# First record of vertebrates (Actinopterygii, Pseudobeaconiidae) from the Mollar Formation (lower Middle Triassic) of the Cuyana rift basin, Argentina

P. Guillermina Giordano[a*], Cecilia A. Benavente[b], Gonzalo Martínez Palacio[a]

[a]Universidad Nacional de San Luis (UNSL). Ejército de Los Andes 950, D5700HHV San Luis, San Luis, Argentina. *guillerminagiordano@gmail.com*; *tonchisivanmartinez@gmail.com*

[b]Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, CCT-CONICET. Av. Dr. Adrian Ruiz Leal, M5500IRA Ciudad de Mendoza, Mendoza, Argentina. *cebenavente@gmail.com*

*Corresponding author



## ABSTRACT

We present a new record of Actinopterygii from continental Triassic rocks from southern South America, Argentina. The material provenance is the Mollar Formation, Santa Clara subbasin, Cuyana rift basin. We studied three specimens preserved in black finely laminated mudstones with different grades of preservation, most of them incomplete but articulated or in casts. These Actinopterygii specimens have been identified as members of the Pseudobeaconiidae family based on their unique combination of diagnostic characters. Pseudobeaconiidae is endemic to southwestern Gondwanan lacustrine settings and in Argentina is restricted to the Ischigualasto-Villa Unión and Cuyana rift basins, being the fishes reported here the first vertebrate remains from the Mollar Formation. Considering Anisian age previously obtained for the overlying Santa Clara Abajo Formation, the fish remains reported here could represent early Anisian or older times, extending the biochron of Pseudobeaconiidae some Myr back. In this context, we

revised fish remains from the Middle-to-Upper Triassic Estratos El Bordo unit, in northern Chile, previously assigned to Pseudobeaconiidae, and reassign them as cf. Pseudobeaconiidae because the morphological characters observed hinder the confirmation of most of the diagnostic characters of the family. Further exhaustive preparation of the Mollar Formation material will allow more accurate taxonomic assignments, for example, if these specimens represent a new species of the family Pseudobeaconiidae.

*Keywords: Fishes; Lacustrine; Paleolake; Santa Clara subbasin; Gondwana*

**RESUMEN. Primer registro de vertebrados (Actinopterygii, Pseudobeaconiidae) de la Formación Mollar (Triásico Medio inferior) de la cuenca Cuyana, Argentina.** Se presenta un nuevo registro de Actinopterygii de rocas continentales triásicas del centro-oeste de Argentina. El material analizado proviene de la Formación Mollar, subcuenca Santa Clara, cuenca Cuyana. Se estudiaron tres ejemplares preservados en limolitas negras finamente laminadas con distintos grados de preservación, la mayoría de ellos articulados o en moldes. Estos especímenes de Actinopterygii han sido identificados como miembros de la familia Pseudobeaconiidae a partir de una combinación única de caracteres diagnósticos. La familia Pseudobeaconiidae es endémica de sistemas lacustres del suroeste de Gondwana y en Argentina su distribución se encuentra restringida a las cuencas Ischigualasto-Villa Unión y Cuyana, siendo los peces aquí reportados los primeros restos de vertebrados de la Formación Mollar. Al considerar la edad anisiana previamente obtenida para la Formación sobreyacente Santa Clara Abajo, la edad de los peces descritos podría corresponder al Anisiano temprano o tal vez más antigua, lo cual extendería el biocrón de Pseudobeaconiidae algunos millones de años al pasado. En este contexto, se revisaron además restos de peces de la unidad Estratos El Bordo del Triásico Medio-Superior del norte de Chile, previamente asignados a la familia

Pseudobeaconiidae, y se reasignaron aquí como cf. Pseudobeaconiidae debido a que los caracteres morfológicos observados no permiten confirmar la mayoría de los caracteres diagnósticos de esta familia. Futuras preparaciones exhaustivas del material de la Formación Mollar permitirán asignaciones taxonómicas más precisas, como por ejemplo, determinar si estos especímenes representan una nueva especie de la familia Pseudobeaconiidae.

*Palabras clave: Peces; Lacustre; Paleolago; Subcuenca Santa Clara; Gondwana*

## 1. Introduction

Pseudobeaconiidae López-Arbarello and Zavattieri, 2008, is an endemic family of Triassic fishes from lacustrine settings of southwestern Gondwana that lacks a clear phylogenetic position. While some authors have considered them as a stem-group Actinopterygii or "subholosteans" (e.g., López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010; Giordano et al, 2023), others have included them as a stem group of Neopterygii (e.g., Xu et al., 2015; Gouric-Cavalli et al., 2017; Xu, 2021; Yuan et al., 2022). This Triassic fish family was recorded first in Argentina (López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010) and, more recently, a putative record was described in northern Chile (Otero et al., 2023).

Triassic fish remains of Pseudobeaconiidae up to this contribution were known from upper Anisian to Carnian rocks. In Argentina, their distribution is restricted to the Cuyana (López-Arbarello et al., 2010) and to the Ischigualasto-Villa Unión (Gouiric-Cavalli et al., 2017) rift basins, being the majority of the material available to date collected from the first basin (Table 1). Within the Cuyana basin, the remains attributed to Pseudobeaconiidae have been reported from the Potrerillos subbasin, particularly from the Potrerillos Formation with the records of *Pseudobeaconia celestae* and *Mendocinichthys brevis* (Bordas, 1944; Schaeffer, 1955; López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010). In addition, there are records of Pseudobeaconiidae from the Santa Clara subbasin, particularly from the Santa Clara Abajo Formation, represented by *Pseudobeaconia bracaccinii*, *Pseudobeaconia elegans,* and *Pseudobeaconia cuyana* (Bordas, 1944; Hutchinson, 1973; Breglia, 2000; López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010; Trotteyn et al., 2023). On the other hand, within the Ischigualasto-Villa Unión basin, indetermined pseudobeaconiids have been

recovered from levels of the Chañares Formation (Marsicano et al., 2015; Gouiric-Cavalli et al., 2017; Mancuso et al., 2020; Irmis et al., 2022).

The Santa Clara subbasin is part of the Cuyana basin, in central-west Argentina (Stipanicic and Marsicano, 2002; Fig. 1). The infilling of the subbasin corresponds to five continental sedimentary units, all of which are part of the Peñasco Group (Spalletti and Zavattieri, 2009; Fig. 2). The lowermost unit is the ~250 m-thick Cielo Formation, which outcrops at the southernmost margin of the subbasin and represents alluvial-fluvial sedimentary paleoenvironments. The overlying ~250 m-thick Mollar Formation, which bears the reported fish remains of this study, represents a fluvial-lacustrine depositional environment (Spalletti and Zavattieri, 2009). The Montaña Formation is a ~500 m-thick unit representing a fluvial system that gradually transitions into the fluvial-deltaic-lacustrine paleoenvironments of the ~100 m-thick Santa Clara Abajo Formation (Benavente et al., 2018, 2023). Fish remains of Pseudobeaconiidae have been reported from the Santa Clara Abajo formation (López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010; Giordano et al., 2023). The uppermost unit of the group is the ~680 m-thick Santa Clara Arriba Formation, which represents a deltaic-fluvial-lacustrine system (Benavente al., 2018, 2023).

The goal of this note is to present the first vertebrates from the Mollar Formation, constituting a new record of Actinopterygii from continental Triassic rocks from southern South America. This is the oldest record of the family Pseudobeaconiidae. In addition, in order to provide regional comparisons, fish remains from the Middle-to-Upper Triassic Estratos El Bordo unit in northern Chile, previously assigned to Pseudobeaconiidae, are analyzed.

## 2. Geologic setting

The Cuyana basin is an entirely continental infilled extensional basin developed between the Early and Late Triassic (Irmis et al., 2022, and references therein). Radioisotopic

dating from the Santa Clara subbasin suggest that was one of the earliest on the rifting system to open up (Benavente et al., 2024). The infill of the Santa Clara subbasin has been constrained to the Middle Triassic: volcanic material from lowermost Santa Clara Abajo Formation was dated at 243.74±0.41 Ma, whereas tuffs from the upper section of the Santa Clara Arriba Formation yielded an age of 242.78±0.64 Ma (U-Pb zircon ages, Benavente et al., 2024; Fig. 2). The lacustrine episodes of those two units are therefore assigned to the late Anisian, which implies that the underlying formations (Cielo, Mollar, and Montaña) are significantly older.

The Mollar Formation consists of a succession of very fine, well-sorted yellowish to white sandstones alternating with reddish and greenish siltstones and black mudstones. It also includes significant tuffaceous contributions present as ~50 cm-thick beds interbedded with ~30 cm-thick greenish massive and rippled siltstones and black finely laminated mudstone layers up to 2 m thick. The reported thicknesses vary throughout the subbasin (Harrington, 1971).

The first general descriptions of the Mollar Formation unit are from Harrington (1971), who provided a general stratigraphic column at the type locality. Subsequently, Spalletti and Zavattieri (2009) conducted a sedimentary and palynological study of this formation, identifying and describing different cycle patterns for the lacustrine system as well as reporting the presence of plant remains and organic matter towards the base of the section. However, a unique sedimentary column was presented making the ciclostratigraphic interpretation difficult. In this contribution we have followed the sedimentary scheme of Spalletti and Zavattieri (2009) to reference the fish bearing levels (Fig. 2).

## 3. Materials and methods

### 3.1 Material

**Institutional abbreviations: IANIGLA:PV**, Colección de Paleovertebrados del Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; **MUHNCAL**, Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Chile.

We collected 35 fish specimens from the Mollar Formation. Most of these are under current preparation process and will be presented in subsequent publications. Material revised for this research includes three specimens catalogued as: IANIGLA:PV:2223, IANIGLA:PV:2210, and IANIGLA:PV:2229, all of them collected with a precise stratigraphical control. The specimens are preserved in black finely laminated mudstones with different grades of preservation, with most of them incomplete but articulated or in casts. Most specimens do not feature the enamel of ganoine preserved. In parallel, the specimen MUHNCAL.20233 from the lower Upper Triassic of northern Chile was revised.

### 3.2 Methods

The specimens were mechanically prepared with manual tools including needles under a binocular microscope. They were studied under a binocular microscope (Leica M80) with a camera lucida attachment at the Universidad Nacional de San Luis, Argentina. Measurements were taken with a digital caliper. Photographs were taken with a digital camera Canon EOS Rebel T3i and mobile phone cameras (Motorola Edge 30 Neo and Samsung Galaxy A21s).

## 4. Results

The new actinopterygian specimens were identified as members of the family Pseudobeaconiidae based on the following unique combination of diagnostic characters (*sensu* López-Arbarello and Zavattieri, 2008):

1. Small size (<10 cm total length). Only the standard length could however be measured, that is, the length from the snout to the beginning of the caudal fin, with an average of 6.33 cm (Fig. 3A).
2. Body depth ~2-2.5 times in standard length (Fig. 3A).
3. Pelvic fins closer to the anal fin than to pectoral fins (Fig. 3A).
4. Presence of an incomplete dorsal ridge of spine-like scales between the skull and the dorsal fin (in the studied specimens the series includes seven elements) (Fig. 3B, C).
5. Flank scales three times deeper than long (Fig. 3A).
6. Scales with straight posterior margin, elevated central region, and concentric ridges of ganoine (Fig. 3D, E). Regarding the presence of an elevated central region and a concentric ridge of ganoine, these two features were very difficult to observe due to the poor preservation of the specimens, as the ganoine enamel was hardly preserved. Only in a few specimens these features were visible.

## 5. Discussion

Up to this contribution, fish remains from the Mollar Formation were previously unknown. Considering a late Anisian age for the Santa Clara Abajo and Santa Clara Arriba formations (Benavente et al., 2024; Fig. 2), and a thickness of ~500 m for the interbedding Montaña Formation (which represents a fluvial system) the new fish findings would represent the oldest record of Pseudobeaconiidae, potentially extending its biochron to early Anisian or even earlier ages. Known specimens of this family in Argentina are: *Pseudobeaconia bracaccinii*, *Pseudobeaconia elegans,* and *Pseudobeaconia cuyana* from the Santa Clara Abajo Formation (Bordas, 1944; Hutchinson, 1973; Breglia, 2000; López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010); *Pseudobeaconia celestae* and *Mendocinichthys brevis*

from the Potrerillos Formation (Bordas, 1944; Schaeffer, 1955; López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010); and indeterminate pseudobeaconiid records from the Chañares Formation (Gouiric-Cavalli et al., 2017) (Table 1).

In terms of potential regional correlations, a partial postcranial specimen assigned to Pseudobeaconiidae, recovered from an informal unit known as Estratos del Bordo of Middle-to-Late Triassic age in northern Chile, was reported by Otero et al. (2023). The determination of this material (MUHNCAL.20233) was based on a single incomplete sample (Fig. 4), with the authors interpreting the preserved portion as part of the dorsal flank region, anterior to the dorsal fin. During the course of this study, we had the opportunity to investigate this material first-hand, providing an interpretation that disagrees with that of Otero et al. (2023). Below we give an alternative and more parsimonious explanation for this material. This new interpretation allows us to revise the observed diagnostic characters and synapomorphies of the family from a different perspective.

The specimen MUHNCAL.20233 is incomplete, showing a small portion in front of an incomplete dorsal fin up to the caudal peduncle reaching the first elements of the caudal fin (Fig. 4A). The dorsal fin is recognized by the presence of support elements or pterygiophores and some fragments of possible rays preserved in the specimen (Fig. 4B). Additionally, some basal fulcra and possible procurrent rays are observed associated to the dorsal fin (Fig. 4B). Posteriorly, the caudal fin is recognized because of the presence of a series of basal fulcra (pairs and unpairs) preserved at the dorsal margin (Fig. 4C), which presents a common arrangement of the epaxial lobe of the caudal fin with an oblique orientation with respect to the anterior-posterior axis of the body (Arratia, 2009). Furthermore, this caudal section is accompanied by the typical scale pattern (rhomboidal scales) in contrast to the deep flank scales that would otherwise be expected in the anterior region of the body (Fig. 4A). In transverse view, a ’cavity’

interpreted as a coelom was identified by Otero et al. (2023); however, contrasting this interpretation with the external anatomical features in our studies, we suggest that, probably, it is not a real body cavity but an artifact produced by taphonomic processes. In relation to the transverse body section of the specimen, Otero et al. (2023) indicated that ventral musculature enclosed the trunk; however, we interpret that this structure is the external integument, only that muscles were not preserved.

The above reinterpretation suggests that most of the diagnostic characters of the family Pseudobeaconiidae (according to López-Arbarello and Zavattieri, 2008) cannot be verified in MUHNCAL.20233. The only two characters that could be confirmed are the presence of an incomplete dorsal ridge of spine-like scales between the skull and dorsal fin, and the scales with straight posterior margin. Among the unverifiable diagnostic characters are: body depth ~2-2.5 times the standard length; pelvic fins closer to the anal fin than to pectoral fins; flank scales three times deeper than long, because there are rhomboidal scales not rectangular flank scales in the preserved body section; and scales with elevated central region and concentric ridges of ganoine. In conclusion, considering our reanalysis and that the identification of the Chilean material was based on a single and incomplete specimen (Otero et al., 2023), we therefore propose MUHNCAL.20233 be classified as cf. Pseudobeaconiidae, because the morphological characters observed do not allow confirmation of most of the diagnostic characters of the family Pseudobeaconiidae.

## Conclusions

The Pseudobeaconiidae remains identified here represent the very first vertebrate remains reported from the Mollar Formation (Santa Clara subbasin, Cuyana rift basin). They likely constitute the oldest record reported so far for this family, potentially extending its

biochron to early Anisian or even earlier age. This finding reinforces the endemic nature of this family restricted to lacustrine basins of southwestern Gondwana, and suggest that it might have existed for at least 10 Myr, considering that records of the family are known up to the Carnian.

**Acknowledgements**

We dedicate this contribution to the memory of Dr. L.A. Spalletti who was the first and only sedimentologist to this day to publish a high-resolution sedimentary log of the Mollar Formation. We thank the Suárez family for granting access to their property to recover the fossils; Geol. Z. Larena and Mr. M. Bourguet are thanked for fieldwork assistance; O. Rojas Mondaca, Head of the Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Chile, and R. A. Otero and S. Soto-Acuña are thanked for insightful discussions about fish material revised in the fossil collection of the museum. Also, Dr. A. Arcucci is thanked for improving the manuscript with suggestions and Dr. F. Gianechini is thanked for helping with photographs. We are grateful to G. Arratia and an anonymous reviewer for the revision of the manuscript. Funding was provided by grants ANPCyT PICT 2020-00258 (PGG), PICT 2020-2739 (CAB), and PROICO 02-0523 (SECYT UNSL) (Arcucci).

**References**

Arratia, G. 2009. Identifying patterns of diversity of the actinopterygian fulcra. Acta Zoologica *90*: 220-235.

Benavente, C.A.; Bohacs, K.M.; Mancuso, A.C. 2023. Integrated Analysis of Balanced-Fill Lake Basin Strata using Vertebrate and Invertebrate Trace Fossils. Journal of Sedimentary Research, 94, 76-102. doi.org/10.2110/jsr.2021.124

Benavente, C.A.; Irmis, R.B.; Pedernera, T.E.; Mancuso, A.C.; Mundil, R. 2024. Triassic Gondwanan floral assemblages reflect paleogeography more than geologic time. Gondwana Research 130: 140-157.

Benavente, C.A.; Zavattieri, A.M.; Mancuso, A.C.; Abarzúa, F.; Gierlowski-Kordesch, E.H. 2018. Paleolimnology of the Santa Clara Arriba paleolake (Triassic Cuyana rift basin): integrating sedimentology and palynology. Journal of Paleolimnology 59: 5-20.

Bordas, A.F. 1944. Peces triásicos de la formación Santa Clara (Mendoza y San Juan). Physis 19: 454-460.

Breglia, S. 2000. Peces actinopterigios de la Quebrada de Santa Clara, norte de Mendoza. Aspectos taxonómicos y relaciones evolutivas. Undergraduate Thesis (Unpublished), Universidad de Buenos Aires: 106.

Giordano, P.G.; Benavente, C.A.; Suárez Davi, S. 2023. Macro- and micromorphology of scales from an endemic South American actinopterygian family (Pseudobeaconiidae, Triassic, Cuyana Basin). Ameghiniana 60: 164-177.

Gouiric-Cavalli, S.; Desojo, J.B.; Ezcurra, M.D.; Fiorelli, L.E.; Martinelli, A.G. 2017. First fish remains from the earliest Late Triassic of the Chañares Formation (La Rioja, Argentina) and their paleobiogeographic implications. Ameghiniana 54 (2): 137-150.

Harrington, H.J. 1971. Descripción geológica de la Hoja 22c, 'Ramblon', provincias de Mendoza y San Juan. República Argentina Dirección de Geología y Minería Boletín 114: 4-86.

Hutchinson, P. 1973. *Pseudobeaconia*, a perleidiform fish from the Triassic Santa Clara Formation, Argentina. Breviora 398: 1-24.

Irmis, R.B.; Mundil, R.; Mancuso, A.C.; Carrillo-Briceño, J.D.; Ottone, E.G.; Marsicano, C.A. 2022. South American Triassic geochronology: Constraints and uncertainties for the tempo of Gondwanan non-marine vertebrate evolution. Journal of South American Earth Sciences 116: 103770.

López-Arbarello, A.; Rauhut, O.W.; Cerdeño, E. 2010. The Triassic fish faunas of the Cuyana Basin, Western Argentina. Palaeontology 53: 249–276.

López-Arbarello, A.; Zavattieri, A.M. 2008. Systematic revision of *Pseudobeaconia* Bordas, 1944 and *Mendocinichtys* Whitley, 1953 (Actinopterygii "Perleidiformes") from the Triassic of Argentina. Palaeontology 51: 1025-1052.

Mancuso, A.C.; Benavente, C.A; Irmis, R.B.; Mundil, R. 2020. Evidence for the Carnian Pluvial Episode in Gondwana: New multiproxy climate records and their bearing on early dinosaur diversification. Gondwana Research, 86: 104-125.

Marsicano, C.A.; Irmis, R.B.; Mancuso, A.C.; Mundil, R.; Chemale, F. 2015. The precise temporal calibration of dinosaur origins. Proceedings of the National Academy of Sciences 113 (3): 509-513.

Otero, R.A.; Rubilar-Rogers, D.; Soto-Acuña, S.; Vargas, A.; Rojas, G.M.; Ugalde, R.; Rojas, O.; Rojas, J.; Novas, F.E. 2023. New records of continental vertebrates from the

Triassic of the Atacama Desert, northern Chile. Journal of South American Earth Sciences 121: e104155. doi.org/10.1016/j.jsames.2022.104155

Schaeffer, B. 1955. *Mendocinia*, a subholostean fish from the Triassic of Argentina. American Museum novitates; no. 1737.

Spalletti, L.A.; Zavattieri, A.M. 2009. El sistema lacustre de la Formación Mollar en el depocentro Triásico de Santa Clara (Provincia de Mendoza, Argentina). Andean Geology 36: 236-263.

Stipanicic, P.N.; Marsicano, C.A. 2002. Léxico Estratigráfico de la Argentina. Asociación Geológica Argentina, volúmen 8: 379 p. Buenos Aires.

Trotteyn, M. J.; Apaldetti, C.; Santi Malnis, P.; Abelín, D., Giordano, P. G.; Jofré, M. C., Correa, G.; Rothis, M. 2023. Una nueva localidad fosilífera de la Formación Santa Clara Abajo (Triásico). Cuenca Cuyana, en la provincia de San Juan. Libro de resúmenes: en 36° Jornadas Argentinas de Paleontología de Vertebrados. La Rioja, Argentina: 83.

Yuan, Z.; Xu, G. H.; Dai, X.; Wang, F.; Liu, X.; Jia, E-H.; Miao, L-Y.; Song, H. 2022. A new perleidid neopterygian fish from the Early Triassic (Dienerian, Induan) of South China, with a reassessment of the relationships of Perleidiformes. PeerJ 10: e13448. doi.org/10.7717/peerj.13448

Xu, G.H.; Gao, K.Q.; Coates, M.I. 2015. Taxonomic revision of *Plesiofuro mingshuica* from the Lower Triassic of northern Gansu, China, and the relationships of early neopterygian clades. Journal of Vertebrate Paleontology 35 (6): e1001515.doi.org/10.1080/02724634.2014.1001515

Xu, G.H. 2021. A new stem-neopterygian fish from the Middle Triassic (Anisian) of Yunnan, China, with a reassessment of the relationships of early neopterygian clades. Zoological Journal of the Linnean Society 191 (2): 375-394.

## Figure Captions

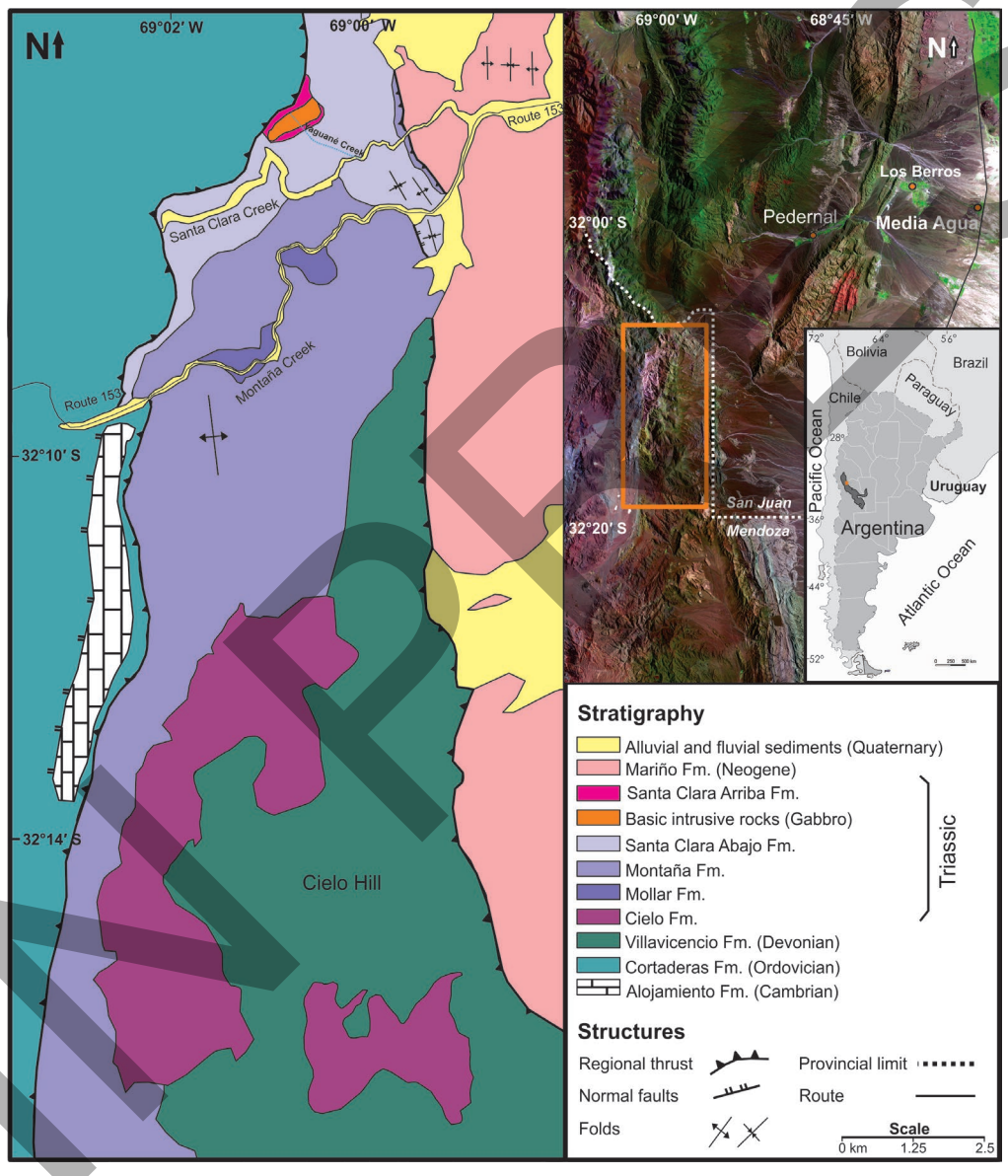


**Fig. 1.** Location, geologic map, and stratigraphy of the Santa Clara subbasin, Cuyana basin, Mendoza Province, Argentina. The extent of the Cuyana basin is shown in dark grey color on the geographic map and the orange square indicates the location of the subbasin within the basin. Towns are shown as orange circles. Modified from Benavente et al. (2018).

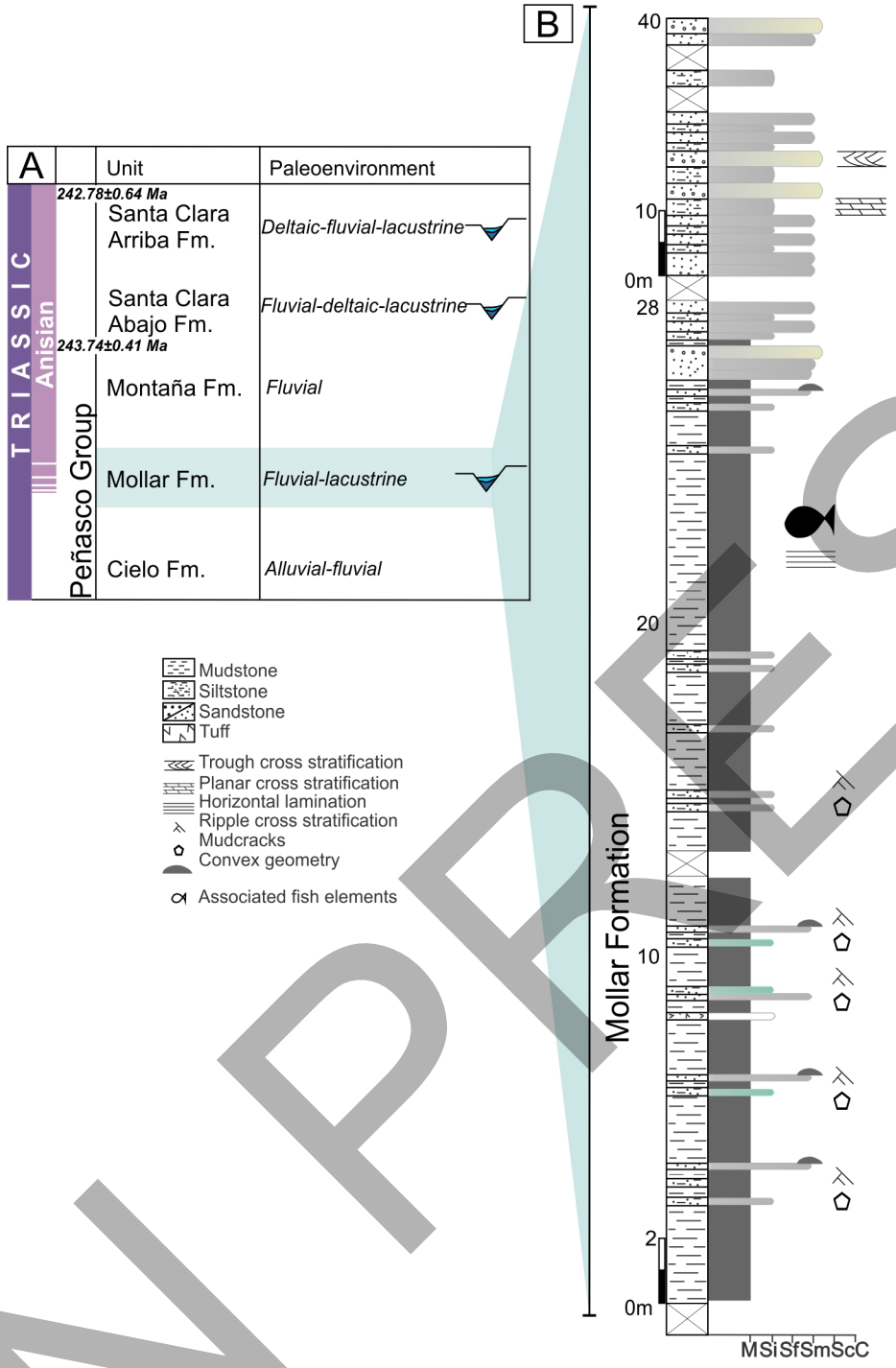


**Fig. 2. A.** Stratigraphic diagram of the Peñasco Group indicating the lacustrine deposits and radiometric ages from Benavente et al. (2024). **B.** Low resolution sedimentary log of the Mollar Formation, showing exclusively the section bearing the fish remains and indicating the fish bearing bed. Modified from Spalletti and Zavattieri (2009). M: mudstone, Si: siltstone, Sf: fine-grained-sandstone, Sm: medium-grained-sandstone, Sc: coarse-grained-sandstone, C: conglomerate.

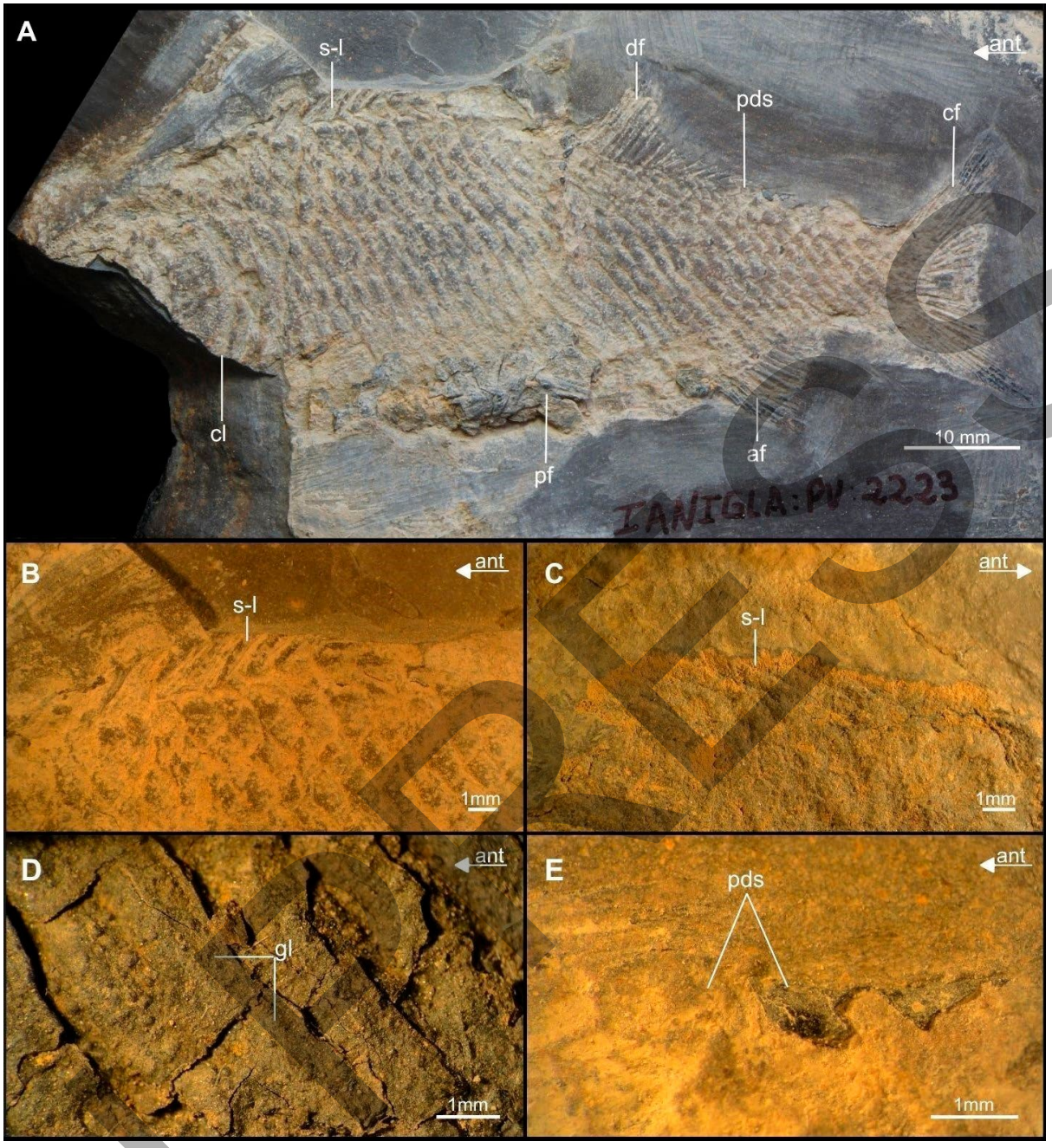


**Fig. 3.** Fish specimens from the Mollar Formation (Santa Clara subbasin). **A.** Specimen IANIGLA:PV:2223 featuring the most relevant anatomical elements. **B.** Detail of incomplete dorsal ridge of spine-like scales of specimen IANIGLA:PV:2223. **C.** Detail of incomplete dorsal ridge of spine-like scales of specimen IANIGLA:PV:2210. **D.** Detail of flank scales of specimen IANIGLA:PV:2229. **E.** Detail of two postdorsal scutes of specimen IANIGLA:PV:2223. Anatomical abbreviations: **af**, anal fin; **ant,** anterior region; **cf**, caudal fin; **cl**, cleithrum; **df**, dorsal fin; **gl**, growth line of ganoine; **pds,** postdorsal scutes; **pf**, pelvic fin; **s-l**, incomplete dorsal ridge of spine-like scales.

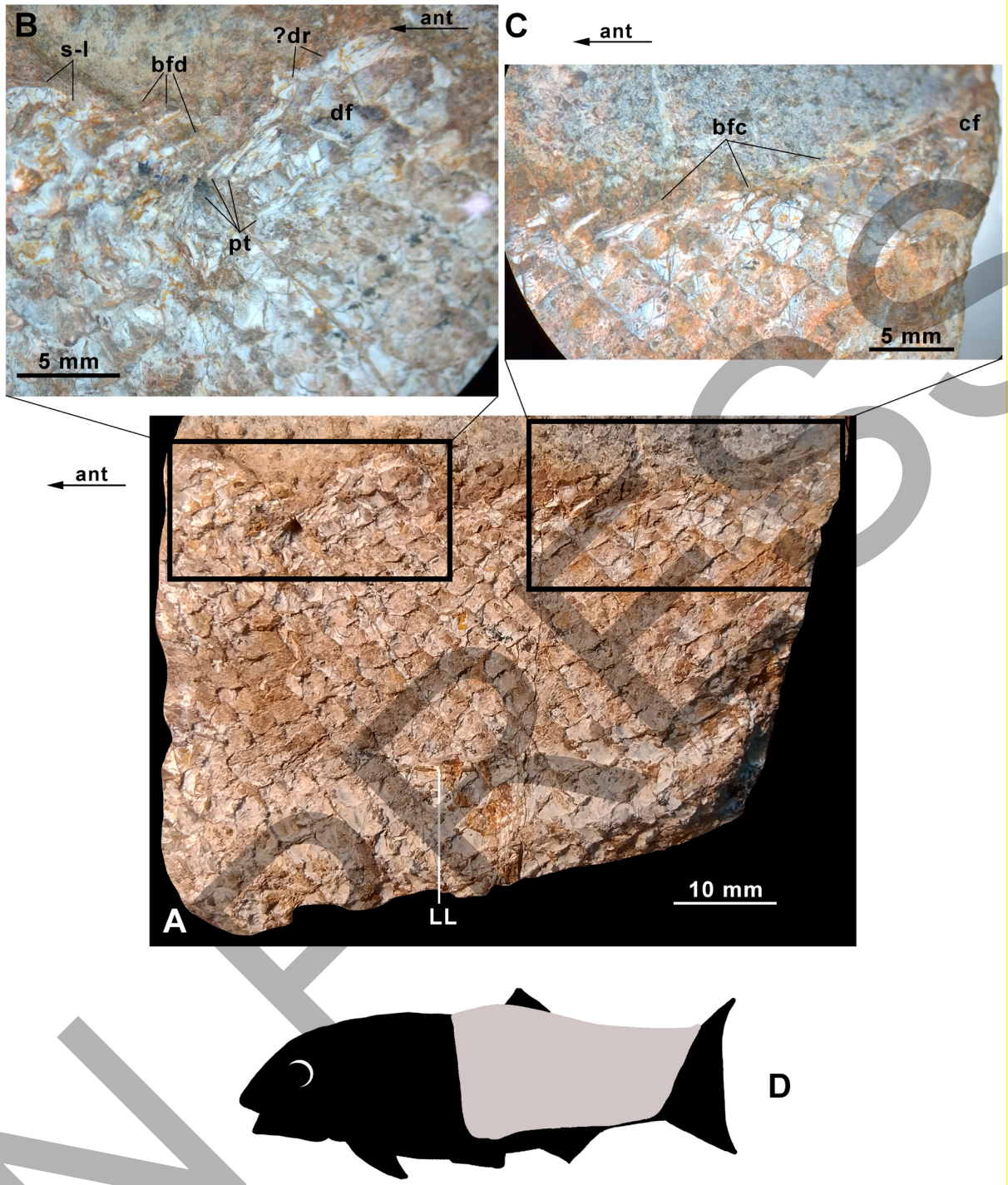


**Fig. 4.** Fish specimen MUHNCAL.20233 *cf.* Pseudobeaconiidae (Estratos el Bordo unit, Middle-to-Upper Triassic). **A.** General view, exposing the rhomboid scales and other relevant morphological elements. **B.** Detailed high-resolution binocular microscope photograph of the anterior dorsal margin. **C**. Detailed high-resolution binocular microscope photograph of the posterior dorsal margin. **D.** Reinterpretation of the preserved anatomical region (in grey shading). Anatomical abbreviations: **ant,** anterior region**, bfc**, caudal basal fulcra; **bfd**, dorsal basal fulcra; **cf**, caudal fin; **df**, anterior part of the dorsal fin; **?dr**, possible dorsal rays; **LL**, lateral line; **pt**, pterygiophores; **s-l**, incomplete dorsal ridge of spine-like scales.