

PALEONTOLOGICAL NOTE

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

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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 a late 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, whether 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 una edad anisiana tardía previamente obtenida para la Formación Santa Clara Abajo, la cual sobreyace a la Formación Mollar, la edad de los peces descritos podría corresponder al Anisiano temprano o tal vez más antigua, lo cual extendería el biocron 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; Gouiric-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 (Stipanovic 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 paleoenvironment (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 *et al.*, 2018, 2023).

The goal of this paleontological 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 revised.

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 suggests that it was one of the earliest subbasins 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 the lowermost section of the Santa Clara Abajo Formation was dated as 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.

TABLE 1. RECORD OF SPECIES OF PSEUDOEACONIIDAE IN THE DIFFERENT FORMATIONS OF THE CUYANA AND ISCHIGUALASTO-VILLA UNION BASINS.

Basin	Subbasin	Formation	Record	Locality
Cuyana	Potrerillos	Potrerillos	<i>Pseudoeaconia celestae</i> López-Arbarello and Zavattieri, 2008	Mendoza Province, Argentina
Cuyana	Potrerillos	Potrerillos	<i>Mendocinichthys brevis</i> (Bordas, 1944) López-Arbarello and Zavattieri, 2008	Mendoza Province, Argentina
Cuyana	Santa Clara	Santa Clara Abajo	<i>Pseudoeaconia bracaccinii</i> Bordas, 1944	Mendoza Province, Argentina
Cuyana	Santa Clara	Santa Clara Abajo	<i>Pseudoeaconia cuyana</i> (Bordas, 1944) López-Arbarello, Rauhut and Cerdeño, 2010	Mendoza Province, Argentina
Cuyana	Santa Clara	Santa Clara Abajo	<i>Pseudoeaconia elegans</i> Bordas, 1944	Mendoza Province, Argentina
Cuyana	Santa Clara	Santa Clara Abajo	Pseudoeaconiidae indet. Trotteyn, Apaldetti, Santi Malnis, Abelin, Giordano, Jofré, Correa and Rothis, 2023	San Juan Province, Argentina
Ischigualasto-Villa Unión	n/a	Chañares	Pseudoeaconiidae indet. Gouiric-Cavalli, Desojo, Ezcurra, Fiorelli and Martinelli, 2017	“All scale patches come from the El Torcido locality (29°48’49.9” S; 67°46’51” W) and were recovered from one meter below the contact between the Chañares Formation and the Los Rastros Formation, upper member of the Chañares Formation” (Gouiric-Cavalli <i>et al.</i> , 2017).

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 are from Harrington (1971), who provided a general stratigraphic column at the type locality. Subsequently, Spalletti and Zavattieri (2009) conducted a sedimentological and palynological study of this unit, 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 cyclostratigraphic interpretations 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; MUHNICAL, 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

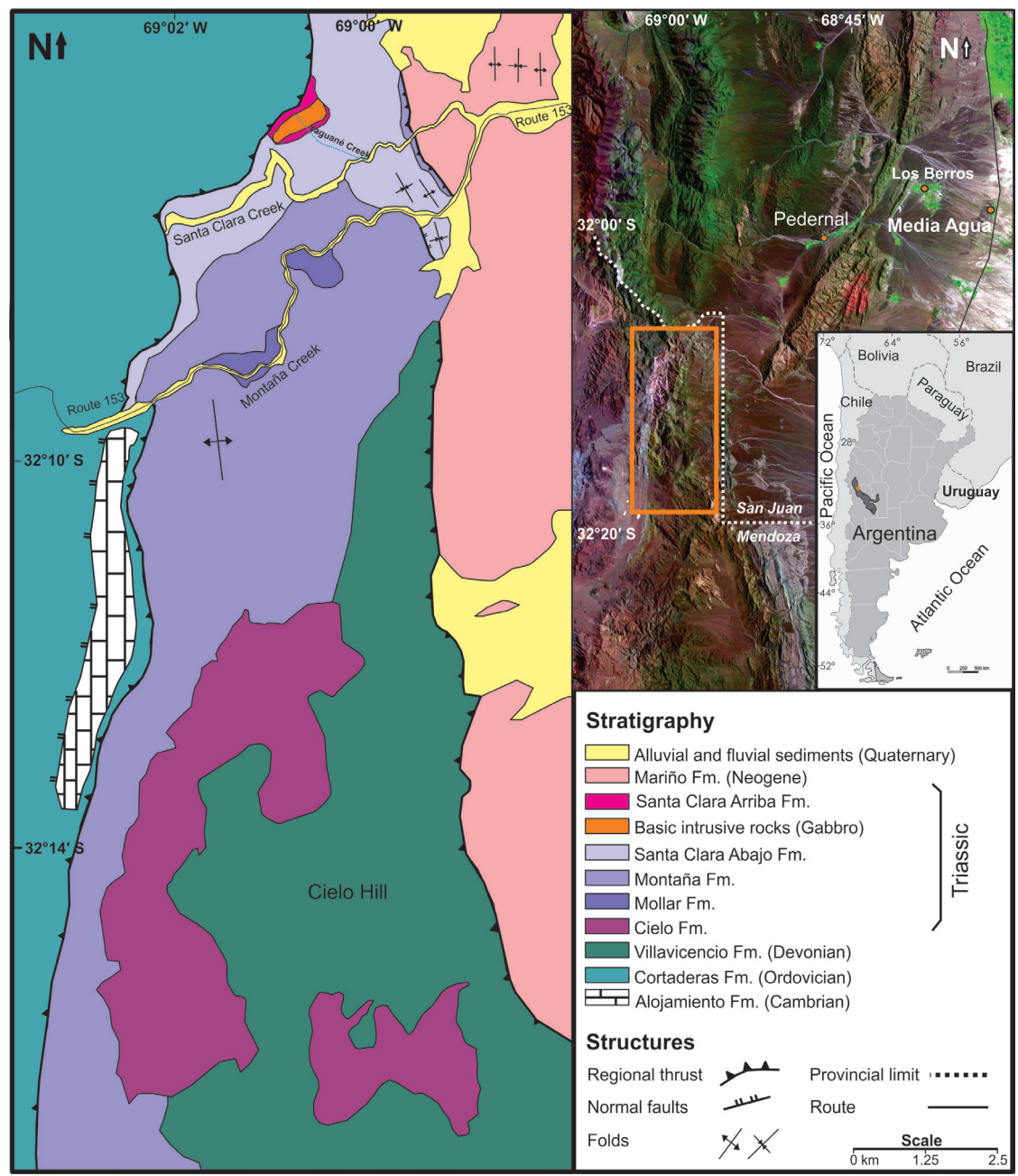


FIG. 1. Location, geologic map, and stratigraphy of the Santa Clara subbasin, Cuyana rift basin, Mendoza Province, Argentina. The extent of the Cuyana basin is shown in dark grey color on the regional map, with the orange square indicating the location of the subbasin within the rift basin. Towns are shown as orange circles. Figure modified from Benavente *et al.* (2018).

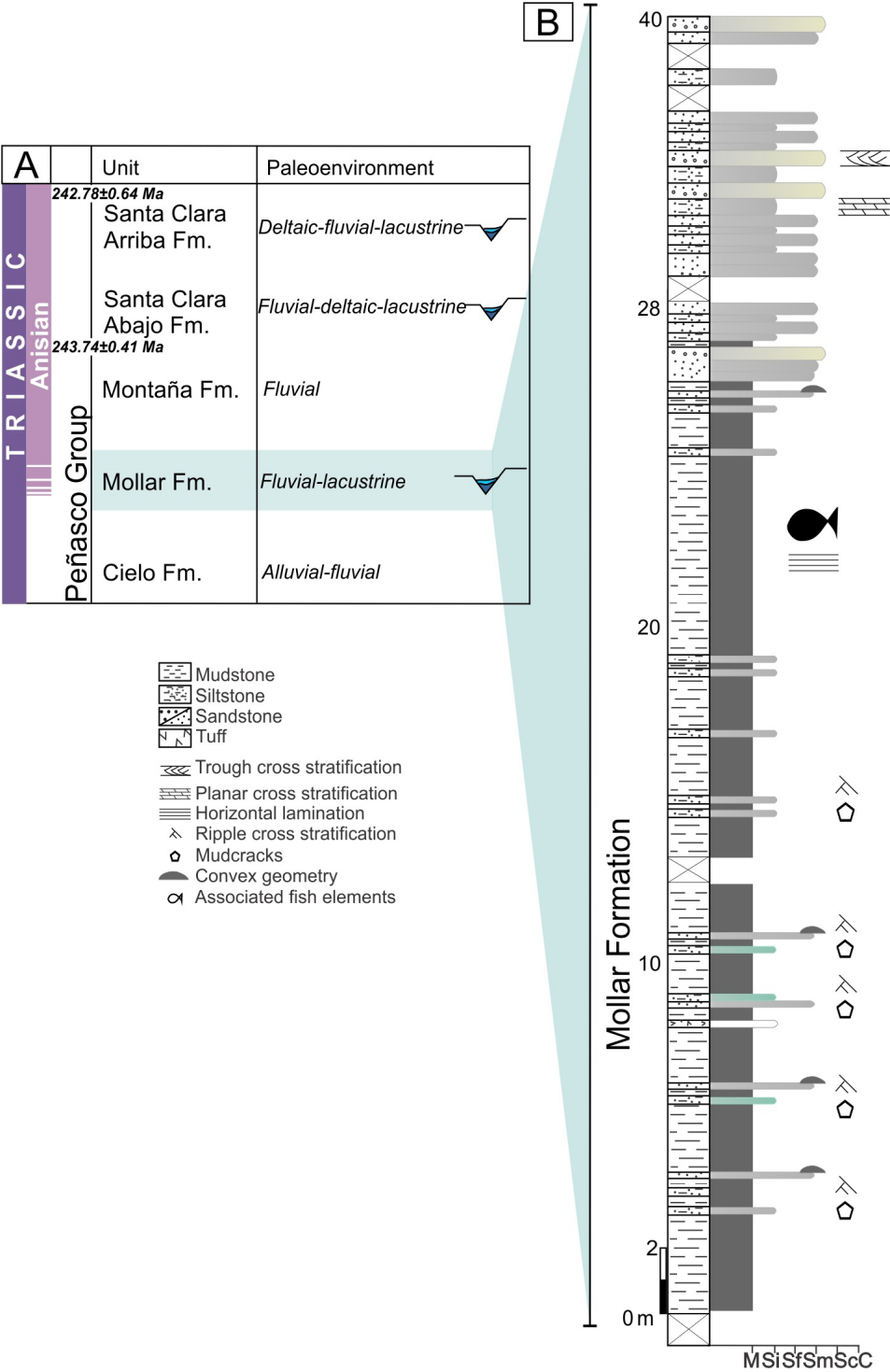


FIG. 2. **A.** Stratigraphic diagram of the Peñasco Group indicating the lacustrine deposits and radiometric ages from Benavente *et al.* (2024). **B.** Low resolution sedimentary log of the Mollar Formation, showing exclusively the section bearing the fish remains and indicating the fish bearing bed.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

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 collected with a precise stratigraphical control. The specimens were extracted from black finely laminated mudstones with different grades of preservation, 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 Leica M80 microscope 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 (Gouric-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 El 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

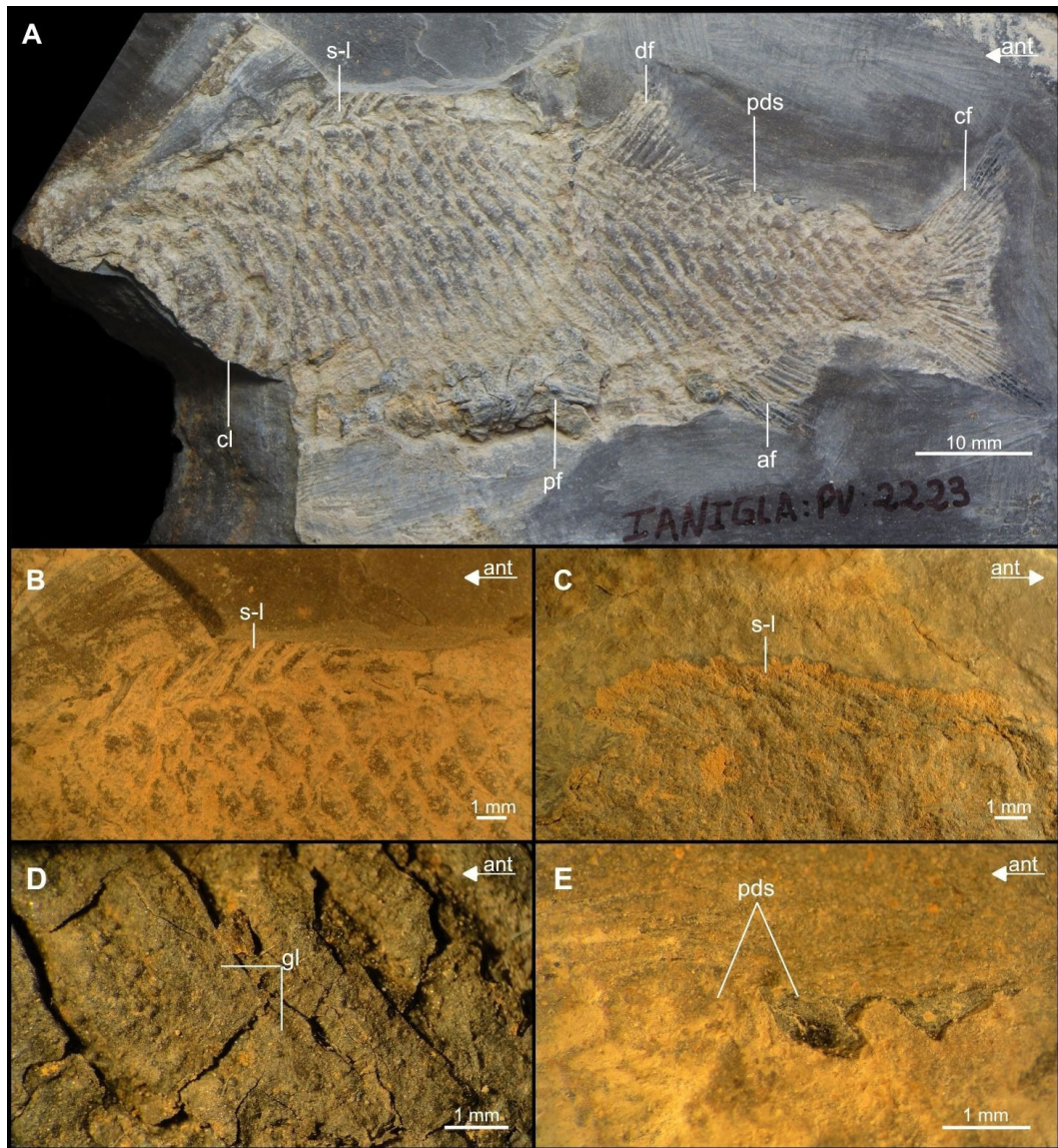


FIG. 3. Fish specimens from the Mollar Formation. **A.** Specimen IANIGLA:PV:2223 featuring the most relevant anatomical elements. **B.** Detail of incomplete dorsal ridge of spine-like scales of specimen IANIGLA:PV:2223. **C.** Detail of incomplete dorsal ridge of spine-like scales of specimen IANIGLA:PV:2210. **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.

preserved in the specimen (Fig. 4B). Additionally, some basal fulcra and possible procurent 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). This caudal section is accompanied by the typical scale pattern (rhomboidal scales) in contrast to the deep flank scales that would otherwise

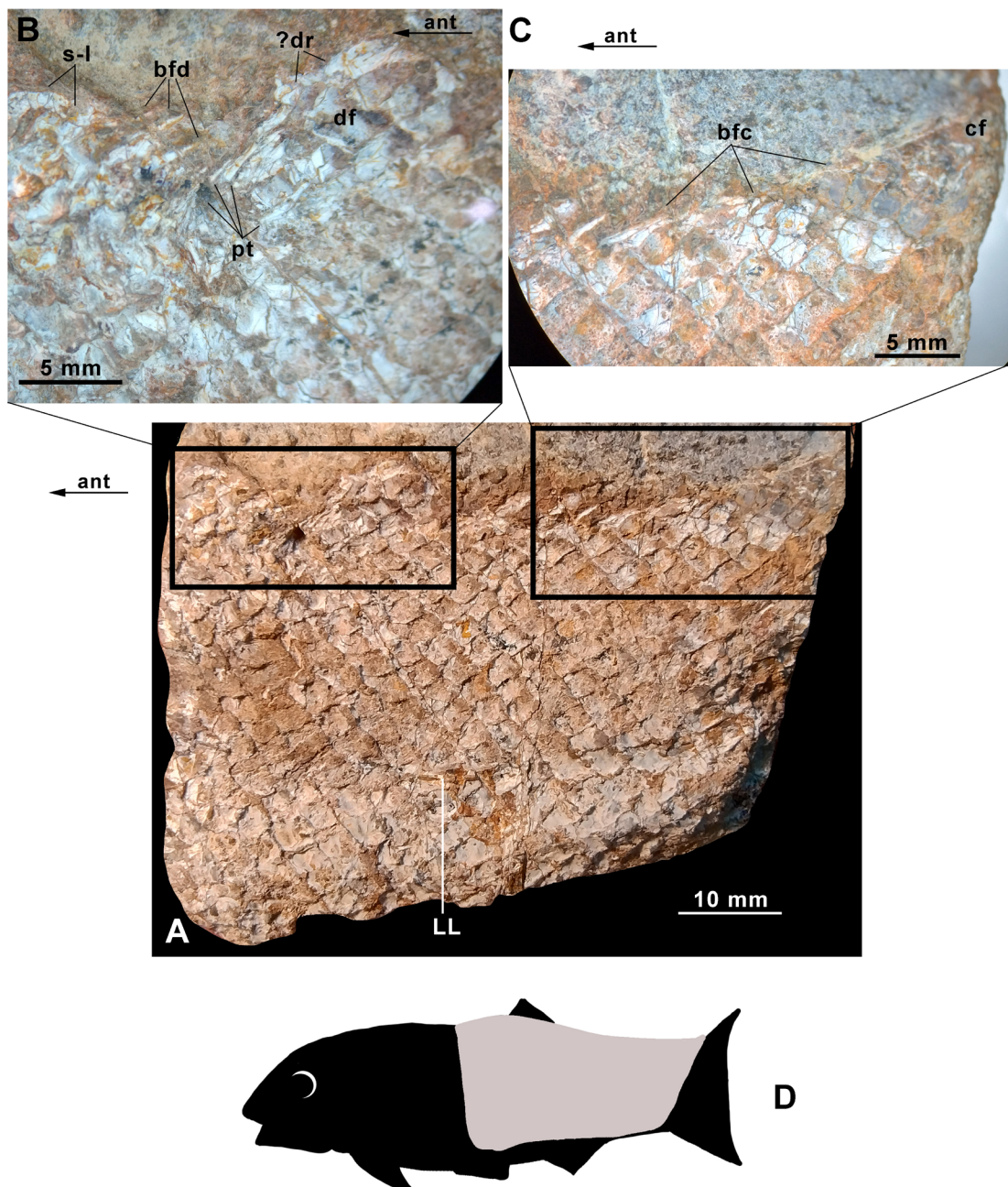


FIG. 4. Fish specimen MUHNCAL.20233 cf. *Pseudobeaconiidae* (Estratos El Bordo unit, Middle-to-Upper Triassic). **A.** General view, exposing the rhomboid scales and other relevant morphological elements. **B.** Detailed high-resolution binocular microscope photograph of the anterior dorsal margin. **C.** 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 fulcrum; **bfd**, dorsal basal fulcrum; **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.

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, after 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 in fact be confirmed are the presence of an incomplete dorsal ridge of spine-like scales between the skull and the dorsal fin, and the scales with straight posterior margin. Among the unverifiable diagnostic characters are: 1) body depth ~2-2.5 times the standard length; 2) pelvic fins closer to the anal fin than to pectoral fins; 3) flank scales three times deeper than long, because rhomboidal scales (and not rectangular scales) are present in the preserved body section; and 4) 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, we 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.

6. 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 ages. 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. 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) (A. Arcucci).

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