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INCREASING THE FISH DIVERSITY OF THE TRIASSIC FAUNAS OF GONDWANA: A NEW REDFIELDIIFORM (ACTINOPTERYGII) FROM THE MIDDLE TRIASSIC OF ARGENTINA AND ITS PALAEOBIOGEOGRAPHICAL IMPLICATIONS

by SOLEDAD GOUIRIC-CAVALLI[1], ANA M. ZAVATTIERI[2],
PEDRO R. GUTIERREZ[3], BÁRBARA CARIGLINO[3] *and* LUCÍA BALARINO[3]

[1]División Paleontología Vertebrados, Museo de La Plata, Consejo Nacional de Investigaciones Científicas y Técnicas CONICET, Universidad Nacional de La Plata, Paseo del Bosque s/n, W1900FWA, La Plata, Argentina; sgouiric@fcnym.unlp.edu.ar
[2]Departamento de Paleontología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Centro Científico Tecnológico, Consejo Nacional de Investigaciones Científicas y Técnicas CONICET, Casilla de Correo 131, M5502IRA, Mendoza, Argentina; amz@mendoza-conicet.gob.ar
[3]Área de Paleobotánica y Paleopalinología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Consejo Nacional de Investigaciones Científicas y Técnicas CONICET, Av. Ángel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina; prgutierrez@macn.gov.ar, barichi10@gmail.com, lubalarino@macn.gov.ar

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Abstract: A new actinopterygian, *Calaichthys tehul* gen. et sp. nov. is described on the basis of a few, well-preserved specimens from the Anisian Cerro de Las Cabras Formation, Cuyo Basin in Mendoza Province. The new genus shows a combination of primitive characters (e.g. deep posterior region of the maxilla contacting the preopercle, a suspensorium backwardly oriented) and more advanced characters (e.g. distally segmented fin rays, hemiheterocercal caudal fin) and is thus considered to be a 'subholostean' fish. The new taxon is assigned to Redfieldiiformes on the basis of its single branchiostegal plate-like ray, a median gular plate, pectoral fins with stout, stiff, mainly non-segmented and distally branched fin rays, long and robust fringing fulcra in all fins, basal fulcra bordering both lobes of the caudal fin, and opposite dorsal and anal fins. *Calaichthys* is characterized by a combination of characters some of which are unique among redfieldiiforms (i.e. strongly ornamented but thin scales with a serrated posterior margin, smooth skull roof bones, extrascapulars with a bifid posterior margin, three suborbital bones, a hatchet-shaped preopercle, rectangular and slender opercle, deep mouth gape, entopterygoid and ectopterygoid with small pointed teeth disposed in several series, unornamented rostral bone, massive pectoral fins and delicate dorsal, pelvic and anal fins). *Calaichthys* provides novel information about the anatomy of redfieldiiforms, in particular in relation with the fins and associated scaly elements, as well as the scale morphology and their disposition over the body. Our work confirms for the first time that redfieldiiforms occur in South America. Redfieldiiforms seem to have originated in Gondwana and shown two diversity peaks: in the Anisian and the Carnian. *Calaichthys* is coeval with those redfieldiiforms of the Middle Triassic (Anisian) of Africa and Australia dwelling in ephemeral lakes.

Key words: 'Subholostean', Anisian, Mendoza, Cuyo Basin.

'SUBHOLOSTEAN' fishes make up a large portion of the Middle Triassic fish faunas and are mainly represented by Peltopleuriformes and Perleidiiformes, but also by other groups including Redfieldiiformes (see discussion in Brough 1936; Romer 1945; Schaeffer 1955; Lombardo & Tintori 2004; Lombardo 2013). Redfieldiiformes is an order of 'subholosteans' which are recorded with certainty from the Middle Triassic to Early Jurassic freshwater deposits of Australia, southern and northern Africa, and eastern and western USA (Schaeffer 1984; Murray 2000; Brinkmann *et al.* 2010). However, there are also putative redfieldiiform taxa in the Middle–Late Triassic of Argentina (López-Arbarello 2004) and in the uppermost Middle–Late Triassic of England, Germany, Poland, Ireland and Switzerland (Deecke 1889; Schaeffer & McDonald 1978; Dzik & Sulej 2007; Lombardo 2013; Schoch & Seegis 2016).

Currently, Redfieldiiformes is composed of 16 genera (see Table 1). The group comprises fishes with an elongated and fusiform body covered by ganoid scales, dorsal

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and anal fins back positioned and opposite to one another and a hemiheterocercal tail (Schaeffer 1984). The earliest and most generalized redfieldiiforms have been found in Australia and South Africa whereas the most specialized forms have been recovered from North America and Morocco (Schaeffer 1984).

The goals of this paper are to describe a new redfieldiiform from the Anisian of Cerro de Las Cabras Formation at the type section, Potrerillos in Mendoza Province, Cuyo Basin, central western Argentina, and to discuss the palaeobiogeographical implications of the new taxon in the context of the global Triassic fish record.

Institutional abbreviation. IANIGLA, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina.

TABLE 1. Recognized redfieldiiform taxa from around the world (not including putative redfieldiiform records from Europe and Argentina).

Taxon	Period/Age	Locality	Reference
Atopocephala	Middle Triassic (Anisian)	Upper Beaufort Series, Bekkerskaal, South Africa	Brough (1934); Schaeffer (1984); Murray (2000); López-Arbarello (2004); Brinkmann *et al.* (2010)
Brookvalia	Middle Triassic (Anisian)	Hawkensbury Sandstones, Brookvale, New South Wales, Australia	Wade (1933); Schaeffer (1984); Murray (2000); López-Arbarello (2004); Brinkmann *et al.* (2010)
Calaichthys	**Middle Triassic (Anisian)**	**Cerro de Las Cabras, North of the Cerro Bayo, Potrerillos, Cuyo Basin, Mendoza Province, Argentina (Fig. 1)**	**This paper**
Daedalichthys	Middle Triassic (Anisian)	Upper Beaufort Series, Bekkerskaal, South Africa	Brough (1931); Schaeffer (1984); Murray (2000); López-Arbarello (2004); Brinkmann *et al.* (2010)
Geitonichthys	Middle Triassic (Anisian)	Hawkensbury Sandstones, Brookvale, New South Wales, Australia	Wade (1935); Schaeffer (1984); Murray (2000); López-Arbarello (2004); Brinkmann *et al.* (2010)
Helichthys	Middle Triassic (Anisian)	Upper Beaufort Series, Bekkerskaal, South Africa	Broom (1909); Schaeffer (1984); Murray (2000); López-Arbarello (2004); Brinkmann *et al.* (2010)
Ischnolepis	Middle Triassic (Anisian)	Madumabisa shales, Lumpsempfwa Valley, Zambia	Haughton (1934); Hutchinson (1973); Schaeffer (1984); Murray (2000); López-Arbarello (2004); Brinkmann *et al.* (2010)
Molybdichthys	Middle Triassic (Anisian)	Hawkensbury Sandstones, Brookvale, New South Wales, Australia	Wade (1935); Hutchinson (1973); López-Arbarello (2004)
Phlyctaenichthys	Middle Triassic (Anisian)	Hawkensbury Sandstones, Brookvale, New South Wales, Australia	Wade (1935); Hutchinson (1973); López-Arbarello (2004)
Schizurichthys	Middle Triassic (Anisian)	Hawkensbury Sandstones, Brookvale, New South Wales, Australia	Wade (1935); Hutchinson (1973); López-Arbarello (2004)
Cionichthys	Upper Triassic (Carnian)	Chinle Formation, Dockum Group, Texas, North America	Schaeffer (1967); Schaeffer & Mangus (1970)
Dictyopyge	Upper Triassic (Middle–Late Carnian)	Newark Supergroup, Richmond, Virginia, North America	Lyell (1847); Schaeffer & Mangus (1970); Schaeffer & McDonald (1978); Olsen *et al.* (1982); Brinkmann *et al.* (2010)
Lasalichthys	Upper Triassic (Middle Carnian)	Argana Valley, Morocco; Chinle Formation, Dockum Group, Texas, North America	Schaeffer (1967); Schaeffer & Mangus (1970); Murray (2000)
Mauritanichthys	Upper Triassic (Carnian)	Argana Valley, Morocco	Martin (1980, 1982); Murray (2000)
Synorichthys	Upper Triassic (Middle–Late Carnian)	Chinle Formation, Texas, North America	Schaeffer (1967); Schaeffer & Mangus (1970)
Redfieldius	Upper Triassic Lower Jurassic (Hettangian–Sinemurian)	Upper part of the Newark Supergroup, Massachusetts, Connecticut, New Jersey, Virginia, North America, New Mexico	Schaeffer & McDonald (1978); Olsen (1980) Murry (1987); Whiteside *et al.* (2011); Schaeffer & Mangus (1970)

MATERIAL AND METHOD

Fossil fishes came from two fossiliferous levels of the Cerro de Las Cabras Formation (Fig. 1). All the specimens are housed at IANIGLA vertebrate palaeontological collections, Mendoza city, Argentina, under the prefix IANIGLA-Pv: numbers 320 a–b, 321a–b, 322. The material needed little preparation; the senior author used fine steel needles and peroxide to remove matrix. Specimens were studied using a stereomicroscope, with drawings made with a camera lucida attachment and later compiled using graphic software. Photographs were taken under a stereomicroscope, using a scanning electron microscope, and directly. The meristic measurements follows Grande (2010) and were taken with a Vernier caliper on the specimens and using Fiji software (https://fiji.sc/) based on high resolution photographs (see Fig. 2; Tables 2, 3). The standard length (SL) and total length (TL) were calculated using the IANIGLA-Pv 321 a–b (holotype) and IANIGLA-Pv 322 (paratype); the head length (HL) was calculated using the IANIGLA-Pv 321 a–b (holotype) and IANIGLA-Pv 320 a–b (paratype). The descriptive terminology follows that applied by most authors (Brough 1931, 1933, 1934, 1936; Wade 1933, 1935; Watson 1925, 1928; Schaeffer 1984) to actinopterygians. Caudal fin ray interpretation and naming follows Arratia (2008, 2009). Scale terminology follows Schultze (1966, 1996, 2016). Skull roof bones are named based on homology criteria (Westoll 1943; Schultze 2008). The relative position of the fins and scale counts follows Westoll (1944).

GEOLOGICAL SETTING

The Cuyo Basin is the largest Triassic rift basin of central western Argentina (Fig. 3). The sedimentary infilling of the basin began around the Middle Triassic (López Gamundí & Astini 2004; López Gamundí 2010) after the magmatic and volcanic event represented by the basement rocks of the Choiyoi Group (Ramos & Kay 1991). The complete Triassic continental succession is represented by the Uspallata Group (Stipanicic & Zavattieri 2002) and comprises a sedimentary succession of alluvial, fluvial, deltaic and lacustrine depositional systems composed of the Río Mendoza, Cerro de Las Cabras, Potrerillos, Cacheuta and Río Blanco formations (Fig. 4). Details of the depositional sequence analysis and tectonic evolution of the sedimentary and volcaniclastic Triassic infilling of the Potrerillos–Cacheuta depocenter are given in Kokogian & Mancilla (1989), Kokogian *et al.* (1989, 1993) and Barredo (2012) among others, and are here summarized in Figure 4. Charrier *et al.* (2007) recognized three major stages in the tectonostratigraphical evolution of the Andes. These tectonic cycles were related to the episodes

FIG. 1. Aerial view from Google Earth (2017) of the northern flank of the Cerro Bayo, Potrerillos area, Mendoza Province (Argentina) showing the mentioned outcropping stratigraphic units. The studied section of the Cerro de Las Cabras Formation is indicated by 'A'. Colour online.

of the supercontinent evolution separated from each other by regional unconformities or by significant palaeogeographical changes indicated by the occurrence of drastic tectonic events on the southern South American continental margin. The distinctive features of their 'Pre-Andean tectonic cycle' (latest Permian to earliest Jurassic) was the development of abundant and widely distributed, essentially siliciclastic magmatic activity, and a palaeogeography dominated by NNW–SSE orientated extensional basins (Charrier 1979; Ramos 1994; Mpodozis & Ramos 2008). The essentially Triassic deposits of the 'Pre-Andean tectonic cycle' in Chile and adjacent Argentina formed more or less continuous NNW–SSE grabens, or half grabens, and horsts oblique to the continental margin of southern Gondwana. In the NNW (northern and central Chile, between 22°S and 42°S) grabens were occupied by the sea and the deposits in those areas are marine, whereas, in the same grabens, the deposits located further SSE correspond to continental successions. Basins formed inland contain only continental deposits (e.g. Ischigualasto–Villa Unión and Cuyo basins of central western Argentina).

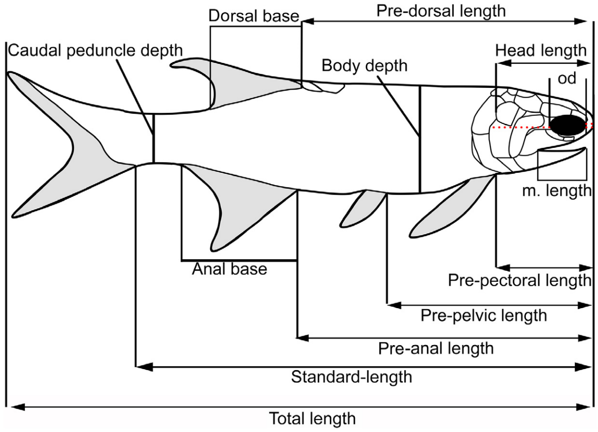

FIG. 2. Redfieldiiformes meristic measurements. *Abbreviations*: od, orbit diameter; m. length, mandibular length. Single dotted line indicates postorbital length; double dotted line indicates preorbital length Colour online.

TABLE 2. Measurements for *Calaichthys tehul* gen. et sp. nov.: body proportions.

Measurements	IANIGLA-Pv 321 a–b (holotype) (mm)	IANIGLA-Pv 320 a–b (mm)	IANIGLA-Pv 322 (mm)
Total length	*c.* 55–60	?	?
Standard length	*c.* 40	?	?
Body depth (% of SL)	12 (30%)	?	?
Pre-pectoral length (% of SL)	10 (25%)	11 (?)	?
Pre-pelvic length (% of SL)	19 (47%)	?	?
Pre-dorsal length (% of SL)	25 (62%)	*c.* 25 (?)	?
Pre-anal length (% of SL)	25 (62%)	?	?
Dorsal fin base	*c.* 3 (?)	?	*c.* 5
Anal fin base	*c.* 6 (?)	?	*c.* 6
Caudal peduncle length	?	?	*c.* 12
Caudal peduncle depth	?	?	*c.* 4

Total length and standard length (SL) are an average of the holotype and paratypes. ? indicates missing data and/or uncertainty due to preservation.

The Cerro de Las Cabras Formation at Potrerillos

The type succession of the Cerro de Las Cabras Formation is located in a tectonically disturbed region on the north and north–north-western flank of the Cerro Bayo and eastern flank of the Cerro de Las Cabras in the Potrerillos area (Fig. 1). The boundaries and outcrops of this unit, as well as its historical background were reviewed in detail in a recent contribution by Cariglino *et al.* (2016). The Cerro de Las Cabras Formation shows a remarkably diverse palaeontological content including continental vertebrates (Báez *et al.* 1993; Marsicano *et al.* 2001; Zavattieri & Arcucci 2007; Abdala *et al.* 2009; López-Arbarello *et al.* 2010), invertebrates (Gallego *et al.* 2004; Vaz Tassi *et al.* 2015), plants (Cariglino *et al.* 2016) and palynofloras (Zavattieri 1990; Zavattieri & Batten 1996). At present, the palaeontological content of the Cerro de Las Cabras Formation suggests a Middle Triassic age, supported also by U–Pb SHRIMP dating on tuff beds from the top of the

TABLE 3. Measurements for *Calaichthys tehul* gen. et sp. nov.: head bones.

Measurements	IANIGLA-Pv 321 a–b (holotype) (mm)	IANIGLA-Pv 320 a–b (mm)	IANIGLA-Pv 322 (mm)
Standard length	*c.* 40	?	?
Head length (% of SL)	*c.* 10–13 (25%)	*c.* 12 (?)	?
Mandibular length (% of HL)	*c.* 8 (62%)	*c.* 8 (?)	?
Pre-orbital length (% of HL)	*c.* 2 (15%)	?	?
Post-orbital length (% of HL)	*c.* 7 (54%)	?	?
Orbit diameter (% of HL)	*c.* 3 (30%)	?	?

Standard length (SL) and head length (HL) are an average of the holotype and paratypes. ? indicates missing data and/or uncertainty due to preservation.

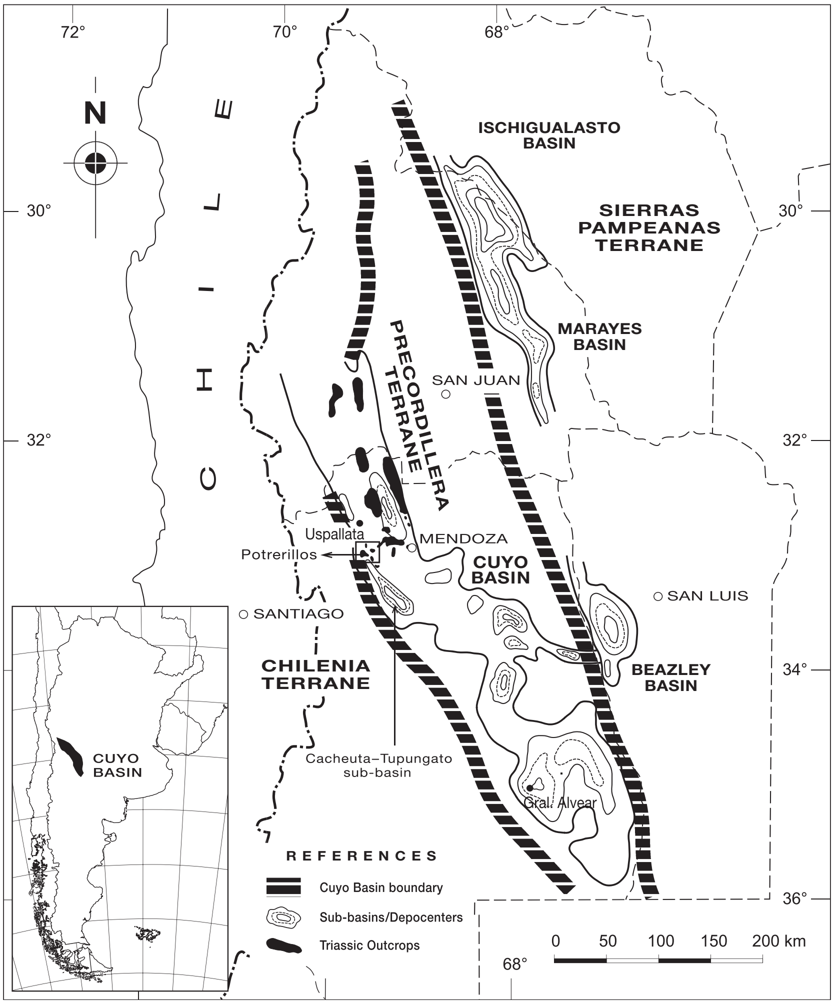

FIG. 3. Generalized reconstruction of the Triassic basins of central-western Argentina, showing the location and extent of the Cuyo Basin. Triassic outcrops and the locations of the sub-basins of the Cuyo Basin are indicated.

Cerro de Las Cabras and the base of the Potrerillos formations, constraining its deposition to the initial infilling of the Cacheuta sub-basin during the early Anisian (Synrift I) to the Anisian–Ladinian boundary (beginning of the Synrift II), respectively (Spalletti *et al.* 2008; Ávila *et al.* 2006; Cariglino *et al.* 2016) (Fig. 4).

The studied section of the Cerro de Las Cabras Formation is located near the International Road 7, km 1102 (32° 55′ 48″ S, 69° 13′ 46, 5″ W) at the southern side of the Río Mendoza river (Fig. 1) and is *c.* 100 m thick. The sedimentological profile comprises the uppermost part of the Cerro de Las Cabras Formation at its type locality, below the coarse conglomeratic basal levels of the Potrerillos Formation (with clasts up to 40 cm in diameter) which locally mark the unconformity between both units (Días & Massabié 1974). The succession is characterized mainly by fine-grained sediments, sandstones and conglomerates interbedded with pyroclastic rocks (Fig. 5). Three tabular whitish pink (rhyolitic?) ignimbrite mantles 2.5–4 m thick are interbedded in the middle to upper part of the studied section. The base of the section (*c.* 55 m) is dominated by grey-greenish to dark grey carbonaceous siltstones and claystones, frequently interbedded with fine to coarse-grained tuffaceous sandstones, fine gravels and conglomerates. They are massive or finely horizontally laminated (fine shales) and frequently contain abundant spinicaudatans (conchostracans), scarce plant debris and fish remains (mainly scales). The middle part of the section is dominated by a succession composed of finely parallel to massive dark-grey to dark-green siltstone–shales containing scarce conchostracans and plant debris. Finely laminated, fine-grained grey sandstones lenses with wavy, planar or even massive structures, alternate with these levels (Fig. 5). Coarse-sandy channels with slightly erosive bases occur sporadically. The upper part of the studied section is dominated by fine to medium-grained, grey-greenish to grey-whitish to purple tuffaceous sandstones with wavy lamination and are frequently mottled, interbedded by tabular laminated purple and light brownish siltstones. The upper fine-

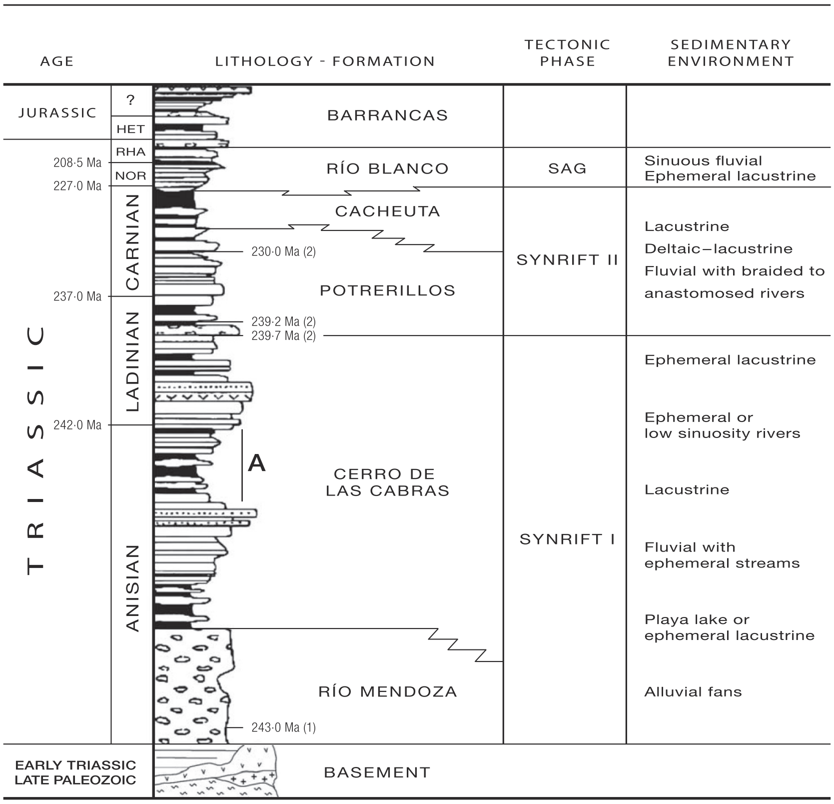

FIG. 4. Generalized and schematic stratigraphical column of the Cacheuta sub-basin, Cuyo Basin, northern Mendoza Province and the corresponding interpretation of tectonic phases and palaeoenvironments (adapted from Kokogian *et al.* 1993). Boundary ages according to the International Chronostratigraphic Chart v 2017/02 (Cohen *et al.* 2017) (1) Ávila *et al.* (2006); (2) Spalletti *et al.* (2008); locations of these radiometric dates are approximate. ‘A’ indicates approximate location of the studied profile. Stages are not to scale.

grained levels show abundant small tubular structures interpreted as rhizoliths.

Fish remains were recovered from two levels located at 20 m (NF1) and 23 m (NF2) respectively from the base of the section. Both fish levels (NF1 and NF2) are characterized by the abundance of spinicaudatans, fish scales and scarce plant debris (mainly sphenophytes) (Fig. 5). The associated spinacaudatan assemblages were assigned to *Euestheria martinsnetoi* (Vaz Tassi *et al.* 2015).

The whole sequence of the Cerro de Las Cabras Formation at its type locality comprises a low sinuosity river system with ephemeral streams, playa lakes, or ephemeral lacustrine deposits (Días & Massabié 1974; Kokogian & Mancilla 1989; Kokogian *et al.* 1993) with scarce herbaceous vegetation composed mainly of sphenophytes growing at the margins, suggesting a semiarid climate with seasonal rainfall (Barredo 2012). The studied section is interpreted as part of those ephemeral shallow lakes where distributary channels and ephemeral streams prograded as channelized flows. Fish remains and conchostracans recorded in the lower third of the studied section (N1 and N2, Fig. 5) inhabited such ephemeral, shallow, lacustrine deposits.

The profuse presence of pyroclastic deposits as well as the ignimbrite tabular mantles as pyroclastic flows throughout the section indicates the occurrence of explosive volcanic activity coeval with sedimentation. Benavente *et al.* (2015) described in detail the middle part of the Cerro de Las Cabras Formation at its type locality, composed mainly of carbonates associated with volcaniclastic deposits. They interpreted that section of the unit as being a freshwater carbonate shallow palustrine–lacustrine depositional systems fed mainly by an open groundwater supply, as confirmed by geochemical data (Benavente 2014). The surrounding siliciclastic sandflat and mudflat sediments of the succession were interpreted by those authors as playa lake systems developed in the lowest areas of the basin with evidence of subaerial exposure and paedogenesis (vertical soils) indicating ephemeral conditions caused by phreatic level fluctuations or regional water table level oscillations due to lake level changes. Such palaeohydrological changes may have been controlled by tectonics and regional climate, reflecting pulses of subsidence and aggradation alternating with pulses of little to no sedimentation, erosion and palaeosol development. In the Cerro de Las Cabras succession, it is possible to determine an overall increasing subsidence shown by an increase in strata thickness and predominance of palustrine facies associations with non-marine stromatolite (= algal biostructure) development towards the top showing mostly aggradation. This interpretation agrees with the tectonic and climatic setting described for the Triassic Cuyo rift Basin (Benavente *et al.* 2015, and references therein).

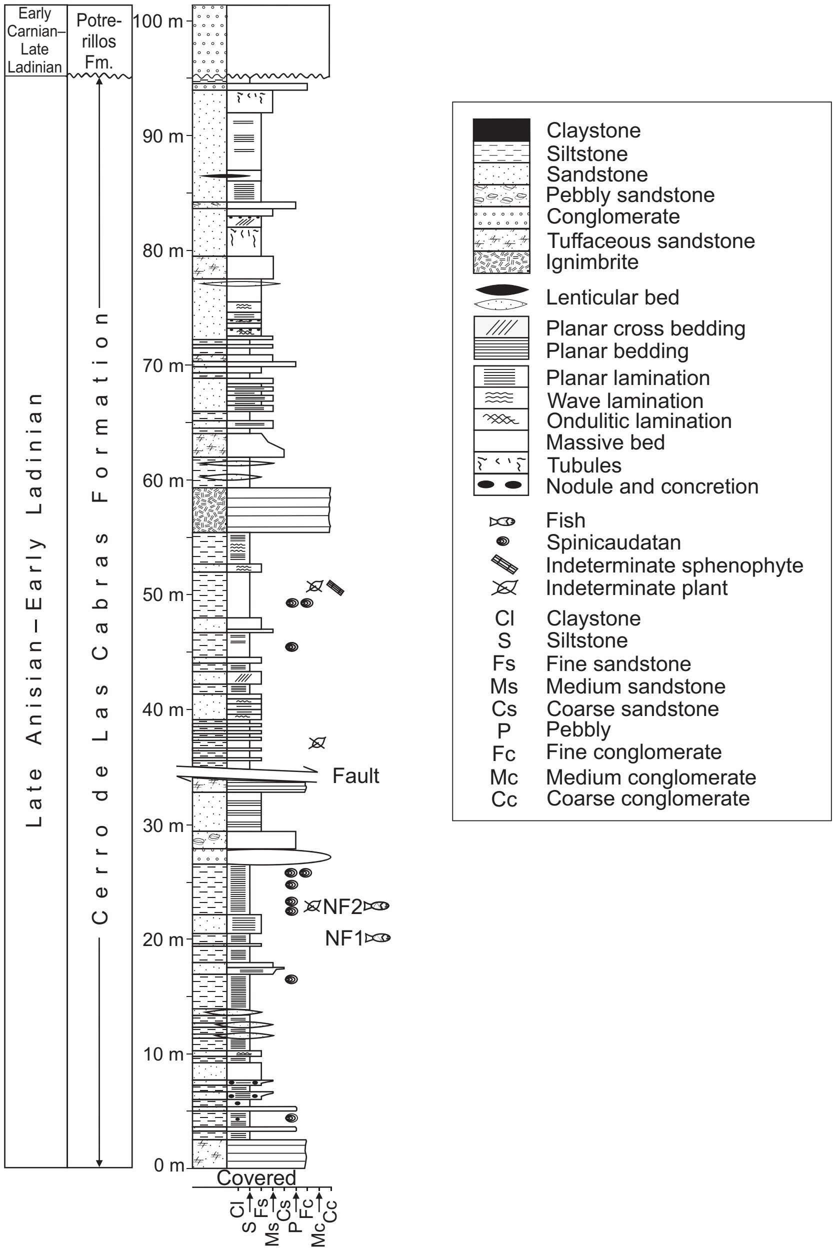

FIG. 5. Sedimentological profile of the Cerro de Las Cabras Formation type locality, at the NNW flank of the Cerro Bayo outcrops, Potrerillos, Mendoza Province (Argentina) showing fossiliferous levels.

Fish taphonomy

The fish remains at Cerro de Las Cabras are represented by: (1) body fragments (i.e. isolated caudal fins, scale patches, isolated skulls, fragments missing the head or the caudal fin); and (2) almost complete fishes that only lack part of the fins or some skull bones. Almost all specimens are articulated, although a few show a small degree of disarticulation and dispersion. Most specimens have a straight spinal cord but some show traces of bending of the spinal cord. Almost all specimens do not show traces of recristalization of bones and/or scales. However, some of those preserved in dark shale facies show a variable degree of recrystallization, cracking and replacement.

SYSTEMATIC PALAEONTOLOGY

OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII Cope, 1887
REDFIELDIIFORMES Berg, 1940
Family INCERTAE SEDIS

Genus *Calaichthys* nov.
Figures 6–15

LSID. urn:lsid:zoobank.org:act:F9958FBA-FDDF-47F4-AC0F-EE4E66289589

Derivation of name. *Cala*, refers to 'water' for a native population of the Cuyo region western of Argentina; it is an Allentiac voice of the aboriginal Huarpe language; *ichthys* (Greek) is for fish.

Type species. *Calaichthys tehul* sp. nov.

Diagnosis. *Calaichthys* is characterized by a combination of characters, including unique features among redfieldiiforms which are marked with [*]. Small-sized and fusiform actinopterygians (>50 mm of TL). Bullet-shaped head with a length of *c.* 10 mm. Large orbit (*c.* 30% of the total skull length) anteriorly placed. Extremely short preorbital region; postorbital region reaching more than 50% of the total length of the skull. Thin and mainly unornamented dermal skull roof bones. Unornamented rostral bone [*]. Two extrascapulars delicately ornamented with very small tubercles and having a bifid posterior margin [*]. Triangular dermosphenotic ornamented with very small tubercles and few rugae [*]. Two wide and quadrangular postparietals of about half the length of the parietals. Three suborbital bones [*]. An anteriorly inclined (in an angle of *c.* 40°) and hatchet-shaped preopercle, which broadly extends over the posterior margin of the maxilla. Rectangular and slender opercle which is much smaller than the subopercle [*]. Deep mouth gape. Unornamented maxilla with a well-developed postorbital plate and an extremely short posteroventral process. Dentary is ornamented with rugae anteriorly [*]. A median gular plate. Conic and slightly backward inclined dentary teeth. Entopterygoid, ectopterygoid and dermopalatine with small pointed teeth disposed in several series. Pectoral fins composed of numerous principal fin rays (17–18) which are stout, stiff, non-segmented, and branched twice distally [*]. Short and tall dorsal fin with thin and barely segmented fin rays [*]. Dorsal and anal fins opposite in origin and located in a posterior position near the origin of the caudal fin. Pelvic fins located midway between pectoral and anal fins and composed of 11–12 segmented fin rays [*]. Falcate anal fin with a long base and highly segmented fin rays. Two rows of bifid scales between the posttemporal and the dorsal fin [*]. Two big and almost circular scutes preceding the dorsal fin base [*]. Well-developed fringing fulcra present in paired and unpaired fins. Robust and long fringing fulcra associated with the pectoral and pelvic fins. Caudal peduncle flanked by well-developed and robust basal fulcra. Thin ganoid scales all over the body. Flank scales with a serrated posterior margin and ornamented with two or three parallel ridges [*]. Serration in flank scales varies between two well-developed serrations and more than three less developed ones; caudal peduncle scales without serration [*]. Rhombic dorsal body scales with three serrations in their posterior margin (two well-developed and a tiny one) [*]. Rectangular ventral body scales with three poorly developed serrations [*]. Ventral body scale rows with highly imbricated scales. More or less rectangular lateral line scales with the lateral line pore between two serrations [*]. Rhombic or lanceolate caudal peduncle scales which lack ornamentation [*]. A series of rectangular plate-like structures or scutes between both pectoral fins [*]. Hemiheterocercal caudal fin with an abbreviated but conspicuous scaly lobe that extends halfway along the dorsal lobe. Very well-developed dorsal and ventral scutes and basal fulcra preceding the caudal fin.

Calaichthys tehul sp. nov.
Figures 6–15

LSID. urn:lsid:zoobank.org:act:82163634-B17B-42F4-B7C8-6958D6052EF7

Diagnosis. As for genus.

Derivation of name. *tehul*, refers to 'under the soil' for a native population of the Cuyo region western of Argentina; it is also an Allentiac voice of the aboriginal Huarpe language.

Holotype. IANIGLA-Pv 321 a–b, an incomplete specimen that has its skull and the anteriormost portion of the body but lacks the caudal fin. The specimen is laterally preserved as a part and counterpart.

Paratypes. IANIGLA-Pv 320 a–b, an incomplete specimen which preserves the skull and the anteriormost portion of the body but lacks the caudal fin. This specimen is dorsoventrally preserved as part and counterpart; IANIGLA-Pv 322, an incomplete specimen which has the caudal, dorsal and anal fins but lacks the skull and anteriormost portion of the body. This specimen is laterally preserved.

Stratigraphical and geographical provenance. The specimens were collected from two different levels of the upper part of the Cerro de Las Cabras Formation of the Uspallata Group, Cuyo Basin, at Mendoza Province, Argentina (32° 55′ 48″ S, 69° 13′ 46, 5″ W). The sediments here are Middle Triassic (Anisian) in age.

Description

Skull roof. The skull roof bones of *Calaichthys* are thin and unornamented (Figs 6–8A), an unusual feature among redfieldiiforms which commonly have a marked ornamentation (see

Redfieldius and *Dictyopyge* in Schaeffer & McDonald 1978, figs 4–5, 12–14). Thin skull roof bones without ornamentation are present in some *Helichthys* species (Brough 1931).

The snout region of *Calaichthys* is poorly preserved in the examined material except for a rostral bone identified in the holotype (IANIGLA-Pv 321 a–b) and the paratype (IANIGLA-Pv 320 a–b); this latter is a single median bone that bears the ethmoid sensory canal (= ethmoid commissure) running near the base of the bone (Figs 7, 8A). Due to poor preservation, the presence of nasals and postrostral cannot be established with certainty. *Calaichthys* has an unornamented rostral bone. However, all redfieldiiform genera have more or less developed tubercles in the snout region (e.g. Wade 1933; Hutchinson 1973; Martin 1980; Schaeffer 1984). Tubercles are well-developed in *Cionichthys*, *Redfieldius*, *Dictyopyge*, *Helichthys* and *Synorichthys* (Schaeffer & McDonald 1978; Schaeffer 1984). Like other redfieldiiforms, the holotype of *Calaichthys* shows a single paired nostril surrounded by the 'premaxilla', adnasal and rostral bones (Fig. 7D). The adnasal (= prefrontal of Brough 1931) forms the anterior border of the orbit; it seems to be barely in contact with the dermosphenotic (Fig. 7). The adnasal is common to many redfieldiiforms, its presence being doubtful only in *Ischnolepis*, *Atopocephala* and *Phlyctaenichthys* (Schaeffer 1984). The general shape of parietals (= frontals) of *Calaichthys* is reminiscent of those of *Cionichthys*, *Redfieldius* and *Mauritanichthys* (see Schaeffer 1984, fig. 3) being posteriorly wide and anteriorly thin, and having a small posterior lateral projection (Fig. 7). Parietals form the greatest part of skull roof; they are large (longer than wide) and more or less symmetrical (Fig. 7). The dermopterotic is a large, elongated rectangular bone; it is in contact with the dermosphenotic anteriorly, and with the extrascapulars posteriorly (Fig. 7). While *Redfieldius* had three postparietals (Schaeffer & McDonald 1978), most of redfieldiiforms including *Calaichthys,* had two (Fig. 7). The postparietals of *Calaichthys*

FIG. 6. *Calaichthys tehul* gen. et sp. nov. (IANIGLA-Pv 321a–b, holotype), photograph of the specimen lightly coated with ammonium chloride. A, right lateral view. B, left lateral view. Scale bar represents 10 mm. Colour online.

are quadrangular, shorter than the parietals and have rounded corners (Fig. 7). Similar postparietals are present in *Molybdichthys*, *Daedalichthys*, *Cionichthys* and *Mauritanichthys* (see Schaeffer 1984, fig. 3). *Calaichthys* has two extrascapulars which have a bifid posterior portion (Fig. 7); the supratemporal or extrascapular commissure runs transversely in the posterior portion of the bone (Fig. 7). Extrascapular morphology and number are variable among redfieldiiforms, for example, pentagonal and/or narrow in some *Brookvalia* species (Hutchinson, 1978), and a series of four rectangular extrascapular bones in *Cionichthys*, *Redfieldius* and *Dictyopyge* (Schaeffer & McDonald 1978; Schaeffer 1984).

Circumorbital series. Some of the circumorbital bones are slightly displaced in the holotype (Figs 6, 7). As far as can be observed, three infraorbitals are present in the holotype (Fig. 7). They form the ventral and posteroventral margin of the orbit. The infraorbitals are slender bar-like bones, the first are in contact with the dorsal edge of the premaxilla and the second in contact with the dorsal edge of the maxilla (Fig. 7). The infraorbital sensory canal runs along the medio-dorsal margin of the infraorbitals. The third infraorbital forms the posteroventral corner of the orbit (Fig. 7). Most redfieldiiforms have one or two infraorbitals (Schaeffer 1984); only *Calaichthys* and *Dictyopyge* have three infraorbital bones (Schaeffer & McDonald 1978).

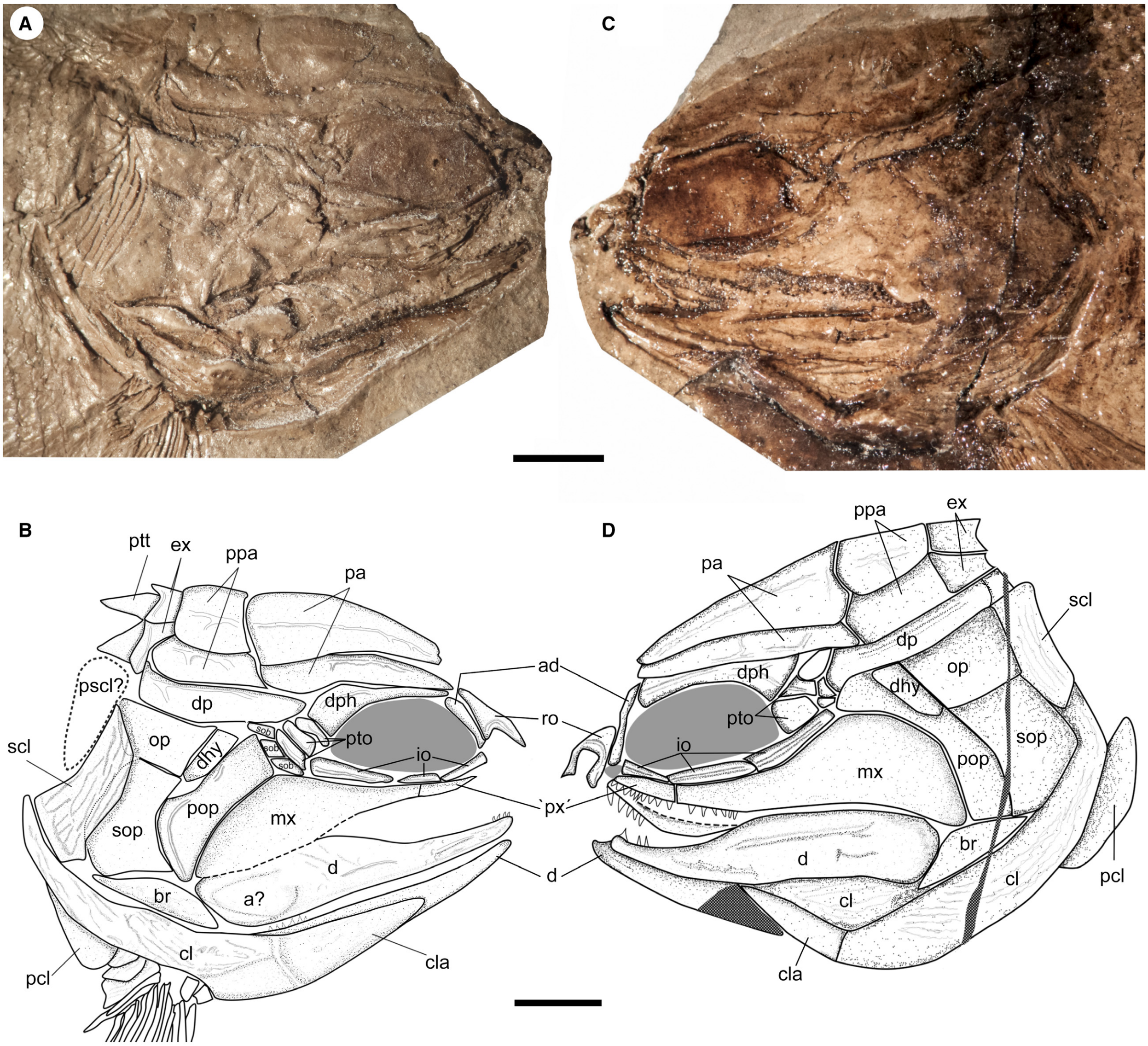

FIG. 7. *Calaichthys tehul* gen. et sp. nov. (IANIGLA-Pv 321 a–b, holotype). A, photograph of head (IANIGLA-Pv 321a). B, drawing of the head and part of the pectoral fin. C, photograph of head (IANIGLA-Pv 321b). D, drawing of the head. Hatched area in D missing from fossil. *Abbreviations*: a?, angular?; ad, adnasal; br, branchiostegal ray; cl, cleithrum; cla, clavicle; d, dentary; dhy, dermohyal; dp, dermopterotic; dph, dermosphenotic; ex, extrascapular; io, infraorbital bones; mx, maxilla; op, opercle; pa, parietal bones; pcl, postcleithrum; pop, preopercle; ppa, postparietal bones; pscl?, presupracleithrum?; pto, postorbital; ptt, posttemporal bones; ‘px’, ‘premaxilla’; ro, rostral bone; scl, supracleithrum; sob, suborbital bones; sop, subopercle. Scale bar represents 2 mm. Colour online.

The three postorbitals preserved in the holotype of *Calaichthys* suffered post-mortem displacement (Fig. 7). The postorbital bones are rectangular and bear a sensory canal (Fig. 7). As far as can be determined, the holotype of *Calaichthys* has three small suborbitals, being a unique character for this genus among redfieldiiforms (Fig. 7A, B). Most redfieldiiforms have a single suborbital, *Phlyctaenichthys* has six and *Redfieldius* has two. *Calaichthys* suborbitals are located in front of the preopercle (Fig. 7), a similar condition is observed in other redfieldiiforms (*Daedalichthys*, *Redfieldius*, *Dictyopyge*, *Atopocephala* and *Brookvalia*). The suborbitals of *Calaichthys* seem to separate the preopercle from the infraorbital series, and partially separate the preopercle from the dermopterotic (this condition is also present in redfieldiiforms like *Daedalichthys* and *Brookvalia*). The opposite is observed in *Redfieldius* and *Dictyopyge*; in these taxa suborbitals fully separate the preopercle from the skull roof but partially separate it from the infraorbital series (see Schaeffer & McDonald 1978 for comparison). The presence of either elongated or reduced postorbital plates is common to both redfieldiiforms and Palaeozoic 'palaeoniscoids' (Mickle 2013).

The dermosphenotic of *Calaichthys* is a sickle-shaped bone that contacts the adnasal and is ornamented with tiny tubercles which are more developed in its postero-ventral region (Fig. 7). The dermosphenotic forms most of the dorsal and postero-dorsal margins of the orbit (Fig. 7); a similar condition observed in many redfieldiiforms including *Daedalichthys*, *Helichthys* and *Cionichthys* (Brough 1931; Hutchinson 1978; Schaeffer 1984), as well as in advanced actinopterygians like pachycormids (see Mainwaring 1978; Poplin 2004). However, many Palaeozoic 'palaeoniscoids' have a more or less reduced dermosphenotic (Poplin 2004) with the supraorbital being the bone that dorsally closes the orbit (Lehman 1952).

Opercular series. The preopercle of *Calaichthys* is hatchet-shaped, anteriorly inclined and is in contact with the posterior and dorsal margins of the maxilla (Fig. 7). Typically, redfieldiiforms have a hatchet-shaped preopercle which shows small developmental variations in shape (see Schaeffer 1984, fig. 2). Commonly, an anteriorly inclined and hatchet-shaped preopercle is also present in Palaeozoic 'palaeoniscoids' (Mickle 2013). The opercle is square or almost rectangular, being smaller than the subopercle (Fig. 7). A similar opercle shape is observed in *Dictyopyge* (Schaeffer & McDonald 1978) but in this taxon the opercle is strongly ornamented. The subopercle is subcircular and larger than the opercle (Fig. 7). Redfieldiiforms commonly have a large subopercle (e.g. *Cionichthys*, *Phlyctaenichthys* and *Brookvalia*). However, the subopercle is smaller than the opercle in *Daedalichthys*, equally as large as the opercle in *Synorichthys* and extremely larger in *Dictyopyge* (Schaeffer 1984).

The dermohyal of *Calaichthys* is rectangular and, as far as can be observed in the holotype, is free (Fig. 7). Among redfieldiiforms, the presence of a dermohyal and an antopercle is a condition present in generalized taxa (Schaeffer 1984). An antopercle could not be recognized in the available material of *Calaichthys*. The sole, rhombic branchiostegal plate-like ray of *Calaichthys* is ornamented with small ridges (Fig. 7). The presence of a single branchiostegal ray is widely distributed among redfieldiiforms with the exception of *Daedalichthys*, which has two branchiostegal rays (Brough 1931; Hutchinson 1973; Schaeffer 1984). A median, spindle-shaped plate is interpreted as the gular (Fig. 9). The plate is located between the two branches of the lower jaw, appears shorter than it and is diffusely ornamented with ridges of ganoine.

Upper jaw. Calaichthys upper jaw bones are smooth and thin (Figs 7–9). The 'premaxilla' (or premaxilla–antorbital of e.g. Gardiner 1963; see discussion in Mickle 2015) is elongated and provided with at least two tooth rows (Fig. 7). 'Premaxillary' teeth are conical, the anterior ones being slightly curved backwards. The maxilla of *Calaichthys* is posteriorly expanded and their anterior portion is rather long and narrow (Fig. 7). It extends posteriorly, reaching the posterior margin of the orbit. The maxilla has an extremely short posteroventral process (Fig. 7) and a similar condition is present in *Dictyopyge*, *Brookvalia* and *Atopocephala* (Mickle 2013, fig. 10). Meanwhile, *Redfieldius* and *Daedalichthys* lack the posteroventral process (Mickle 2013, fig. 10). The maxilla has several, tiny and pointed teeth, some of which are slightly curved backwards (Fig. 9). The maxilla of *Calaichthys* has a primitive shape which is common to redfieldiiforms as well as several lower actinopterygians (see Westoll 1944; Lehman 1952; Schaeffer 1984; Bürgin 1992; Mickle 2013).

Lower jaw. Calaichthys' lower jaw is posteriorly deeper (Figs 7, 9) and, as in other redfieldiiforms, does not expose the coronoid process which might be hidden by the maxilla (Fig. 7). The lower jaw comprises the dentary, which is a thin bone that lacks ornamentation except in its anterior portion, where there are strong ridges or rugae (Fig. 7). The dentary has a row of small pointed and stout teeth (Fig. 7). It seems that the anterior teeth are bigger than the posterior ones. The mandibular sensory canal runs medially along the dentary bone (Figs 7–9).

Palatoquadrate and suspensorium. Most bones of the palatoquadrate and suspensorium are hidden by other bones. The suspensorium is oblique and backwardly oriented (Fig. 7), being similar to that of other Middle Triassic redfieldiiforms such as *Brookvalia*, and a feature also widely distributed among Palaeozoic 'palaeoniscoids'. Upper Triassic redfieldiiforms show a vertical suspensorium (Brough 1936). By disarticulation, the specimen IANIGLA-Pv 320 a–b shows the ectopterygoid, entopterygoid and at least two dermopalatine bones. All of these bones bear small and pointed teeth (Figs 8, 9). The dermopalatine is anteriorly thin and posteriorly wide; it bears small teeth which are organized into at least four rows, the inner or lingual teeth row has bigger teeth than the external or labial one.

Pectoral girdle. Dermal bones of the pectoral girdle are well-ossified. *Calaichthys* has triangular posttemporal bones which seem to meet rostrally (Fig. 7). Similar shaped posttemporal bones are present in other redfieldiiforms, such as *Lasalichthys*, *Phlyctaenichthys* and *Atopocephala* (Wade 1935; Hutchinson 1973; Schaeffer 1967), although in these genera the posttemporal are heavily ornamented. Because the supracleithrum in the holotype of *Calaichthys* is displaced, a bone, preserved as an impression, could be referred to the pre-supracleithrum (Fig. 7). A pre-supracleithrum is commonly present in redfieldiiforms (see *Helichthys* in Hutchinson 1978 and the discussion in Schaeffer

1984). The supracleithrum is more or less rectangular, being a rather large bone (*c.* 4 mm length), strongly ornamented with parallel ridges, some of which seem to anastomose and with a smooth posterior margin (Fig. 7). Commonly, the supracleithrum of redfieldiiforms is heavily ornamented having a variable ornamentation pattern (Schaeffer & McDonald 1978; Hutchinson 1973). The posterior margin of the supracleithrum in redfieldiiforms is smooth except in *Daedalichthys* (Brough 1931). *Calaichthys* has one large postcleithrum, which is subtriangular or L-shaped (Figs 7, 8). The cleithrum of *Calaichthys* is robust, sickle- or crescent-shaped and its lateral wing is strongly ornamented with ganoine ridges (Figs 7–9). Clavicles are well-ossified and join the anteroventral margin of the cleithrum (Figs 7–9). *Calaichthys* has at least five postcleithral scales (Fig. 10).

Pectoral fins. The pectoral fins are positioned low in the flank of the fish and close to its ventral margin (Figs 6–8, 10). Pectoral fins have 17–18 principal fin rays, the first one being the wider (Fig. 10). *Calaichthys* pectoral fin rays are mainly non-segmented being scarcely segmented and branched only in their distal portion (Figs 6, 8, 10, 15). This condition is similar to that present in *Daedalichthys* (Brough 1936, fig. 5) and differs from other members of the family which have some of the pectoral fin rays segmented and unbranched distally (see for instance *Brookvalia* in Hutchinson 1973, p. 258). Further, *Calaichthys* fin rays differ from those of Palaeozoic ‘palaeoniscoid’ fishes, which have numerous thin, segmented and branched pectoral fin rays.

In redfieldiiforms the number of principal pectoral fin rays is variable, for instance, 6–7 in *Daedalichthys*, 8 in *Helichthys*, 10–11 in *Redfieldius* and *Dictyopyge* and 17 in *Brookvalia* (Brough 1931; Hutchinson 1973; Schaeffer & McDonald 1978).

Calaichthys has a series of massive, prominent, and large fringing fulcra preceding the first wide pectoral fin ray (Figs 6, 8, 10, 15). A similar pattern of fringing fulcra is also found in *Helichthys* and *Daedalichthys* (Brough 1931, 1936).

Pelvic fin. The pelvic fin of *Calaichthys* originates near or at the midpoint between the pectoral and anal fins (Figs 6, 8A, C, 11). It has a more or less long base, being fan-shaped, and is composed of 11–12 lepidotrichia. The first two pelvic rays are robust, stout and wider than the remaining one (Fig. 11). At least one scute and five basal fulcra precede the pelvic fin (Fig. 11). All pelvic fin rays are scarcely segmented (two or three segments each ray), they become distally thinner and branch at least twice (Fig. 11). The first ray supports massive fringing fulcra (Fig. 11). Redfieldiiform pelvic fins may have about 8–11 bifurcated and segmented lepidotrichia in *Redfieldius* and *Dictyopyge* (Schaeffer & McDonald 1978), 14 in *Molybdichthys*, 21–22 in *Brookvalia*, 25 in *Schizurichthys* and 29 in *Ischnolepis* (Hutchinson 1973).

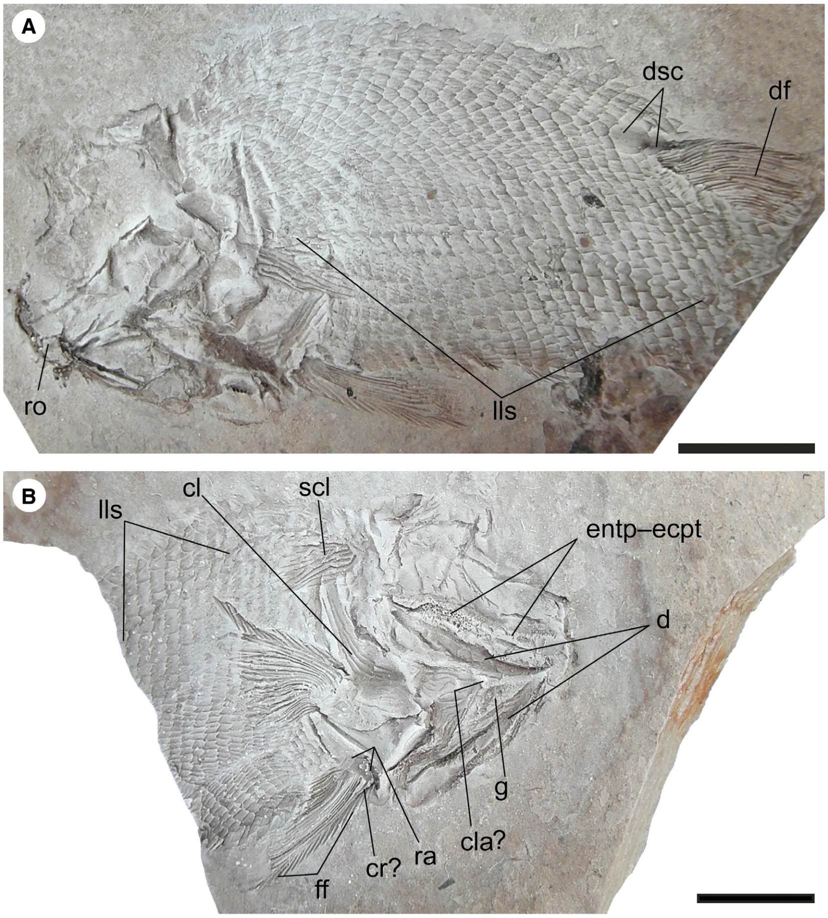

FIG. 8. IANIGLA-Pv 320 a–b, *Calaichthys tehul* gen. et sp. nov. preserved in ventral view. *Abbreviations*: cl, cleithrum; cla?, clavicle?; cr?, compound ray?; d, dentary; df, dorsal fin; dsc, dorsal scutes; entp–ecpt, entopterygoid–ectopterygoid; ff, fringing fulcra; g, gular plate; lls, lateral line scales; ra, radials; ro, rostral bone; scl, supracleithrum. Scale bar represents 5 mm. Colour online.

Dorsal fin. The dorsal fin of *Calaichthys* is inserted at the 21st scale row, being triangular with a rather long base (Fig. 12). The dorsal fin is located opposite to the anal fin (Fig. 6). The fin rays are thin and barely segmented, having two or three large segments each about 1 mm in length. The dorsal fin has 17–20 principal rays and two procurrent rays (Fig. 12). The first two principal dorsal fin rays are branched twice in their distal region. Two rounded and big (*c.* 2 mm) dorsal scutes precede the dorsal fin; the anterior scute is overlapped by three rows of scales (Fig. 12). At least four basal fulcra precede the dorsal fin. Fringing fulcra are well developed, being not as massive as the ones in the pectoral or pelvic fins (Figs 10–12). Each fulcrum seems to be lanceolate, similar to pattern C of Arratia (2009) (Fig. 12). Elongated accessory fulcra are located between some basal fulcra (Fig. 12). Among redfieldiiforms, the pectoral fin of *Calaichthys* is reminiscent of that present in *Daedalichthys* mainly because of the development of big scutes preceding the fin and because it has well-developed basal and fringing fulcra (see Brough 1931).

Anal fin. The anal fin is falcate, originates at the 22 scale row and is preceded by a small scute (Fig. 6). It comprises at least 30 stout and stiff principal rays, which are scarcely segmented (having six more or less long segments per ray). Segments are in contact by a straight union. Each anal fin ray branches distally at least twice. Two or three basal fulcra precede the anal fin. Also, a series of well-developed fringing fulcra is present.

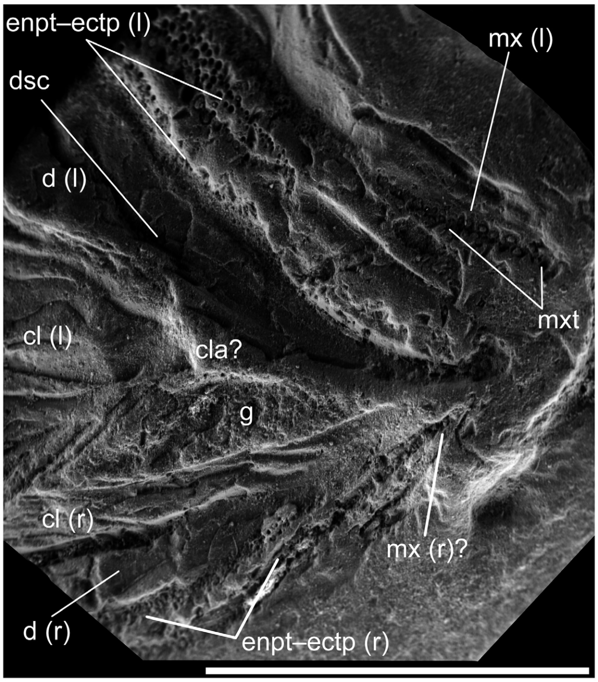

FIG. 9. IANIGLA-Pv 320 a, *Calaichthys tehul* gen. et sp. nov., SEM photograph of the skull in ventral view. *Abbreviations*: cl, cleithrum; cla?, clavicle?; d, dentary; dsc, dentary sensory canal; entp–ecpt, entopterygoid–ectopterygoid; g, gular plate; (l), left; mx, maxilla; mxt, maxillary teeth; (r), right. Scale bar represents 4 mm.

Caudal fin. The distal part of the caudal fin's dorsal lobe is broken off and the ventral one is completely preserved (Fig. 13). The caudal fin is hemiheterocercal and slightly forked. The caudal fin comprises at least 37 principal caudal fin rays (Fig. 13). These rays are thin and segmented; those of the ventral lobe branch distally at least four times (Fig. 13). Segments are more or less equal in size and the union between segments is straight. Due to the state of preservation, the organization of the dorsal lobe of the caudal fin is not clear. However, it can be observed that the ventral lobe

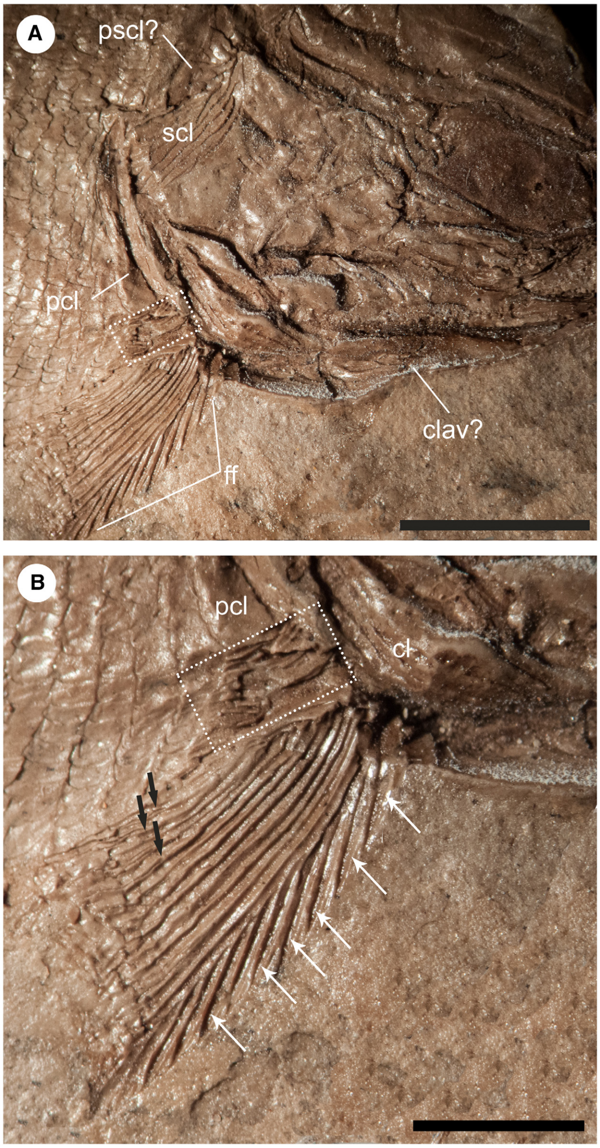

FIG. 10. *Calaichthys tehul* gen. et sp. nov. (IANIGLA-Pv 321 a–b, holotype), detail of the pectoral fin and pectoral girdle. A, general view; B, close-up of A. Dotted rectangles highlight the peculiar postcleithral scales. White arrows in B denote fringing fulcra; black arrows denote the first bifurcation of pectoral fin rays. *Abbreviations*: cl, cleithrum; clav?, clavicle?; ff, fringing fulcra; pcl, postcleithrum; pscl?, presupracleithrum?; scl, supracleithrum. Scale bars represent 4 mm (A); 2 mm (B). Colour online.

comprises three procurrent caudal fin rays and at least nine basal fulcra (Fig. 13). The preserved region of the caudal fin's dorsal lobe has at least 12 elongated, massive and prominent basal fulcra (Fig. 13). A series of lanceolate fringing fulcra and accessory fulcrum are located in the margins of both, dorsal and ventral caudal fin lobes (Fig. 13). Although incompletely preserved, the dorsal lobe of the caudal fin has an abbreviated (but not inconspicuous) scaly lobe that projects into the dorsal lobe (Fig. 13B). The scaly lobe is composed of at least 15 scales and reaches the half of the dorsal lobe (Fig. 13). While most redfieldiiforms have among 50–65 caudal fin rays (52 in *Synorichthys* Schaeffer 1967; 60 in *Ischnolepis* Hutchinson 1973; 63 in *Brookvalia* Hutchinson 1973; and 65 in *Helichthys* Brough 1934) *Calaichthys* has 37 caudal fin rays (Fig. 13), similar to *Atopocephala* and *Geitonichthys*, which have 40 fin rays (Brough 1934; Hutchinson 1978) and *Cionichthys*, which has 33 (Schaeffer 1967).

Squamation. Calaichthys specimens have exquisitely preserved, thin ganoid scales covering the body (Fig. 14). The squamation comprises 24–30 transverse scale rows (Fig. 6). Anterior body flank scales are more or less quadrangular (Figs 6, 14D). Scales near the dorsal margin of the body are rhombic (Fig. 14C) and those of the ventral margin are rectangular (Fig. 14E). Scales at the caudal peduncle are lanceolate (Fig. 13). Most of the scales have a bifid posterior margin with a ventral denticle bigger than the dorsal one; others have a serrated posterior margin and the caudal peduncle scales lack the serrations (Fig. 14). *Calaichthys* scales are ornamented with two or three parallel ridges (Fig. 14), being smooth in the caudal peduncle region of the fish (Fig. 13). A total of 35 lateral line scales are preserved in the holotype and 28 in IANIGLA-Pv 320 a–b (Figs 6, 8, 13A).

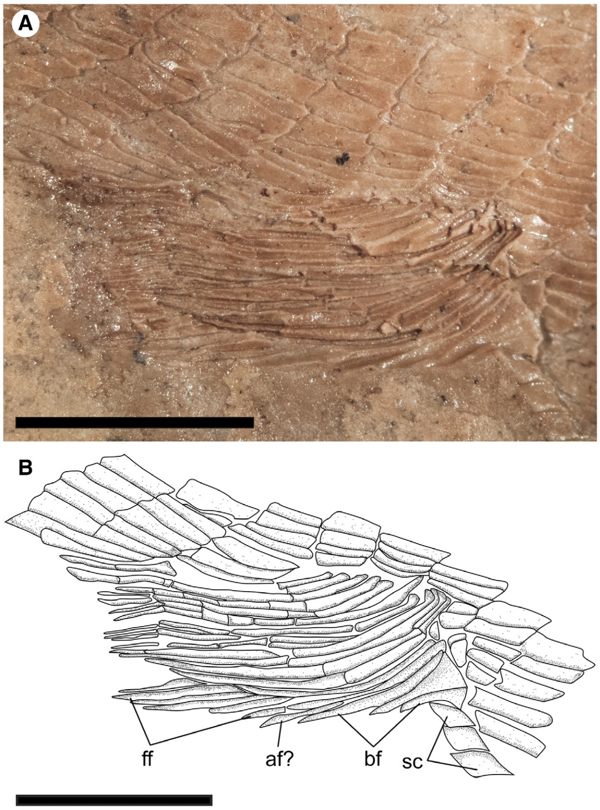

FIG. 11. *Calaichthys tehul* gen. et sp. nov. (IANIGLA-Pv 321 a–b, holotype), pelvic fins. A, photograph of the pelvic fin. B, interpretative drawing of A. *Abbreviations*: af?, accessory fulcrum?; bf, basal fulcra; ff, fringing fulcra; sc, scutes. Scale bars represent 2 mm. Colour online.

IANIGLA-Pv 320, which is preserved in ventral view, shows a series of plate-like and rectangular scales between pectoral fins (Fig. 15); these scales decrease in size caudally and are ornamented with small tubercles and punctuations (Fig. 15). This specimen also has a well-developed ventral keel (Fig. 8B).

The dorsal scales between the posttemporal and the dorsal fin are shield-like, with a small posterior spine (Figs 6, 8, 14A–B). IANIGLA-Pv 322 has six scale rows in front of the dorsal lobe of the caudal fin, the scales on the axial body lobe being smaller and rhombic in shape (Fig. 13).

The posterior margin of redfieldiiforms scales varies between species, being smooth in *Cionichthys dunklei* or denticulated in *C. greeni* (Schaeffer 1967) and *Daedalichthys* (Hutchinson 1973). Also, the ornamentation pattern is variable among redfieldiiforms, having tubercles in *Atopocephala* (Brough 1934), *Schizurichthys* and *Ischnolepis* (Hutchinson 1973), ridges in *Brookvalia* and *Daedalichthys* (Hutchinson 1973), or even lacking any ornamentation, as in *Helichthys* species (Hutchinson 1978). The condition present in *Calaicththys* scales (flanked with a denticulate posterior margin ornamented with ridges, and caudal peduncle scales which lack ornamentation and serrations) is unique to this taxon among redfieldiiforms (Figs 6, 8, 14).

DISCUSSION

Our work confirms for the first time that Redfieldiiformes occur in South America. Previously only a putative redfieldiiform taxon had been recorded from the Middle–Upper Triassic of the Los Rastros Formation (López-Arbarello 2004; Gouiric-Cavalli *et al.* 2017, appendix S1) for which a collection number, anatomical description and precise locality are unknown.

The anatomy of *Calaichthys* includes a mixture of characters that are generalized among Mesozoic 'subholostean' redfieldiiforms and Palaeozoic 'palaeoniscoids' (see above). *Calaichthys* is regarded as a 'subholostean' because it shows a mixture of primitive ('palaeoniscoid') characters (fixed maxilla with a deep posterior region that is in contact with the preopercle, a suspensorium backwardly oriented) and more advanced (holostean) ones (distally segmented fin rays, hemiheterocercal caudal fin). Moreover, many characters (i.e. cheek pattern reflecting an oblique and backwardly directed suspensorium, a hatchet-shaped preopercle, a large head with a large orbit and a skull with a long and posteriorly deep maxilla) agree with a generalized 'subholostean' and Palaeozoic 'palaeoniscoid' fish grade (e.g. Lehman 1952; Schaeffer 1955; Lombardo & Tintori 2004; Lombardo 2013; Mickle 2013).

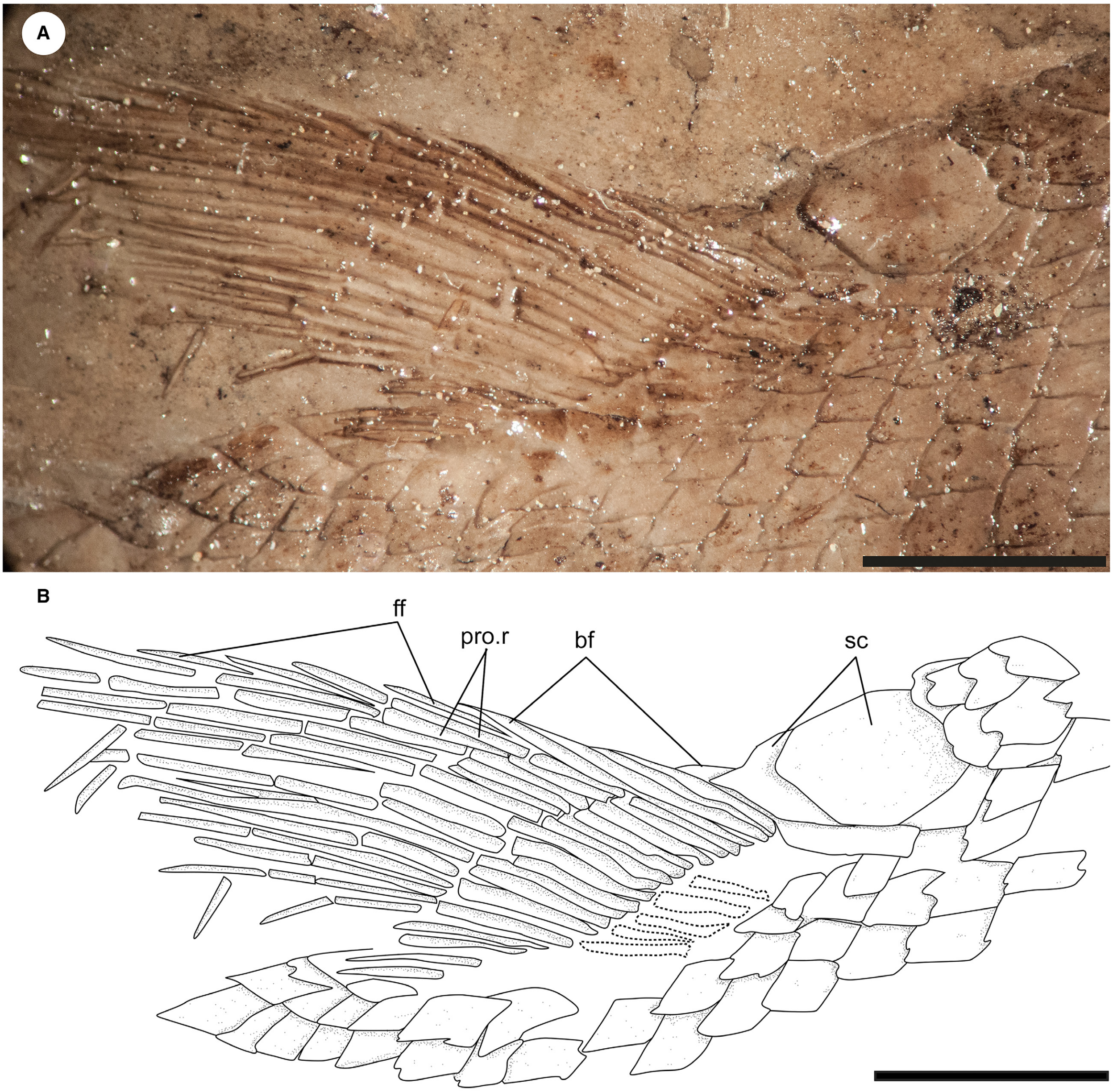

FIG. 12. *Calaichthys tehul* gen. et sp. nov. (IANIGLA-Pv 321 a–b, holotype). A, photograph of the dorsal fin. B, interpretative camera lucida drawing of dorsal fin. *Abbreviations*: bf, basal fulcra; ff, fringing fulcra; pro.r, procurrent ray; sc, scutes. Scale bars represent 2 mm. Colour online.

Calaichthys is included within Redfieldiiformes because it presents many of the diagnostic characters for the group, as proposed by Hutchinson (1978) and Schaeffer (1984), such as the presence of an adnasal bone, reduced branchiostegal series to one branchiostegal plate-like ray, pectoral fins with stout, opposite dorsal and anal fins, stiff, mainly non-segmented and distally branched fin rays, leading rays usually bearing long and robust fringing fulcra, basal fulcra bordering both lobes of the caudal fin and hemiheterocercal caudal fin. Although a single branchiostegal ray is not a unique character of redfieldiiforms, being also present in other actinopterygians (Westoll 1944; Poplin 1997, 2001; López-Arbarello *et al.* 2006), the combination of characters showed by *Calaichthys* does not allow its inclusion within any of these actinopterygian groups. Among redfieldiiforms we consider *Calaichthys tehul* to be a new taxon given its unique combination of characters (see Diagnosis above).

Like other redfieldiiforms, *Calaichthys* has a wide mouth gape, small teeth and an inclined suspensorium,

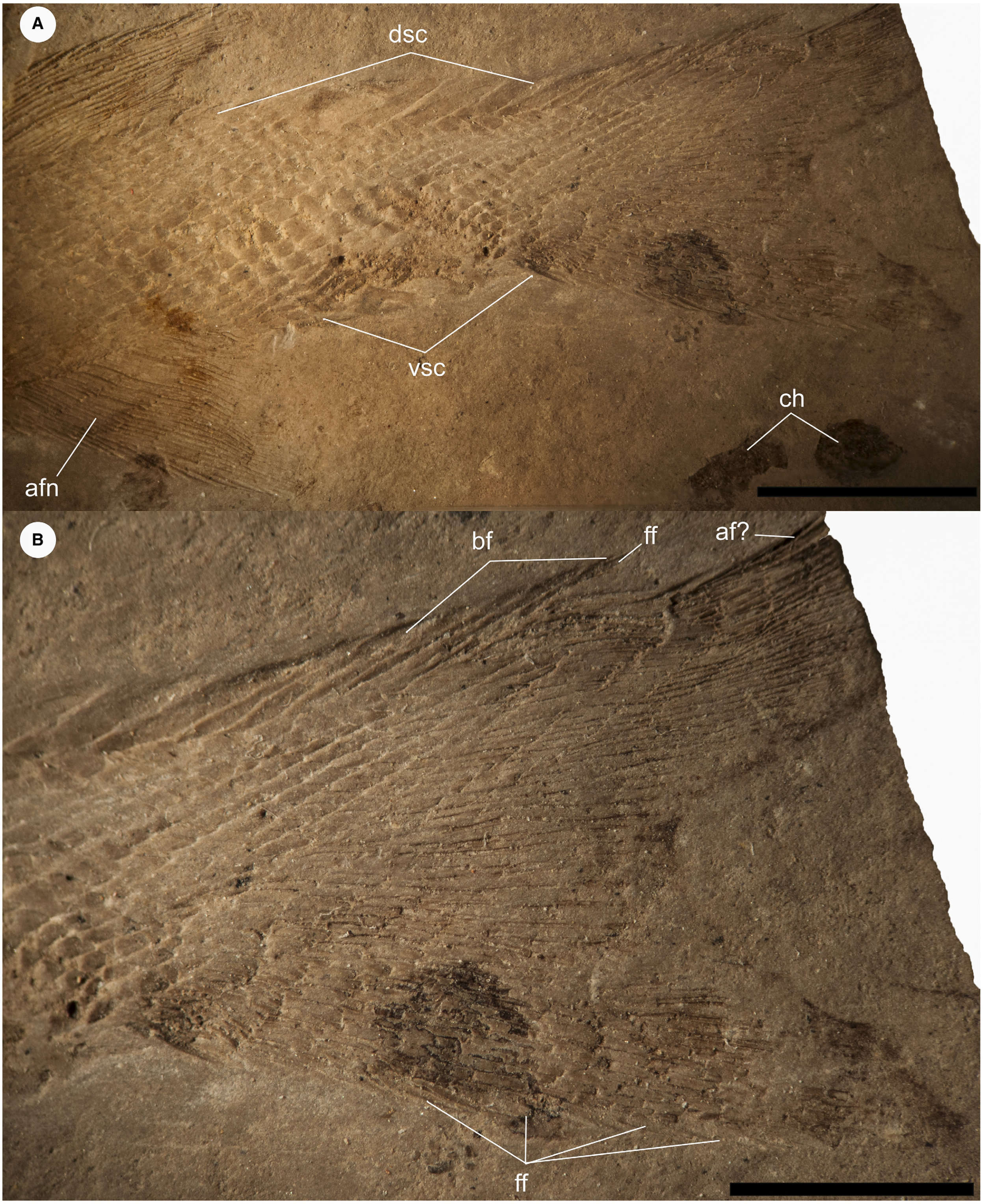

FIG. 13. IANIGLA-Pv 322, *Calaichthys tehul* gen. et sp. nov. caudal fin. A, the preserved specimen. B, detail of the caudal fin. *Abbreviations*: af?, accessory fulcrum?; afn, anal fin; bf, basal fulcra; ch, conchostracans; dsc, dorsal caudal peduncle scutes; ff, fringing fulcra; vsc, ventral caudal peduncle scutes. Scale bars represent 5 mm (A); 3 mm (B). Colour online.

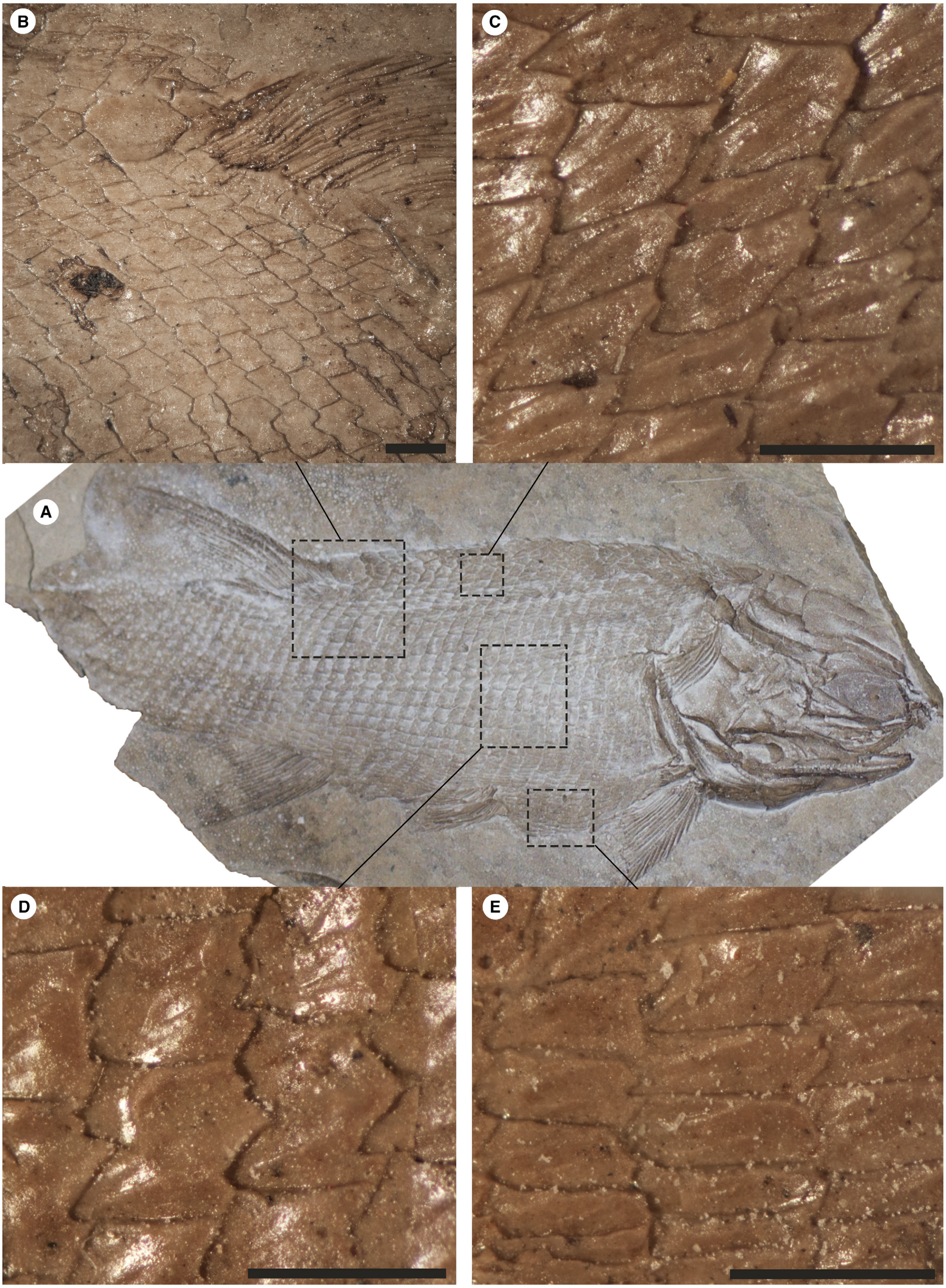

FIG. 14. *Calaichthys tehul* gen. et sp. nov. (IANIGLA-Pv 321 a–b, holotype) squamation. A, IANIGLA-Pv 321 a–b in lateral right view, dashed rectangles indicate each squamation section. B, dorsal scale rows and scales preceding the dorsal scutes of the dorsal fin. C, dorsal scale rows. D, flank scale rows. E, ventral scale rows. All scale bars represent 1 mm (A not to scale). Colour online.

all characters associated with ram feeding (Lauder 1980; Kriwet 2001; Whiteside *et al.* 2011).

Notably, redfieldiiforms show variation in the scaly elements (basal, fringing and accessory fulcra and scutes) associated with their fins (e.g. Schaeffer & McDonald 1978; Schaeffer 1984). Considering the large variability associated with these elements in paired and unpaired fins of actinopterygians as a whole (e.g. Arratia 2009; Schultze & Arratia 2013) and their possible taxonomic relevance, a detailed study of these structures in redfieldiiforms as well as in other basal actinopterygians is required.

Remarks on the ichthyofauna of the Cerro de Las Cabras Formation

During the Middle to Late Triassic, significant lacustrine innovations have been hypothesized, the so-called Mesozoic Lacustrine Revolution (Buatois *et al.* 2016) which involved the diversification and increase in morphological disparity of aquatic organisms after the reduction in lacustrine biodiversity during the end of the Palaeozoic to Middle Triassic (Cohen 2003).

The Middle Triassic ichthyofauna of the Cerro de Las Cabras Formation is composed of the chondrostean *Neochallaia tellecheai*, the acrolepids *Challaia magna* and *Ch. multidentata* (Rusconi 1949*a*, *b*; López-Arbarello *et al.* 2010) and the redfieldiiform, *Calaichthys tehul*. A preliminary assessment of other fish remains associated with those described herein suggests that acrolepids and ‘perleidiforms’, but not pseudobeaconiids, were also present at the formation (SGC, pers. obs. 2017). No sarcopterygians have been so far recovered from Cerro de Las Cabras type locality.

Calaichthys was collected in facies dominated by finely laminated grey-greenish to dark grey carbonaceous siltstones and claystones associated with conchostracans referred to *Euestheria martinsnetoi* (Vaz Tassi *et al.* 2015) and plant remains related to a ‘*Dicroidum* Flora’ (Cariglino *et al.* 2016). Both conchostracans and fishes coexisted, being autochthonous to the ephemeral shallow lacustrine bodies.

Palaeobiogeographical remarks. Gondwanan Triassic ichthyofaunas are relatively poorly known (López-Arbarello 2004). South American continental Triassic fishes are known from only three countries: Brazil, from where fragmentary and mostly undescribed material has been reported, along with the lungfish *Ptychoceratodus* cf. *phillipsi* (Richter & Toledo 2008); Chile, where specimens include poorly preserved indeterminate ‘perleidiforms’ and *Arratiaichthys chilensis* recovered from marine sediments (Richter & Breitkreuz 1997; Arratia & Schultze 1999; Arratia 2015); and Argentina (Cuyo and Ischigualasto–Villa Unión basins) from where several specimens, most of them badly preserved, have been recovered, described and reviewed on various occasions (e.g. Bordas 1944; Cabrera 1944; Rusconi 1946*a*, 1948*a*; López-Arbarello *et al.* 2006; López-Arbarello & Zavattieri 2008; Johns *et al.* 2014; Gouiric-Cavalli *et al.* 2016; Agnolin *et al.* 2016; and see Gouiric-Cavalli *et al.* 2017, appendix S1).

Although the continental deposits of the Cuyo and Ischigualasto–Villa Unión basins of Argentina present the most numerous fish faunas in South America, most collected specimens are still unstudied or their taxonomy is problematic (López-Arbarello & Zavattieri 2008). Almost all of the taxa previously erected are based on poorly preserved or even undiagnostic material. Thus, a taxonomic

FIG. 15. *Calaichthys tehul* gen. et sp. nov. (IANIGLA-Pv 320 a, holotype) in ventral view, the dashed rectangle highlights the ventral big plate-like scales. *Abbreviations*: ff, fringing fulcra; vk, ventral keel. Scale bar represents 1 mm. Colour online.

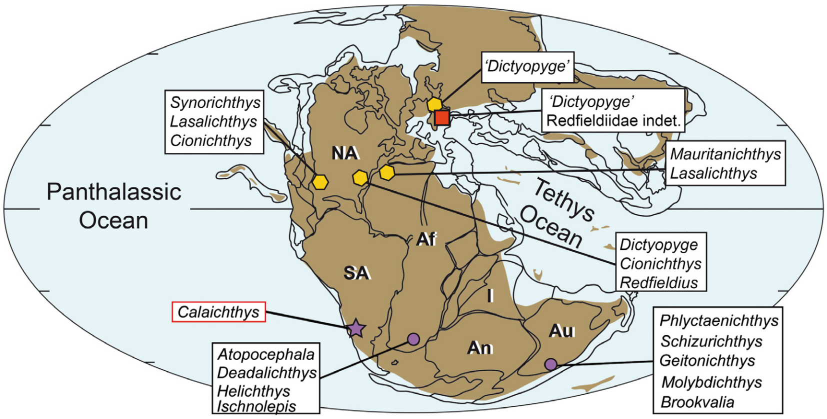

FIG. 16. Triassic Redfieldiiformes palaeobiogeography. *Abbreviations:* Af, Africa; An, Antarctica; Au, Australia; I, India; NA, North America; SA, South America. Palaeobiogeographical map modified from Scotese Palaeomap project: http://www.scotese.com/. Data of redfieldiiform distribution from: Brinkmann *et al.* (2010); Brough (1931, 1934); Broom (1909); Cavin (2017); Deecke (1889); Dzik & Sulej (2007); Haughton (1934); Hutchinson (1973); Lombardo (2013); López-Arbarello (2004); Lyell (1847); Murray (2000); Murry (1987); Olsen (1980); Schaeffer (1984, 1967); Schaeffer & Mangus (1970); Schaeffer & Mc Donald (1978); Schoch & Seegis (2016); Wade (1935); Witheside *et al.* (2011). Circles, Middle Triassic (Anisian) records; rectangle, Middle Triassic (Ladinian) records; hexagons, Upper Triassic (Carnian) records; star, *Calaichthys* record. Colour online.

revision of these faunas is necessary and essential for a better understanding of the evolution of basal actinopterygians in Gondwana.

Redfieldiiformes as a whole has a Pangaeic distribution (e.g. Schaeffer 1984; Fig. 16) being related to hot climate zones in Laurasia and Gondwanan lakes. However, the redfieldiiforms might have originated in Gondwana, undergoing rapid diversification to reach a diversity peak during the Anisian (Table 1, Fig. 16). Yet, during the late Middle Triassic (Ladinian) and the Late Triassic, redfieldiiforms seem to be present in Europe (Dzik & Sulej 2007; Brinkmann *et al.* 2010; Schoch & Seegis 2016; Cavin 2017; but see Brough 1931; Lombardo 2013; Schaeffer & McDonald 1978 for a discussion) but not so diversified. Redfieldiiforms seem to have been suffered a second diversity peak during the Late Triassic (Carnian) in North America, from where the last (Sinemurian) records of the group, come.

CONCLUSIONS

We report a new taxon, *Calaichthys tehul* gen. et sp. nov. which is the first 'subholostean' Redfieldiiformes described from South America. Thus, we improve the knowledge of the fish taxonomic diversity in the Triassic lakes of the Cacheuta sub-basin, Cuyo Basin, as well as in Gondwana. The fossil fish population of the Cerro de Las Cabras Formation has a similar taxonomic composition to those of other Triassic localities of the Cuyo and Ischigualasto–Villa Unión basins (Gouiric-Cavalli *et al.* 2017, appendix S1).

Recent studies have highlighted the importance of post-cranial characters in systematic studies of this group. Consequently, the newly taxon described above, which provides detailed post-cranial information, could be useful in future systematic and phylogenetic studies. The structure of the fins, their associated scaly elements as well the squamation pattern could be crucial in understanding the relationships between taxa.

Calaichthys which, at present, is endemic to Cerro de Las Cabras Formation, is coeval with those redfieldiiforms from the Middle Triassic (Anisian) of Africa and Australia being part of the first diversity peak of Redfieldiiformes. The new Argentinian record supports a Gondwanan distribution for Redfieldiiformes during the Middle Triassic (Anisian) being related to hot climate conditions (Fig. 16). Triassic European 'redfieldiiforms' need to be revisited, and new and better preserved material are needed to clarify their taxonomic affinity.

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