fam nov. gen et sp [B] (unpublished results). Scale bar = 5 mm. (d) MIC-V569: basal Actinopterygii. Scale bar = 5 mm. (e) MIC-V191 a and b: *Neosemionotus punctatus* Bocchino, 1973. Scale bar = 1 cm. (f) MIC-V190: *Neosemionotus punctatus* Bocchino 1973. Scale bar = 5 cm. (g) MIC-V62 a and b: Pleuropholidae nov. gen et sp. (manuscript on preparation). Scale bars = 5 mm.

#### 4.2 Lagarcito Formation (Fig. 4 e-g)

Rather than by the actinopterygian assemblage, Lagarcito Formation is more renowned by *Pterodaustro guinazui* (Chiappe *et al.* 1998 a, b). However, fishes are no less interesting.

Among the total set of Actinopterygii, more than 50 specimens of 'Semionotiformes' have been recovered. Unexpectedly, only two specimens of Pleuropholidae have been found along more than 20 years of paleontological excavations.

Previous studies described more than one species of semionotiforms from Lagarcito Formation (Bocchino, 1973; 1974) (Fig. 4 e-f). However, a recent revision, which included more material, confirmed a unique taxon corresponding to *Neosemionotus punctatus* Bocchino, 1973 (López-Arbarello and Codorniú, 2007). Remarkably, this species constitutes an endemic ginglymodian fish that, according to latest studies, occupies an uncertain position among Ginglymodi (López-Arbarello, 2012).

It is well-known that the family Pleuropholidae presents a rare fossil record worldwide, so this scarcity increases the significance of the pleuropholids from Lagarcito Formation (Fig. 4 g). These specimens have been submitted to a detailed morphological study, being com-

pared with other members of the family. Results indicate that it is a new taxon among Pleuropholidae (Succar and Giordano, 2012; Giordano *et al.*, in prep). It is interesting to remark that, so far as known, most Semionotiformes of the Early Cretaceous from Africa, Asia, Europe and South America, inhabited freshwater environments (Cavin, 2013). Following the same pattern, most Cretaceous Pleuropholidae were continental species, while most Jurassic forms were marine.

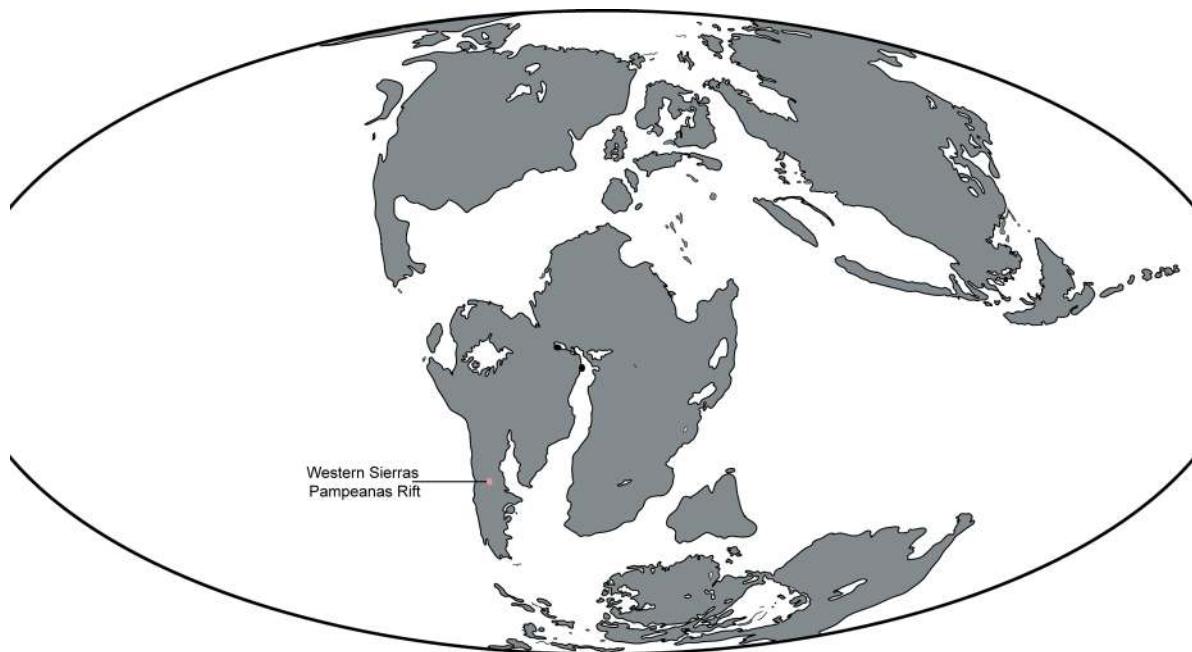
#### 5. Discussion and conclusions

Various aspects of the knowledge concerning Cretaceous continental actinopterygian faunas from Argentina have been improved in last years, especially those related to morphology and alpha taxonomy (e.g., López-Arbarello and Codorniú, 2007; Giordano, 2015; Giordano *et al.*, 2016). However, other issues such as phylogeny and biogeography, are unknown or on its beginning. An interesting topic of study is the endemism component which characterized the continental actinopterygians of the Early Cretaceous from Argentina. This aspect is presented at genera and family levels and besides it is reflected in other animal taxa of these assemblages (species level) like insects from La Cantera Formation and *Pterodaustro guinazui* (Ar-

ucci *et al.*, 2015).

An endemic species is that circumscribed to a unique place, regardless the size of the area (Rapoport and Monjeau, 2001). Thus, the endemism observed in continental Cretaceous actinopterygian assemblages from Southern South America, might not be explained apart from the geological framework. The rift system of Western Sierras Pampeanas (Fig. 1 a) was developed when Gondwana separated during the Aptian-Albian. According to Maisey (2000), these events had a long-term impact upon the distribution patterns of marine and freshwater organisms. The Western Sierras Pampeanas system, was composed by several discrete intermountain basins (Castillo-Elías *et al.*, 2016 a) where biotas were confined. So, actinopterygians most likely developed as local faunas, building their own population dynamics, and sharing a common and a unique spatial history. A high degree of endemism is related to isolation time of an area together with its habitats diversification (Espinosa Organista *et al.*, 2001). Rift basins suffer continue modifications which could be translated in a variety of habitats (Guinot and Cavin, 2015). In this changeable context, barriers<sup>3/4</sup>which

obstructs the dispersal and the gene flow among populations<sup>3/4</sup>are in continue development (Morrone and Escalante, 2016). In a dynamic tectonic scenario, where intermittent barriers are developed, not only vicariant events explains fish species distribution, also the dispersal by intermountain temporary corridors (Craw *et al.*, 2008). Considering the regional paleogeographical reconstruction of South America (Scotese, 2014) (Fig. 5), in addition to the geological and paleobiological local data, there is no evidences of marine ingressions for the Aptian-Albian interval in Western Sierras Pampeanas rift system. This condition made these basins different from those rift basins from the Salta Group of the Upper Cretaceous, Argentina, which present epicontinental marine facies (Cónsole Gonella *et al.*, 2012). Moreover, Argentinian Lower Cretaceous central rift basins differ from those well-known basins from northeast Brazil (Fig. 5). By the Aptian-Albian a marine transgression of western Tethys has been recorded in several Brazilian interior basins, including numerous formations such as Crato and Santana from the Araripe Basin and Codó from the Parnaíba Basin (Brito and Yabumoto, 2011; Arai, 2014; Lindoso *et al.*, 2016).



**Figure 5.** Early Cretaceous (Late Aptian) paleogeographic map of emerged areas according to Scotese (2014). It shows the location of the Western Sierras Pampeanas Rift System (red circle) and the location of some of the main Brazilian basins (black circles).

As concluding remarks, continental Actinopterygii-bearing localities of the Cretaceous in Argentina are scarce. Although incompletely known, actinopterygians from La Cantera and Lagarcito Formations provide interesting and unique morphological, systematic and historical aspects of species which differs from those known faunas from Brazil and other regions from Gondwana. Therefore, it is imperative to continue studying Argentinian fish biotas as well as regional and local geology in an integrative way. It will allow to understand the still fragmentary distribution

patterns of these Cretaceous continental actinopterygian faunas from southern South America in the wide context of Gondwana.

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