Anatomical description and taxonomy of †Luisiella feruglioi (Bordas), new combination, a freshwater teleost (Actinopterygii, Teleostei) from the Upper Jurassic of Patagonia

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ARTICLE

ANATOMICAL DESCRIPTION AND TAXONOMY OF †*LUISIELLA FERUGLIOI* (BORDAS), NEW COMBINATION, A FRESHWATER TELEOST (ACTINOPTERYGII, TELEOSTEI) FROM THE UPPER JURASSIC OF PATAGONIA

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ABSTRACT—The teleosts of the Late Jurassic Almada Fauna (Cañadón Calcáreo Formation) from Patagonia have been known for decades, but their taxonomic assignment has remained problematic. Two teleost species were thought to be represented in these lacustrine deposits: †'*Tharrhias*' *feruglioi* and †*Luisiella inexcutata*. In recent years, numerous complete and excellently preserved specimens have been collected, justifying revision of all available material. After a detailed anatomical study, we conclude that only one species of teleost is present in this fauna. †'*Tharrhias*' *feruglioi* and †*L. inexcutata* are synonyms and represent a single species, and due to the erroneous referral to the genus †*Tharrhias*, which designates a different fish, the new combination †*Luisiella feruglioi* is proposed. This study has revealed great morphological variability, which can be explained as intraspecific variability (ontogenetic and individual) as discussed herein. The overall morphology of †*L. feruglioi* resembles that of basal teleosts. In particular, †*L. feruglioi* is intriguingly similar to †*Cavenderichthys talbragarensis* from the continental Late Jurassic Talbragar Beds in Australia, owing to the presence of features not commonly found in known basal teleosts (hyomandibular bone with preopercular process, lower jaw with deep coronoid process and lacking a 'leptolepid' notch in the dentary, and first uroneural anteriorly reaching the second preural centrum) and probably derived features such as a preopercular canal with few simple tubules. The resemblance between the Almada and Talbragar faunas has been recently proposed in reference to the coccolepidid species present in both Gondwanan faunas and is here discussed regarding the anatomical similarities shown by teleosts.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The earliest unquestionable teleosts are recorded in the early Mesozoic, represented by some Late Triassic 'pholidophoriforms' and the Early Jurassic †*Dorsetichthys bechei* (Agassiz, 1844), and †*Leptolepis coryphaenoides* (Bronn, 1830). According to the fossil record, teleosts experienced a first significant radiation during the Late Jurassic (Arratia, 2004). Except for the possible teleosts †*Jiangilichthys* Su, 1983 (Late Triassic), and †*Hengnamia* Wang, 1977 (Early Jurassic), which are regarded as freshwater forms, the oldest known teleosts were marine animals, whereas the first records of continental teleosts occur in the Upper Jurassic. These oldest freshwater teleosts are known from a few, widely distributed geological units: the Morrison Formation (Kimmeridgian–Tithonian) in the U.S.A. (Kirkland, 1998), the Cañadón Calcáreo Formation (Oxfordian–Tithonian) in central Chubut, Argentina (López-Arbarello et al., 2008), the continental sequence of the Late Jurassic to Early Cretaceous Stanleyville Beds, Democratic Republic of Congo (Myers et al., 2011), and the Talbragar Beds (Kimmeridgian–Tithonian) in Australia (Turner et al., 2009). The broad distribution of Late Jurassic continental teleosts is in accordance with a Pangean origin of Teleostei, as already proposed for several lineages of modern teleosts (Diogo, 2004; Conway et al., 2010; Nakatani et al., 2011). In general, studies on Mesozoic teleosts are based on excellently preserved marine fishes from Europe and Chile but rarely include freshwater teleosts (Patterson and Rosen, 1977; Arratia, 1997, 1999). Therefore, studies on freshwater teleosts are critical to improving knowledge of the origin and early diversification of this major vertebrate clade.

The so-called Almada Fish Fauna (López-Arbarello et al., 2008) from the Cañadón Calcáreo Formation in Patagonia has been known for more than 70 years, but the taxonomy and systematic position of its teleosts are still problematic. Among four nominal species, only †'*Tharrhias*' *feruglioi* Bordas, 1942, and †*Luisiella inexcutata* Bocchino, 1967, have been accepted as valid taxa since the revision by Cione and Pereira (1987). These authors noted the erroneous referral of these fishes to the order Clupeiformes and instead considered them as Teleostei incertae sedis. They also confirmed the opinion of Bocchino (1978) that †'*Tharrhias*' *feruglioi* is not a species of the genus †*Tharrhias* Jordan and Branner, 1908, from the Cretaceous of Brazil, although they did not resolve its generic assignment.

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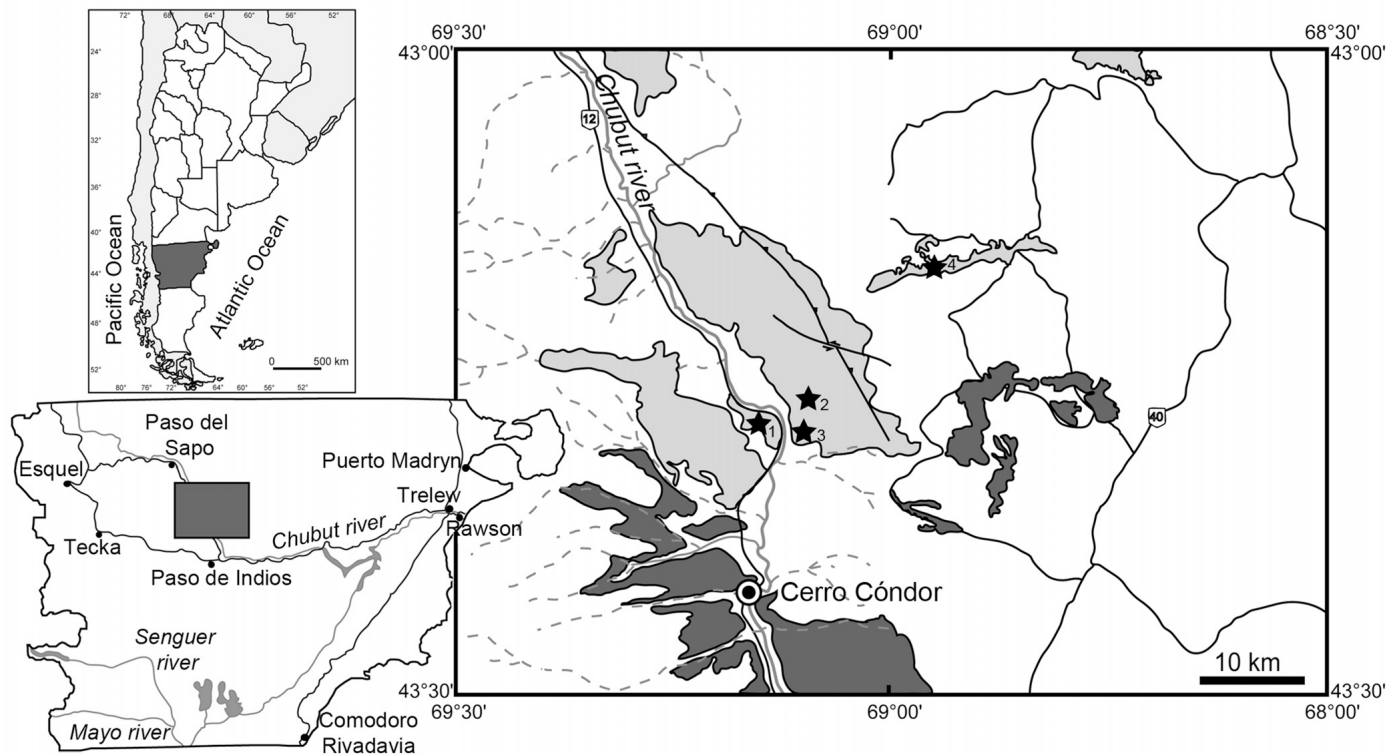
FIGURE 1. Geographical and geological setting of the Cañadón Calcáreo Formation (light grey) in central Chubut, Argentina. Outcrops of the Cañadón Asfalto Formation are shown in dark grey. Numbers indicate different outcrop localities where teleost specimens have been recovered: **1**, Puesto Almada; **2**, Estancia Fernandez; **3**, Puesto Limonao; **4**, Sierra de la Manea.

Since 2001, numerous well-preserved specimens of teleosts have been collected from the Cañadón Calcáreo Formation, Central Chubut, Argentina (Fig. 1) through intensive field work led by Oliver Rauhut of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany, in a joint project with the Museo Paleontológico Egidio Feruglio (MEF) of Trelew, Argentina. The study of this material motivated a systematic revision of the teleosts, the taxonomic conclusions of which are presented and discussed in this paper.

Institutional Abbreviations—**BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **MACN**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MPEF- PV**, Vertebrate Paleontology Collection, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

Anatomical Abbreviations—**a.ch**, anterior ceratohyal; **a.lat.pr**, anterolateral process; **a.pl**, anterior pit line; **a.r**, anal rays; **ang-art**, anguloarticular; **ao**, antorbital bone; **art**, articular; **axp**, axillar process; **ber.for**, beryciform foramen; **bpt**, basipterygium; **br. r**, branchiostegal rays; **cl**, cleithrum; **d**, dentary; **d.hyp**, dorsal hypohyal; **d.r**, dorsal rays; **d.sct**, dorsal scute; **dsph**, dermosphenotic bone; **ectp**, ectopterygoid; **endp**, endopterygoid; **e**, epurals; **ep**, epineural bones; **epx.r**, epaxial rays; **ex**, extrascapular bone; **fr**, frontal bone; **fr.fu**, fringing fulcra; **H1–8**, hypurals 1–8; **h.sp**, hemal spine; **hy**, hyomandibular bone; **ihm**, infrahemal spine; **io1–5**, infraorbital bones 1–5; **io.c**, infraorbital canal; **iop**, interopercle; **m.c**, mandibular canal; **m.pl**, middle pit line; **mes**, mesethmoid, a compound ossification formed by fusion of the dermal rostrodermethmoid and the endoskeletal supraethmoid; **mx**, maxilla; **mx.cc**, maxillary cranial condyle; **n.a**, neural arches; **n. sp**, neural spines; **na**, nasal bone; **op**, opercle; **op.hy**, opercular process of hyomandibula; **p.ch**, posterior ceratohyal; **p.n.sp**, paired neural spines; **pa**, parietal bone; **pap**, parapophysis; **pcl**, postcleithrum; **pec.r**, pectoral rays; **pel.r**, pelvic rays; **PH**, parhypural; **pmx**, premaxilla; **pop**, preopercle; **pop.c**, preopercular sensory canal; **pop.hy**, preopercular process of the hyomandibula; **PR 1–19**, principal caudal rays 1–19; **pr.r**, procurrent rays; **psph**, parasphenoid; **pt**, pterygiophores; **pto**, pterotic bone (fused auto- and dermopterotics); **ptt**, posttemporal bone; **ptt.c**, posttemporal sensory canal; **Pu1–5**, preural centra 1–5; **q**, quadrate; **r**, ribs; **s. co**, supratemporal commissure; **scl**, supracleithrum; **smx1–2**, supramaxillae 1–2; **sn**, supraneural bone; **so**, supraorbital bone; **so.c**, supraorbital sensory canal; **soc**, supraoccipital bone; **sop**, subopercle; **sr**, sclerotic ring; **t.c**, temporal sensory canal; **U1– 2**, ural centra 1–2; **u.n.sp**, unpaired neural spines; **un**, uroneurals; **ur**, urohyal; **v**, vertebra; **v.hyp**, ventral hypohyal; **v.sct**, ventral scute; **vo**, vomer. An 'l' and 'r' between parentheses after the abbreviations indicates left and right elements, respectively.

SYSTEMATIC PALEONTOLOGY

NEOPTERYGII Regan, 1923
TELEOSTEI Müller, 1844, sensu Arratia, 1999
Order and family indet.
†*LUISIELLA* Bocchino, 1967

Type Species—†*Luisiella inexcutata* Bocchino, 1967.
Diagnosis—same as for the type and only known species.

†*LUISIELLA FERUGLIOI* (Bordas, 1942), new combination
(Figs. 2–12)

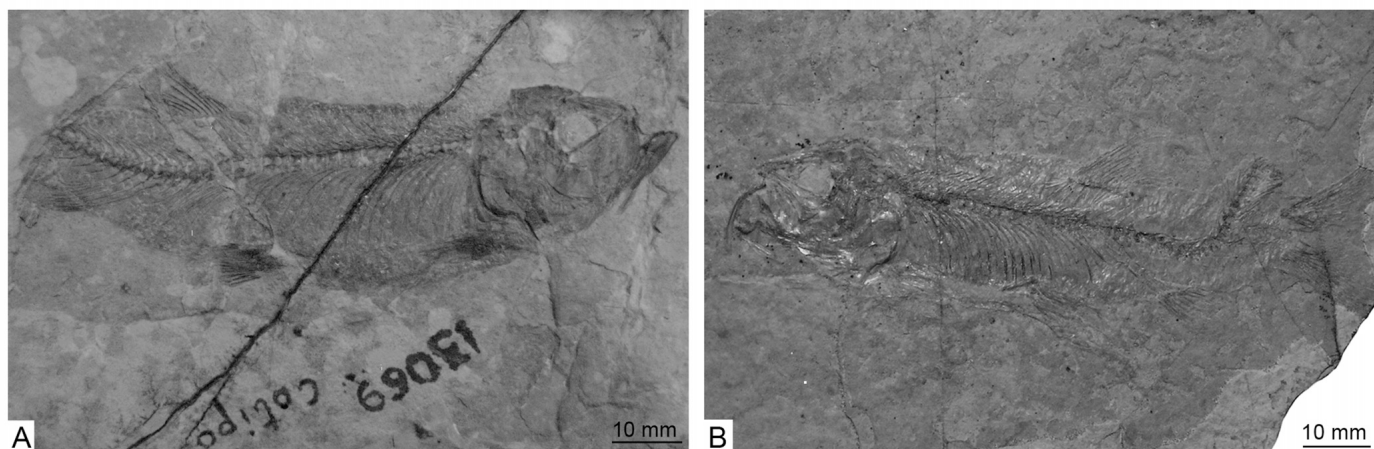†*Diplomystus longicostatus* Cope, 1887: Piatnitzky, 1936:105 (referred).

FIGURE 2. †*Luisiella feruglioi*, new combination. **A**, lectotype (MACN 13069); **B**, holotype of †*Luisiella inexcutata* (MLP 35-III-1-4).

†*Tharrhias feruglioi* Bordas, 1942:316–317, pl. 1 (original description).
†*Luisiella inexcutata* Bocchino, 1967:92–95, figs. 2–3 (original description).
†*Leptolepis feruglioi* (Bordas, 1942): Bocchino, 1978:303–309, pl. 1 (new combination).
†'*Tharrias*' *feruglioi* Bordas, 1942: Cione and Pereira, 1987:290–292, pls. 3 and 5c (emended spelling).

Lectotype—MACN 13068–9, single specimen preserved as part and counterpart (Lectotype designation by Bocchino, 1978; Fig. 2A).

Paralectotypes—MACN 13026, 13036, 13056.

Additional Material—See Supplementary Data.

Type Locality—According to Bordas (1942:316), the type specimen (MACN 13068–9) comes from "Valle medio del Río Chubut, en el Lote 24, sección I, cerca de la casa de Marcos Almada, aguas arriba de Paso de los Indios, Chubut" [Middle valley of the Chubut River, in the parcel 24, section I, near the house of Marcos Almada, upstream from Paso de Indios, Chubut]. The house of Marcos Almada is locally known as Puesto Almada, Estancia El Torito; it is located about 20 km north of the village of Cerro Cóndor at the Ruta Provincial No. 12 in the central valley of the Chubut River (S43°18′25.6″, W69°10′11.5″; Fig. 1).

Type Horizon—'Estratos de Almada,' basal lacustrine section of the Cañadón Calcáreo Formation (Late Jurassic: Oxfordian–Tithonian).

Distribution—Localities of Puesto Almada, Puesto Limonao, Estancia Fernández including Cañadón Los Chivos I and II and Cañadón Las Minas, and Sierra de La Manea (Fig. 1); outcrops of the basal lacustrine section of the Cañadón Calcáreo Formation (Late Jurassic: Oxfordian–Tithonian) in the middle valley of the Chubut River, Chubut Province, Argentina.
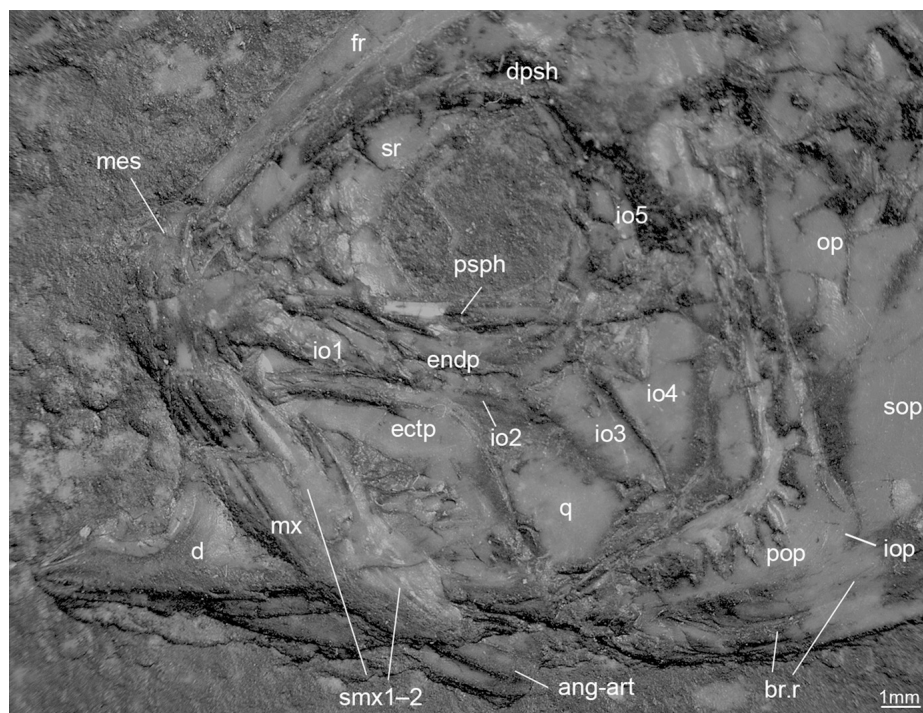

FIGURE 3. †*Luisiella feruglioi*, new combination. Photograph of skull in left lateral view (MPEF-PV 3185).

Diagnosis—Fusiform small teleost of up to ca. 90–100 mm of standard length (SL); length of the skull 1/4 SL; skull longer than it is deep; snout length shorter than orbital diameter; infraorbital sensory canal with few and simple tubules; preopercular sensory canal with seven to eight simple tubules not reaching the ventral margin of the preopercle; preopercle without posteroventral extension; suborbital bone absent; frontal bones strongly sculptured; anterior pit line in a groove in parietal; middle pit line in a groove in parietal and pterotic; maxilla sculptured with longitudinal grooves; abdominal neural arches expanded and hourglass-shaped, with neural spines originating from the middle portion of the posterior border of each half of the neural arch; dorsal fin origin immediately posterior to the origin of the pelvic fins; first anal pterygiophore notably large.

Other distinct features of the species, which are not preserved in the lectotype, include vertebral column with 39–41 vertebrae (22–24 abdominal + 15–17 caudal) visible behind the skull and first preural centrum with a short neural spine.

DESCRIPTION

The following description is based on the type and referred material (see Supplementary Data). Specimen numbers are indicated in brackets when a feature is especially well preserved in a particular individual. †*Luisiella feruglioi*, new combination, is a small, fusiform fish of 90–100 mm of maximum standard length (SL), reaching ca. 110–115 mm in total length. The head depth is 79.3% of the head length, and this length is 25.8% of the standard length. The snout length is 87.8% of the orbital diameter and represents 22.4% of the head length, whereas the orbital diameter is 25.6% of the head length. The opercular region is 29.2% of the head length. The dorsal fin origin is located at the midlevel of the standard length, immediately posterior to the origin of the pelvic fins. Percentages correspond to average values of body proportions; individual measurements and body proportions expressed as percentages are provided in Supplementary Data, Tables S1–S4.

Skull Roof—The frontal, parietal, and pterotic bones are the main components of the skull roof; deep grooves and wrinkles strongly sculpture the parietal and pterotic and the posterior portion of the frontals (Figs. 3, 4). The nasals are small, elongate, tube-like bones mainly bearing the anterior portion of the supraorbital sensory canal. These paired bones are lateral to the anterior portion of the corresponding frontal and not in contact with each other (MPEF-PV 1477#1, 1489#2b, MLP 35-III-1-4). The frontals are the largest bones of the cranial roof; they are slightly separated from one another anteriorly (e.g., MPEF-PV 10534a), whereas posteriorly they are in contact through a smooth suture that becomes sinuous caudally. Each frontal has a subtriangular shape, anteriorly narrow and broader behind the orbit (e.g., MPEF-PV 3431, 3959). The posterior margin of the frontal is irregular (generally sinuous) and asymmetric (MPEF-PV 3851), and it sutures the anterior portion of the corresponding parietal, slightly overlapping it. The frontals bear the supraorbital sensory canals, which extend in enclosed bony tubes (see Sensory Canals and Lateral Line for the trajectory and tubules of the supraorbital sensory canals in the frontals). The parietals articulate anteriorly with the frontals and posteriorly with the extrascapulars and supraoccipital bones, overlapping most of the latter. Although the shape of these bones is difficult to trace because they are usually partially overlapped by the frontals, it is possible to describe them as small, quadrangular to rectangular bones superficially sculptured with grooves and wrinkles (MPEF-PV 1488#2b, 3415, 10534a; Fig. 5). However, variation in the shape of the parietals (rectangular, quadrangular, trapezoidal) and their irregular posterior margins among individuals and/or in the same individual is evident. The parietals are in contact with each other along the midline with a straight suture but are slightly separated posteriorly by the supraoccipital bone (e.g., MPEF-PV 1488#2a, 10534a); they do not participate in the formation of the supraoccipital crest. The supraorbital sensory canal extends within the lateral portion of each parietal for about one-half of its length, giving off a pore. Additionally, there is a shallow anterior pit line groove, which crosses the bone in an anterior to posterior direction, and a deeper middle pit line groove crossing it and extending onto the pterotic bone (e.g., MPEF-PV 3419, 3851, 3882a, 10534a; Fig. 5). The pterotics are located lateral to the parietals, posterolateral to the frontals, posteromedial to the
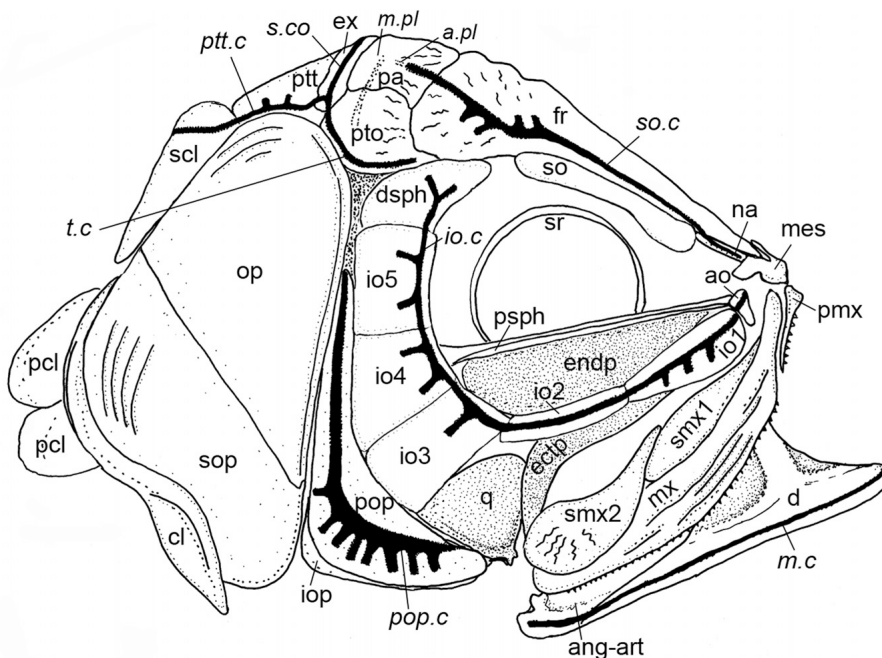

FIGURE 4. †*Luisiella feruglioi*, new combination. Reconstruction of the skull in right lateral view. Elements of the sensory canal system are labeled in italics.

2mm

dermosphenotics, and anterolateral to the extrascapular bones, forming the posterolateral region of the cranial roof. Each pterotic has an irregular shape, with a narrow anterior portion that contacts the frontal medially and a larger, quadrangular posterior portion. The otic or temporal sensory canal extends close to the lateral margin of the pterotic without giving off any tubule, curving posteriorly to reach the corresponding extrascapular. The extrascapulars form the posterior margin of the skull; they contact anteriorly with the parietals and pterotics and posteriorly with the posttemporal bones (Figs. 4, 5). The extrascapulars are separated from each other by the supraoccipital crest. Each extrascapular is a lateromedially oriented, slightly elongated semicircular bone, with a concave anterior margin and an irregularly convex posterior margin (MPEF-PV 3419). They are ornamented with concentric wrinkles that reproduce the shape of the posterior margin of the bone (e.g., MPEF-PV 3415, 3959). Each extrascapular carries part of the temporal sensory canal and bears a lateromedially directed branch of this canal that corresponds to the supratemporal commissure.

Braincase and Parasphenoid—In general, the braincase and its associated dermal and chondral ossifications are not well exposed in teleosts because usually they are laterally and dorsally overlapped by the cranial roofing bones and the bones of the orbital series. Therefore, only the mesethmoid, parasphenoid, vomer, autosphenotic, and supraoccipital of †*L. feruglioi* were identified and are described herein.

The mesethmoid forms the most anterior portion of the skull (Fig. 4). The main part of the mesethmoid is shield-like and has a convex dorsal surface (Fig. 6A, B). Anteriorly, it ends in a small triangular apex that bears a pair of minute anterolateral projections. In dorsal view, the mesethmoid has two symmetrical, well-ossified anterolateral processes, each of which projects anteriorly and distally forms a ventrolaterally oriented facet for the articulation with the corresponding palatine bone (Fig. 6A, B). In addition, the mesethmoid bears a pair of articular facets for the articulation with the cranial condyle of the maxilla anteriorly, whereas posteriorly it bears two short and rounded posterior processes, which apparently overlap the tip of the frontals (MPEF-PV 3419; Fig. 6B).

The parasphenoid is an elongate, dorsoventrally flat bone that contacts the mesethmoid anterodorsally and the vomer anteroventrally. The dorsal surface of the parasphenoid is slightly concave, whereas the ventral surface bears a thin, poorly developed keel. We have not observed any teeth or denticles on the parasphenoid. The presence of the ascending and basipterygoid processes on this bone is uncertain, as well as the nature of the contact of the parasphenoid with the basioccipital. The lateral ethmoid might have contacted the dorsal margin of the

parasphenoid, but this contact was not clearly exposed in the studied specimens.

The vomer is an unpaired bone preserved only in MPEF-PV 1654; it is a small, anteroposteriorly elongated bone (Fig. 7A). This bone is ventral to the mesethmoid and to the anterior portion of the parasphenoid. Proximally, the vomer is anchor-shaped and has two short lateral projections. Posterior to these projections, it extends into two strap-like processes, which define a groove that, according to Patterson (1975), might have contained the anterior branch of the palatine nerve. A displaced cluster of minute teeth is visible on one of the posterolateral projections of the vomer in MPEF-PV 1654.

The autosphenotics are paired bones located at the posterodorsal margin of the orbit, invested laterally by the dermosphenotic. Each autosphenotic is approximately pentagonal in shape, with a ventrally directed main apex and well-developed anterodorsal and lateral processes (MPEF-PV 1489#2b).

The supraoccipital is a small bone that forms the dorsomedial portion of the most posterior region of the neurocranium (MPEF-PV 488#2b, 3871b, 10534a). In dorsal view, its shape resembles a fleur-de-lis, with a pair of posterolaterally directed projections and a short median spine directed backwards that extends dorsally into a very low supraoccipital crest.

Circumorbital Series—The orbit is framed by a sclerotic ring composed of two ossicles, which are oriented anterodorsally and posteroventrally, respectively (MPEF-PV3421, 10534). Each circumorbital series includes an antorbital, infraorbitals 1–5, a dermosphenotic, and a supraorbital bone (Figs. 3, 4). Suborbital bones are absent.

The first two infraorbitals form the ventral margin of the orbit. The succeeding element curves around the posteroventral margin of the orbit, and the last two border its posterior margin (Figs. 3, 4). Occasionally, the io4 is also involved in the formation of the posteroventral curve of the orbit. The first infraorbital is lanceolate in shape, with a rather straight dorsal margin, a slightly curved ventral margin, and a tapering posterior end. The second infraorbital is a narrow, tube-like bone almost reduced to a canal-bearing ossification. The third infraorbital is rectangular, being about two times longer than it is wide. Its major axis has an anterodorsal to posteroventral orientation. Infraorbitals 3 and 4 are in contact with each other, with an oblique suture that may occur opposite the middle portion of the preopercle (e.g., MPEF-PV 3879, 3941), dorsal to that portion (e.g., MPEF-PV 3851, 3959, 3987) or, less frequently, ventral to it (e.g., MPEF-PV 1472#1, 3185). The posterior margins of infraorbitals 3 and 4 do not overlap the anterior margin of the preopercle. The fourth infraorbital is subtrapezoidal; it has
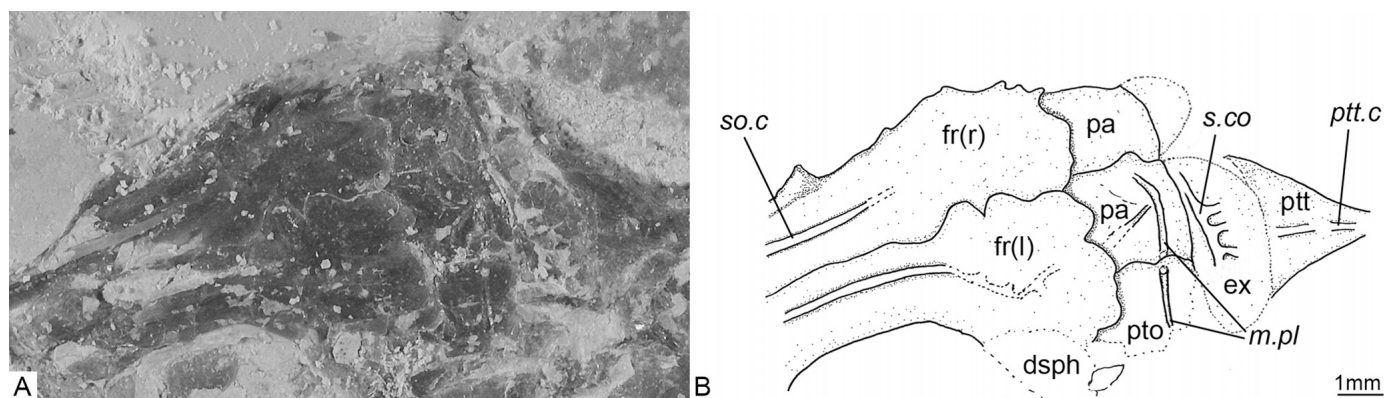

FIGURE 5. †*Luisiella feruglioi*, new combination. **A**, photograph of skull roof (MPEF-PV 3415); **B**, line drawing of skull roof (MPEF-PV 3415).
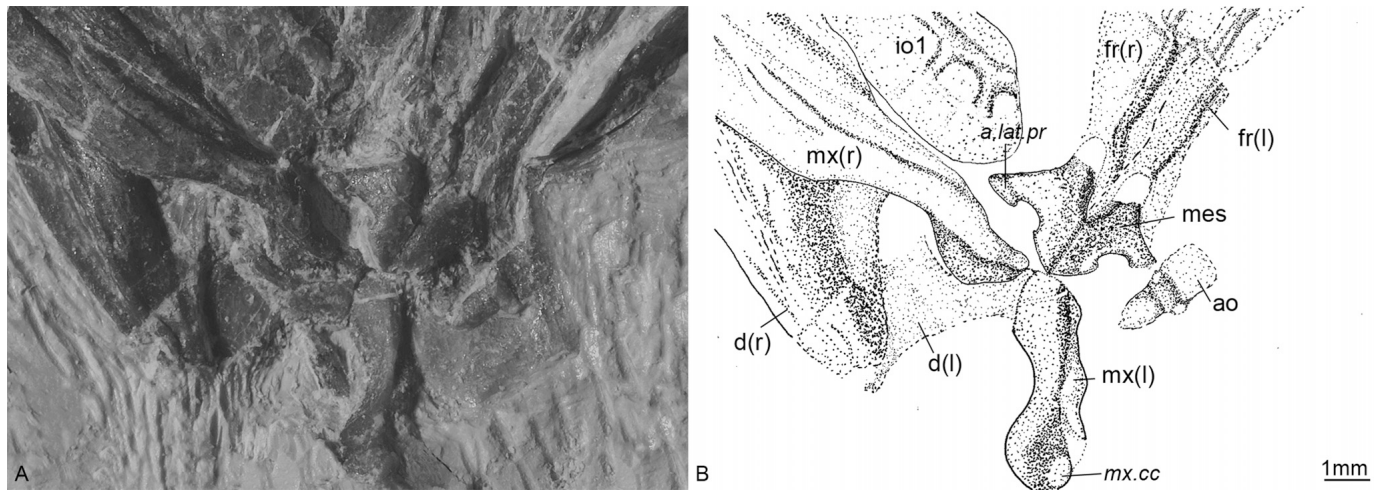
FIGURE 6. †*Luisiella feruglioi*, new combination. **A**, photograph of the anterior portion of the skull in dorsal view (MPEF-PV 3419); **B**, interpretative drawing of the anterior portion of the skull in dorsal view (MPEF-PV 3419).

a long side in contact with the preopercle and a short side delimiting the posterior, or sometimes the posteroventral, margin of the orbit. The fifth infraorbital is also subtrapezoidal, with the long side forming the posterior margin and the short side forming the anterior margin of the bone. The trajectory of the infraorbital canal through these bones and the dermosphenotic is described in detail below, in Sensory Canals and Lateral Line.

The dermosphenotic is lateroventral to the frontal, lateral to the autosphenotic, and anterolateral to the pterotic, forming the posterodorsal margin of the orbit. It has a roughly semicircular shape, with a tapering anterior end, a slightly concave anterior margin, and a convex posterior margin (e.g., MPEF-PV 1354, 3977). This bone is smaller than the posterior infraorbitals (fourth and fifth infraorbitals).

One supraorbital forms the anterodorsal margin of the orbit of †*L. feruglioi*. This bone is anteroposteriorly elongated and ovoid, and it does not reach the posterior margin of the orbit (e.g., MPEF-PV 1354, 2341a).

Hyopalatine Bones—Here we describe the quadrate, metapterygoid, endopterygoid, ectopterygoid, and bones of the hyoid arch. We were unable to identify the palatines.

The quadrate is a triangular bone that is located below the posterior half of the orbit, anteromedial to the third infraorbital (Figs. 3, 4). It has a slightly convex dorsal margin that contacts with the anteroventral margin of the metapterygoid and a straight anterior margin that is in contact with the posterior margin of the ectopterygoid. Anteroventrally, the bone bears a small condyle for the articulation with the lower jaw (e.g., MPEF-PV 3909). Immediately behind this condyle, the anteroventral rim of
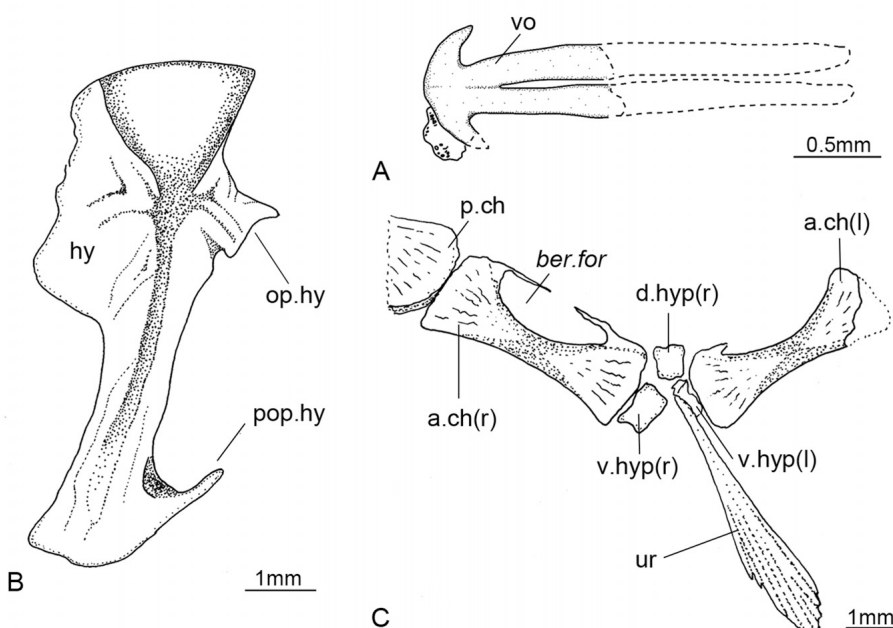

FIGURE 7. †*Luisiella feruglioi*, new combination. **A**, vomer (MPEF-PV 1654); **B**, hyomandibular bone (MPEF-PV 1654); **C**, anterior ossifications of the hyoid arch (MPEF-PV 3414).

the quadrate widens and forms a facet that is related to the post-articular process of the lower jaw (e.g., MPEF-PV 3419). In addition, the bone bears a posteroventral process, which originates near the anteroventral corner of the quadrate and is directed backwards. This process extends to the posterior margin of the quadrate, without reaching beyond it. The main body of the quadrate and the posteroventral process delimit a recess in which a slender symplectic lies (e.g., MPEF-PV 1654, 3936b). The latter bone is not in contact with the lower jaw and, therefore, does not participate in the quadrate-mandibular articulation. The quadrate-mandibular articulation is placed below the posterior half of the orbit. The metapterygoid is a subquadrangular, laminar bone that contacts the quadrate posterodorsally through a rounded anteroventral margin (e.g., MPEF-PV 3414). It is located medial to the third and fourth infraorbitals. Ventral to the parasphenoid and medial to the first infraorbitals lies the anteroposteriorly elongated endopterygoid. Its shape could not be described in detail because it is partially obscured by the infraorbital bones in all examined specimens, although it is evident that ventrally this element is in contact with the dorsal margin of the ectopterygoid and that posteriorly it contacts the metapterygoid. The endopterygoid lacks teeth or denticles. The ectopterygoid is a boomerang-shaped bone ventral to the endopterygoid. Its two limbs taper distally and are oriented subhorizontally and subvertically in the head, defining an almost right angle between them. The vertically oriented limb of this bone contacts the anterior margin of the quadrate, almost reaching its anterior condyle ventrally. Like the endopterygoid, the ectopterygoid lacks denticles.

The hyomandibular is a dorsoventrally elongated bone that broadens both dorsally and ventrally. It has a rounded dorsal margin, and the dorsal portion of the bone is slightly arched forward (MPEF-PV 1654, 3414, 3952; Fig. 7B). The hyomandibular is in contact with the metapterygoid anteroventrally, with the preopercle posteroventrally, and with the opercle posterodorsally. A distinct laterally open groove that served for the passage of the hyomandibular branch of nerve VII (facial) is visible on this bone. Dorsally, its main shaft bears a large anterior and a smaller posterior membranous overgrowth, as well as a posteriorly directed opercular process. This process is short, robust, and nearly cylindrical; it fits in a socket on the anterior margin of the opercle. Furthermore, although closer to its ventral margin, the hyomandibular bears a short, distally tapering, posterodorsally directed preopercular process that contacts the preopercle (Fig. 7B).

The posterior ceratohyal (ceratohyal 1, proximal ceratohyal, or epyhial) is semicircular, with a straight dorsal margin and a rounded ventral margin (Fig. 7C). Anteriorly, it articulates with the anterior ceratohyal and ventrally it is in contact with the posterior spathiform branchiostegal rays (see below). The anterior ceratohyal (ceratohyal 2 or distal ceratohyal) is hourglass-shaped, having concave dorsal and ventral margins in lateral and medial views. It contacts anteriorly with the hypohyals and posteriorly with the posterior ceratohyal. Ventrally, it articulates with the acinaciform branchiostegal rays and also with a few spathiform branchiostegal rays. A delicate bony rod, frequently not preserved, extends dorsally between the anterior and posterior margins, defining an inner oval window known as the beryciform foramen of McAllister (1964) (MPEF-PV 1478#8B, 3418, 3871; Fig. 7C). A pair of small, quadrangular hypohyals forms the anterior portion of each half of the hyoid arch. They are posteriorly in contact with the anterior ceratohyal. The ventral hypohyal is always the largest, being about twice the size of the dorsal hypohyal (e.g., MPEF-PV 1478#8B, 3942a; Fig. 7C). This hypohyal is perforated by a canal for the hyodean artery, which extends dorsally up to the border of the dorsal hypohyal. Whether the hyodean artery also pierced the dorsal hypohyal is uncertain because we were not able to observe any pore for its entrance or exit in this bone. The urohyal is a styliform,

anteroposteriorly oriented bone that is in contact proximally with the ventral margin of the ventral hypohyals (Fig. 7C). Its distal portion is laterally expanded and has a crenulated posterior border (MPEF-PV 1469#1b, 3414), although in some specimens this border is smooth (MPEF-PV 1489#2b).

Jaws—Each half of the upper jaw comprises the premaxilla, the maxilla, and two supramaxillae. The premaxilla is a small, triangular bone that is located above and nearly parallel to the articular process of the maxilla, tapering caudally. A row of uniformly distributed, small, conical teeth extends along most of its oral margin. The medial end of the premaxilla projects dorsally into a blunt process (e.g., MPEF-PV 1354) that probably corresponds to the articular process of the premaxilla of other teleosts (e.g., Patterson, 1975; Stiassny, 1986). The premaxillae are in contact with one another through a high and sinuous medial margin.

The slightly arched, elongate maxillae are the main components of the upper jaw; they are strongly sculptured by irregularly distributed longitudinal grooves (Figs. 3, 4). Anteriorly, each maxilla has a long, medially directed articular process, which is about 25% to 33% of the total length of the bone. A low upwardly directed condyle which, according to Patterson (1975) probably articulated with the mesethmoid, is present on the anterior part of the articular process. In addition, this process bears an inconspicuous dorsolateral ridge. The main body of the maxilla is relatively uniform in height; it has a rounded posterior margin, and it narrows dorsally, where the bone is overlapped by the two supramaxillae. Its oral margin is slightly convex and bears minute teeth that are smaller than those borne by the premaxillae. Often, the posterior portion of the oral margin bears denticles or a toothed lamella instead of well-developed teeth. Posteriorly, the maxilla does not laterally cover the quadrate-mandibular articulation, as it does in some Jurassic teleosts (Arratia, 1987, 1997).

The two supramaxillae are located dorsolateral to the maxilla (Figs. 3, 4). Supramaxilla 1 is lanceolate in shape, with a tapering anterior end and frequently a rounded posterior margin (e.g., MPEF-PV 3418), although sometimes a bilobed posterior margin is present (e.g., MPEF-PV 3415). Anteriorly, this element reaches the base of the articular process of the maxilla, whereas posteriorly it extends for about one-half of the length of the main body of the maxilla. The supramaxilla 2 has a rounded main body, which is often slightly sculptured with irregular striations, and extends rostrally into an anterodorsal spine (e.g., MPEF-PV 3969, MLP 35-III-1-4). This second supramaxilla is posterior to the supramaxilla 1, and its anterodorsal spine borders the dorsal margin of the latter. Ventral to this spine, the supramaxilla 2 has a concave anterior margin, whereas posteriorly it has a convex margin that reaches the level of the posterior margin of the maxilla.

The lower jaw is composed of the dentary and the anguloarticular; there is no trace of an independent retroarticular, the bone being probably fused to the anguloarticular (Figs. 3, 4). The lower jaw is relatively long and the quadrate-mandibular articulation is located below the posterior half of the orbit. The dentary forms the anterior portion of the mandible and has an indented posterior margin in contact with the anguloarticular bone. Its symphyseal region is fairly low, and immediately behind it the anterodorsal margin of the dentary bends up posterodorsally to form the coronoid process, which is high and located rather anteriorly in the bone. Anterior to the coronoid process and forming the anterodorsal border of the dentary, there is a sheet of bone, which is usually not preserved or is broken. Unlike other known Jurassic teleosts, a 'leptolepid' notch is absent in the ascending anterodorsal margin of the dentary, the oral margin of which lacks teeth. The posterior portion of the lower jaw is formed by a laminar anguloarticular bone that has a rather convex anterior margin and an anterodorsally to
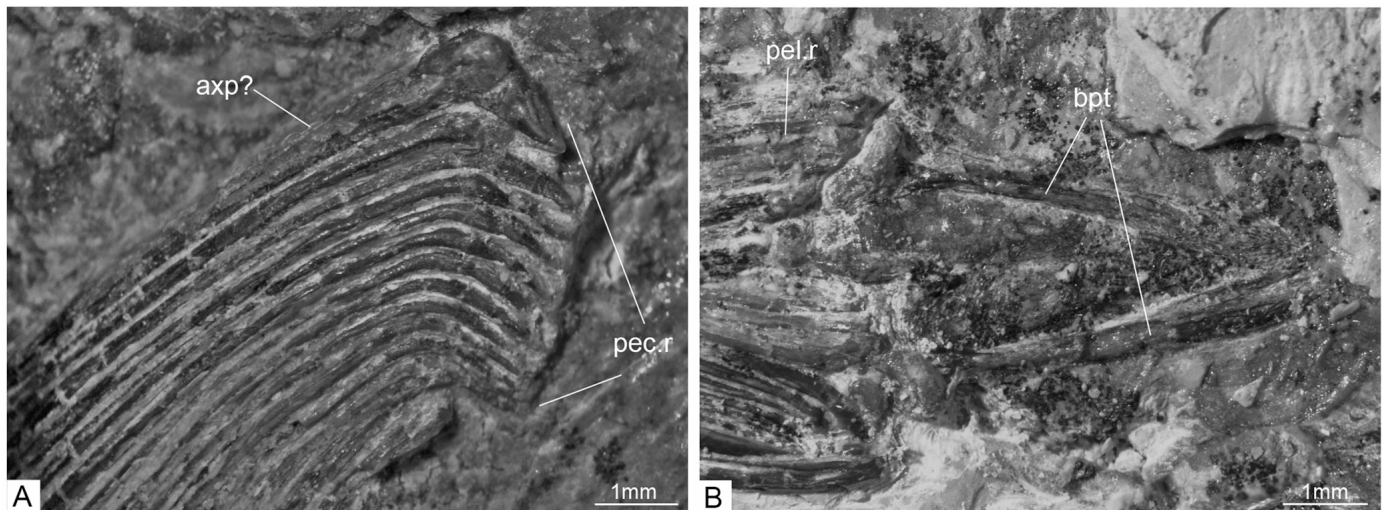
FIGURE 8. †*Luisiella feruglioi*, new combination. **A**, photograph of pectoral fin (MPEF-PV 3198b); **B**, photograph of pelvic fins (MPEF-PV 3198b).

posterodorsally directed dorsal margin. Like the ventral portion of the bone, the posteroventrally located articular area is robust; it exhibits a medial facet for the articulation with the quadrate. In addition, the anguloarticular has a conspicuous, but short, postarticular process.

Opercular Series, Branchiostegal Rays, and Gular Plate—The opercular series is composed of the preopercle, the opercle, the interopercle, and the subopercle; a suprapreopercle is absent (Fig. 4).

The preopercle is a boomerang-shaped bone whose limbs are oriented vertically and subhorizontally in the head. The subhorizontal limb is slightly shorter than the vertical limb, which extends dorsally beyond the level of the contact between infraorbitals 4 and 5 (see Supplementary Data, Table S2, for length and depth measurements of the preopercle). Each limb tapers distally defining an average angle of 110° between both limbs. The preopercle has a rounded and unexpanded posteroventral margin, and, unlike some other known Jurassic teleosts, its posterior margin lacks a notch. The trajectory of the preopercular canal is visible through the median portion of the two limbs; there are one or two tubules in the vertical limb (e.g., MPEF-PV 3876 [2], 3858 [1]) and seven to eight posteroventrally directed simple tubules in the subhorizontal limb (including one tubule present in the area between the limbs).

The interopercle is a rostrally tapering, triangular bone that lies medial to the preopercle. Frequently, only its posteroventral portion is visible, defining a straight angle and extending ventral and posterior to the preopercle (MPEF-PV 3418).

The opercle is the largest bone of the opercular series (Fig. 4). This bone reaches a maximum width at the level of its articulation with the hyomandibular, defining a slightly rounded dorsal portion and a triangular ventral portion. Ventrally, the opercle articulates obliquely with the subopercle; an acute anteroventral angle (of about 40°) is formed between its ventral and anterior margins (Supplementary Data, Table S2). The anterior margin is straight and thicker than the rest of the bone, which is rather laminar. Anterodorsally, there is a low socket or facet for the articulation with the opercular process of the hyomandibular bone (see below; Fig. 7B). The opercle is ornamented with fine concentric lines close to the dorsal and posterior margins of the bone (e.g., MACN 13068).

The subopercle lies posterior to the preopercle and interopercle, and ventral to the opercle. It has an oblique dorsal margin that is partially overlapped by the opercle, a slightly rounded ventral margin, and a rather straight anterior margin in contact with both preopercle and the interopercle (e.g., MPEF-PV 1481). The subopercle of †*L. feruglioi* is relatively high (2/3 of the total length of the bone), and, like the opercle, it is ornamented with fine concentric lines. In addition, the subopercle bears a small anterodorsal process (Fig. 4).

There are about 16 branchiostegal rays. The most anterior ones (8, 9) are acinaciform (scimitar-like) and articulate with the anterior and middle portions of the ventral margin of the anterior ceratohyal. The remaining seven to eight branchiostegal rays are spathiform (paddle-like) and articulate with the posterior portion of the ventral margin of the anterior ceratohyal and also with the ventral margin of the posterior ceratohyal (e.g., MPEF-PV 1469#1, 1472#2, 3424b). The spathiform branchiostegal rays increase in size and length caudally. In addition, the proximal border of each spathiform branchiostegal ray overlaps the previous one, resembling the blades of a fan. The median gular plate is small and lanceolate.

Pectoral Girdle—The cleithra are the largest bones of the pectoral girdle (Fig. 4). In lateral view, each cleithrum is a sigmoid element that narrows at midlength (i.e., inflection point, where the dorsal and ventral halves meet) and is medially vaulted. Each half tapers distally with its greatest width closer to the inflection point; the dorsal half is vertically oriented, whereas the ventral half is subhorizontal. Posteriorly, the bone has a convex dorsal margin that becomes concave in the middle part of the bone and again slightly convex ventrally. The supracleithrum is a dorsoventrally elongated, lanceolate bone that is located posterior to the opercle and dorsal to the cleithrum, slightly overlapping the latter (Fig. 4). The supracleithrum is ventrally narrow; it has a rounded dorsal margin, a straight anterior margin, and a slightly convex posterior margin. The lateral line extends through the dorsal portion of this bone, exiting at its dorsal half. The posttemporal has a triangular shape and is slightly vaulted ventrally (e.g., MPEF-PV 3419). This element narrows posteriorly and contacts anteriorly with the extrascapular bones with a concave anterior margin (Figs. 4, 5). It bears the posttemporal sensory canal, which extends in an anteroposterior direction (e.g., MPEF-PV 1654). Posterior to the dorsal half of the cleithrum, there are generally two postcleithra (Fig. 4). Each of the latter elements is scale-like, although larger and thicker than a scale, and is ornamented with fine concentric lines. The postcleithra are usually almost circular in shape (MACN 13034),
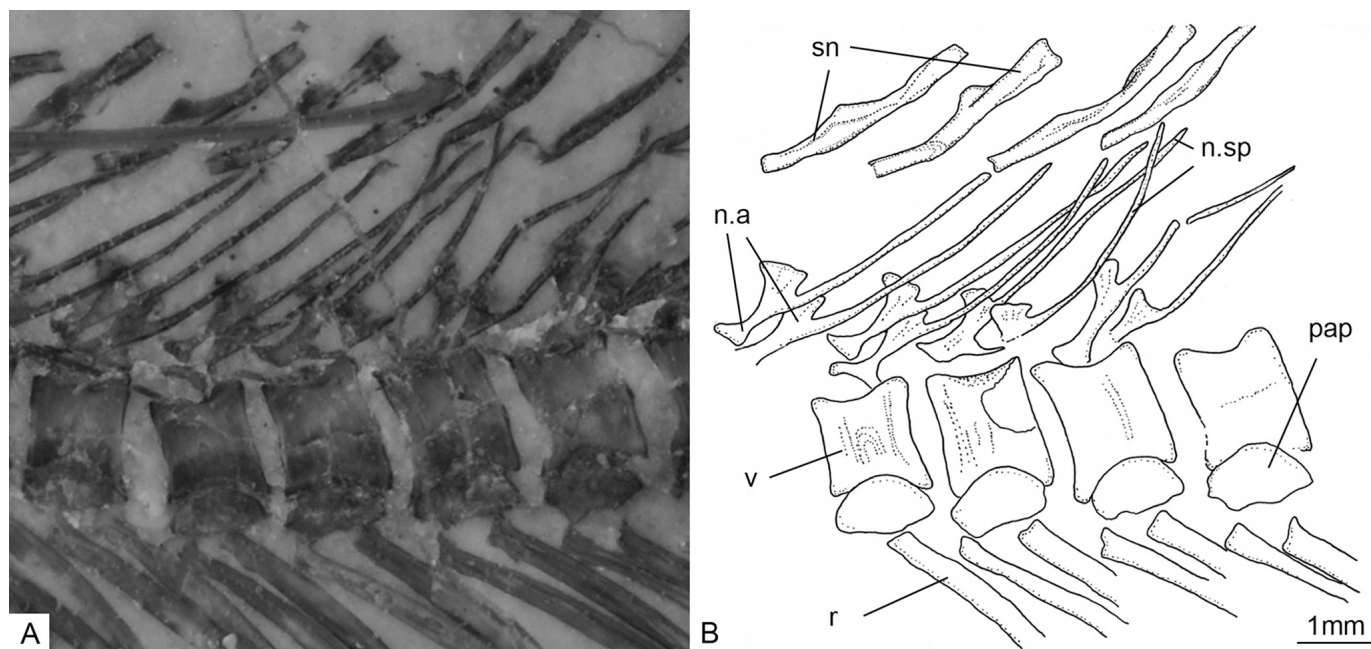
FIGURE 9. †*Luisiella feruglioi*, new combination. **A**, photograph of part of abdominal column (MPEF-PV 3871a); **B**, line drawing of abdominal column (MPEF-PV 3871a).

although sometimes they are lanceolate (MPEF-PV 1388a, 3875).

The scapular bone is an ossification of irregular shape located posteromedially to the cleithrum and in contact with the coracoid anteroventrally. The coracoid, placed ventrolaterally to the cleithrum, is nearly triangular, with a tapering anterior end and a posterior portion with a rounded margin (e.g., MACN 14430, MPEF-PV 3851a). As is typical in teleosts, there are four radials in the pectoral girdle of †*Luisiella feruglioi*. The radials are small, dorsoventrally elongated, rod-like ossifications that slightly abut each other posteriorly (e.g., MPEF-PV 3965). Each radial articulates anteriorly with the scapula and posteriorly with the pectoral fin rays.

Pectoral Fins—The origin of the pectoral fins is located ventral to the middle portion of the cleithrum. In the pectoral fin, there are 14 or 15 long, segmented, robust rays (e.g., MPEF-PV 1471#A, 1654, 3965; Fig. 8A) that are distally bifurcated (at least two times). The first rays are broader than the others and their bases are oriented downwards, almost perpendicular to the main axis of each ray. Dorsal to the most dorsal ray, there is a strap-like ossification (MPEF-PV 1471#A, 3198b, 3965) that may correspond to an axillary process, a common element of the pectoral and pelvic fins of some Jurassic teleosts (Arratia, 1994, 1997).

Pelvic Girdle—The pelvic girdle and fins are placed approximately at 50% of the standard length of the fish, between the pectoral and anal fins, and slightly closer to the latter. The pelvic girdle is quite large; it is formed by a pair of triangular basipterygia or pelvic plates that are horizontally oriented and have posterior articular surfaces for the pelvic fin rays (Fig. 8B). Each basipterygium has a rod-like lateral margin and extends medially into a membranous outgrowth, known as the interior wing. The basipterygia contact each other medially usually overlapping anteriorly. Each basipterygium bears an exiguous external wing posterolaterally and a short anterior process medially.

Pelvic Fins—In the pelvic fins, there are 12 or 13 long rays that are distally segmented and bifurcated, this bifurcation occurring at least twice (MPEF-PV 1354; Fig. 8B). The first pelvic ray has a perpendicularly oriented base with respect to the main axis of the ray. An axillary process appears to have been present because a membranous ossification occurs dorsal to the first pelvic rays.

Vertebral Column—The vertebral column is composed of 39–41 vertebrae (including first preural vertebra), 22–24 of which are abdominal and 15–17 are caudal. Each vertebra has a well-developed chordacentrum that constricts the notochord in the middle portion of each centrum. A fairly thick autocentrum sculptured with longitudinal ridges superficially invests the chordacentrum of each vertebra. In lateral view, the abdominal vertebrae are approximately quadrangular, and slightly constricted in the middle portion (e.g., MPEF-PV 3851, 3871). In contrast, the caudal vertebrae are longer than high (around 1.8 times) and have a characteristic hourglass shape, being strongly constricted in the middle portion of the centrum (e.g., MPEF-PV 3936, 3957).

There are 22–24 pairs of ribs that nearly reach the ventral margin of the body (e.g., MPEF-PV 3851, 3937). In general, they are slightly broader proximally than distally, where they contact the respective parapophyses, which are not fused to the corresponding vertebra (Fig. 9). All ribs have a lateral longitudinal ridge, although their total lengths decrease posteriorly (e.g., MPEF-PV 3097).

With the exception of the last abdominal vertebra, which often bears a single neural spine, the left and right halves of the neural arches remain unfused along the midline in the abdominal region and each half projects dorsally into a neural spine (MACN 13035, 13042, MPEF-PV 3883; Fig. 9). Additionally, each half of the abdominal neural arches have a peculiar hourglass shape in lateral view; they are dorsoventrally elongated, distally expanded, and slightly arched rostrally (MLP 35-III-4-1, MACN 13068, MPEF-PV 1354, 3871a, 3936a; Fig. 9). Each abdominal neural spine originates from the posterodorsal border of the hourglass-shaped neural arch and is directed posteriorly, at an angle lower than 45° with respect to the main axis of the vertebral column. The first unpaired neural spine is found either on the last abdominal vertebra or on the first caudal vertebra (Fig. 10). The unpaired neural spines are always longer than the paired ones (e.g., MPEF-PV 1475#5a). In the caudal region, the neural and hemal arches are not fused (at least laterally) to the

centra, and their respective spines are oriented at 45° with respect to the main axis of the column.

In the vertebral column, a transition zone between the abdominal and caudal regions (more precisely midcaudal) is easily identified below the dorsal fin (Fig. 10). This transition is particularly clear at the level of the first three caudal vertebrae (or often caudal vertebrae 2–4) because their hemal arches and spines are different from those of other vertebrae (Fig. 10). In MACN 13068, for example, the first and second caudal vertebrae lack well-developed hemal spines but bear robust and long hemal processes, which contact distally with short, spine-like ossifications or infrahemal spines (terminology of Goodrich, 1930). The infrahemal spine of the first caudal vertebra is longer than the same element of the second caudal vertebra, but nearly one-half of the length of the succeeding hemal spines. In contrast, the third caudal vertebra of MACN 13068 has a really short hemal process contacting a long infrahemal spine.

There are 14 or 15 supraneural bones located above the paired neural spines of the abdominal vertebrae, extending from the occiput to a few vertebrae placed immediately below the origin of the dorsal fin (e.g., MPEF-PV 1354, 3097; Fig. 9). The most anterior supraneurals are relatively broad, sigmoid bones,

whereas the posterior ones are straight and narrow, rod-like ossifications. Often, the first supraneurals have a lanceolate outline, bearing membranous overgrowths on both sides (MACN 14430).

Paired epineural bones occur in association with the vertebral column from the first rib-bearing vertebra to the vertebrae placed below the posterior pterygiophores of the dorsal fin (Fig. 10). The epineurals are splinter-like bones, which are as long as the abdominal neural spines. Each epineural bone is fused to the dorsal border of the hourglass-shaped neural arch and is oriented at approximately 15° to the main axis of the column in a caudal direction (e.g., MPEF-PV 3872a; Figs. 9, 10). Usually, the last pair of epineural bones is associated with the last abdominal vertebra (MPEF-PV 3873, 3883), but sometimes it is in contact with the vertebra immediately in front (e.g., MACN 14430, MPEF-PV 1493#10) or with the first caudal vertebra (e.g., MACN 13061, MPEF-PV 3908). Epicentral or epipleural bones are absent.

Caudal Skeleton—Anterior to the caudal fin, the neural and hemal spines of the sixth preural vertebra and succeeding ones are gradually straighter and longer than those borne by the preceding ones. Both neural and hemal spines of the preural vertebrae 3–5 increase in width posteriorly, although generally the
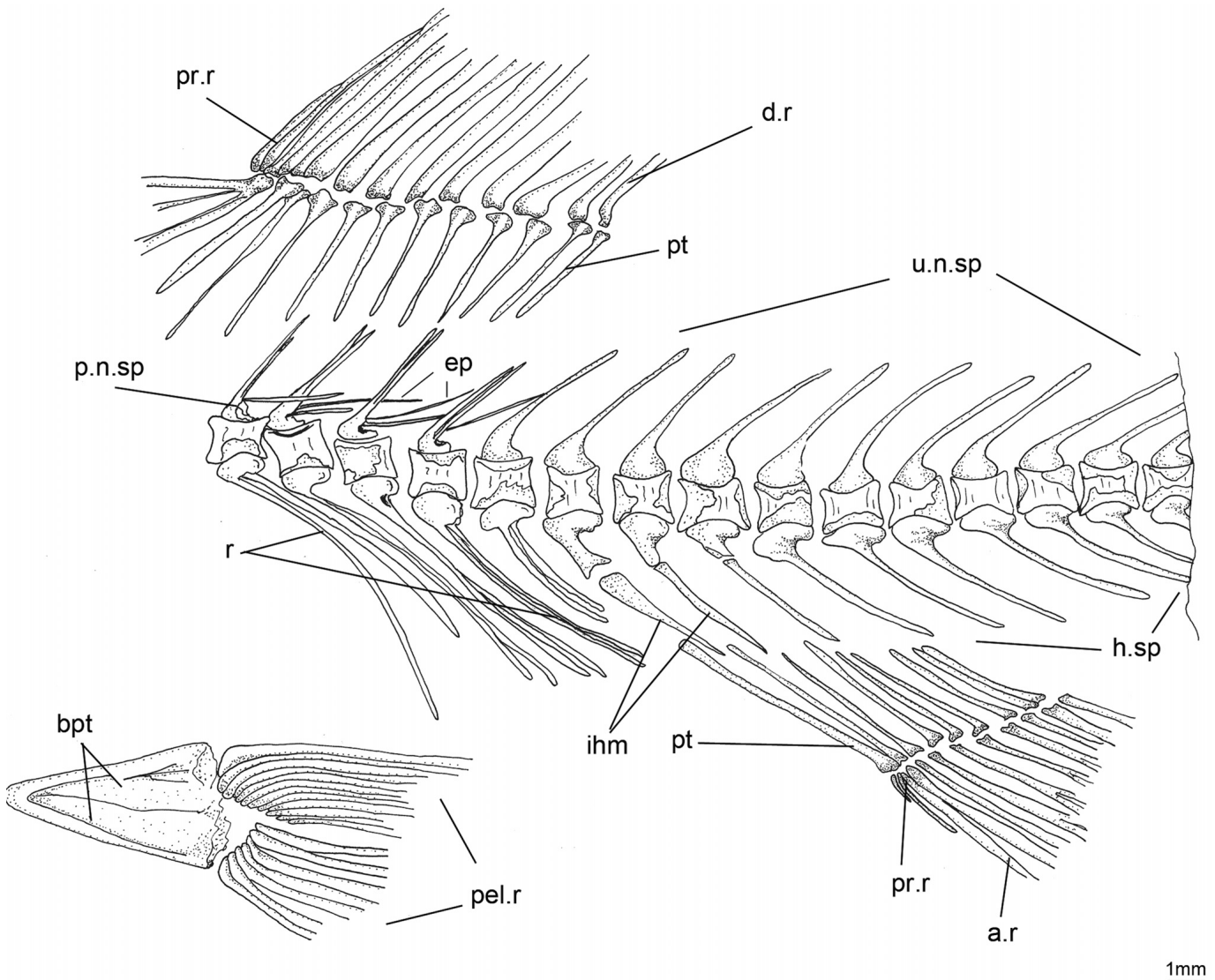

FIGURE 10. †*Luisiella feruglioi*, new combination. Line drawing of middle section of the trunk (MACN 13031).

hemal spines are wider than the neural spines of the same centrum. In addition, the neural spines of preural vertebrae 2–5, and sometimes preural vertebra 6 also, bear a short, anteriorly directed process at their bases (Fig. 11). The neural spine of the second preural is as long as the preceding neural spines in some specimens, but shorter in others. The first preural vertebra has a small neural spine that is shorter than those on preceding vertebrae. The parhypural lacks a hypurapophysis, and its width diminishes distally. The parhypural and the hemal spines of preural vertebrae 2–4 are close to each other (e.g., MPEF-PV 3950); they have truncated distal ends and bear short, rostrally directed processes that fit into a posterior notch of the preceding element.

Unlike the autocentra of the midcaudal vertebrae, which strongly constrict the notochord, the autocentra of the preural vertebra immediately anterior to the caudal fin constrict the notochord gently. With the exception of the first preural vertebra, which is quadrangular, these preural vertebrae are hourglass-shaped like midcaudal vertebrae, although their sizes decrease progressively caudally (Figs. 11, 12). In addition, two ural centra form the most posterior portion of the caudal fin skeleton. The first ural centrum is elongate and slightly narrower in its middle portion. Alternatively, one anteriorly located neural spine (e.g., MPEF-PV 1487#7) or two small neural spines, anterior and posterior (e.g., MPEF-PV 1471#E, 3934), occur on this element. The first ural centrum is in contact with the first and second hypurals. The second ural centrum is smaller than the preceding one and subtriangular in shape. Usually, this centrum is in contact with the hypurals 3–5 but sometimes it is only in contact with hypurals 3 and 4. There is no neural arch or spine on the second ural centrum.

†*Luisiella feruglioi* has nine hypurals, which decrease in size from anteroventral to posterodorsal (MPEF-PV 3195, 3946). Generally, the first and second hypurals are not fused to each other; however, their bases are fused perichondrally in some specimens (MPEF-PV 1611, 3195, 3989). These hypurals are not fused (at least laterally) to the first ural centrum. The first hypural is the largest; it is as long as, or even longer than, the parhypural (Fig. 11). The first hypural bears an anteriorly directed basal process and is broader distally. In addition, and unlike the preceding hemal spines, the first hypural has a posterior notch close to its base. The second hypural is shorter and narrower than the first one, and has an anteriorly directed notch at its base, which together with the posterior notch of the previous hypural form a small circular area that characterizes both bones. There is no diastema between the second and third hypurals, as is known in other Jurassic teleosts (Arratia, 1997). The third hypural is subtriangular, whereas the other hypurals are somewhat rectangular bones.

There are five or six elongate, tongue-like uroneural bones that cover the dorsolateral portions of the caudal centra (e.g., MACN 13042, MPEF-PV 1354, 1487#4a, 3097, 3195a; Figs. 11, 12). The first uroneural reaches the second preural centrum anteriorly and the anterior end of the second ural centrum posteriorly. The second uroneural extends from the first preural centrum to the posterior end of the second ural centrum. The third uroneural reaches anteriorly the posterior end of the first preural centrum and extends over ural centrum 1, whereas the fourth uroneural only reaches the second ural centrum. These four uroneurals become gradually shorter posteriorly. The fifth and sixth (when present) uroneurals are shorter than the
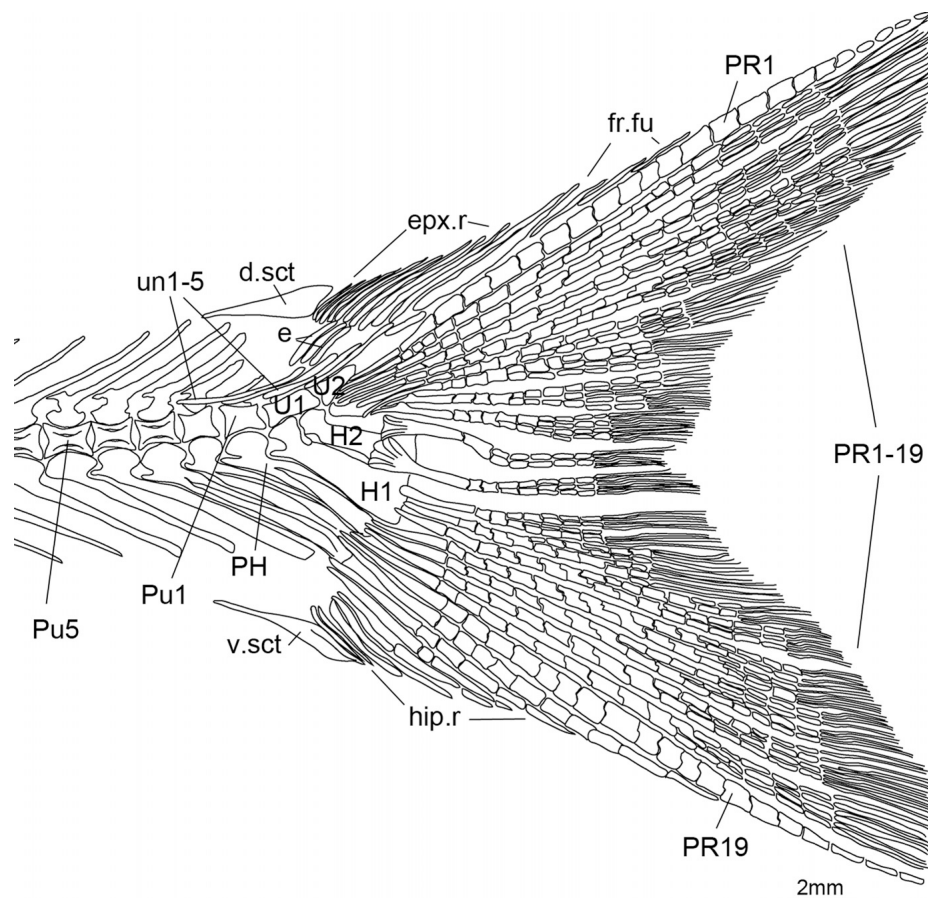

FIGURE 11. †*Luisiella feruglioi*, new combination. Reconstruction of caudal fin skeleton and caudal preural column (based mainly on MPEF-PV 1354 and 3439).
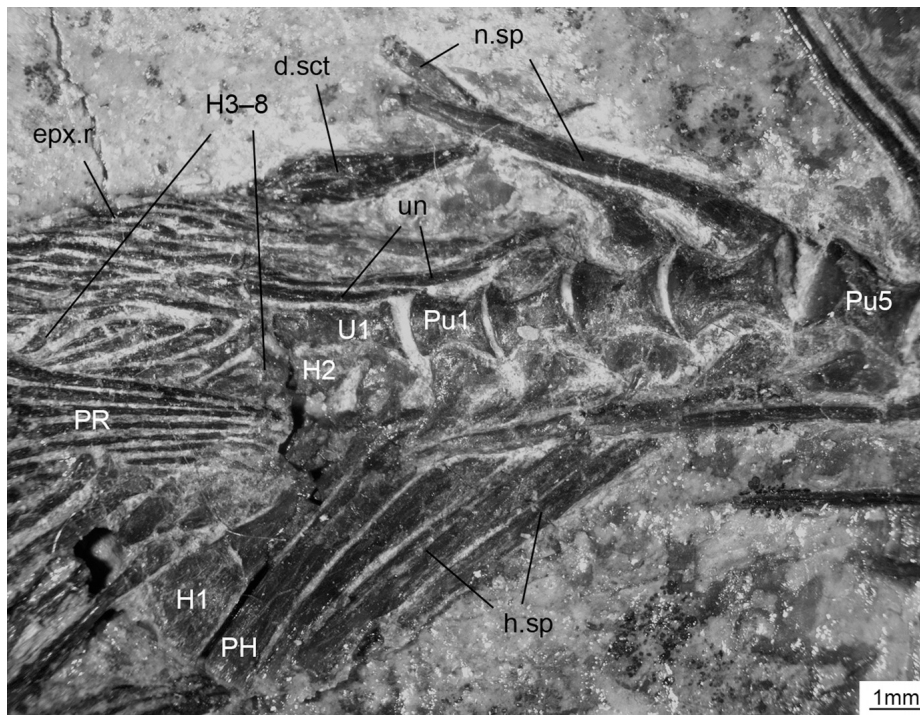
FIGURE 12. †*Luisiella feruglioi*, new combination. Photograph of caudal fin skeleton and preural caudal column (MPEF-PV 3195).

preceding ones and are placed below the bases of the basal fulcra. All the uroneurals are arranged parallel to each other and form a subhorizontally oriented series.

The caudal fin endoskeleton also includes three rod-like epural bones (e.g., MPEF-PV 1471#E, 1558#4, 3934). These bones form an anteroventrally to posterodorsally oriented series above the ural portion of the vertebral column (i.e., ural centra 1 and 2; Fig. 11). Dorsally, they contact with the proximal end of the epaxial rays. Each epural is slightly arched anteriorly.

Dermal Elements of the Caudal Fin—The caudal fin is homocercal, with well-defined dorsal and ventral lobes. Externally, it is limited by one dorsal and one ventral scute. The dorsal scute is located anterior to the epaxial rays of the fin dorsal to the distal tips of the neural spines of the last preural centra, and it is oriented almost horizontally (Figs. 11, 12). This scute is lanceolate, vaulted, and has a rounded main body that narrows rostrally, forming a spine-like process; frequently, it also bears a low dorsal keel. The ventral scute is also lanceolate, although it is smaller in size. It is almost horizontally oriented, and often it is ornamented with fine striae.

There are numerous epaxial and hypaxial rays that form both dorsal and ventral margins of the lobes of the caudal fin (without counting principal caudal rays). In the dorsal lobe, 9–11 epaxial rays are located dorsal to the notochord and, thus, to the first or most dorsal principal caudal ray (MPEF-PV 1491#4a, 3934a, 3195a; Figs. 11, 12). The most anterior elements are basal fulcra, whereas posteriorly it is not clear if the elements are basal fulcra or procurrent rays owing to the lack of segmentation. Each epaxial ray overlaps the succeeding ray; these rays increase in size caudally, so that the last epaxial ray is as large as the first principal ray of the fin. Two or three minuscule, spine-like fringing fulcra occur above the first principal caudal ray, placing posteriorly to the last epaxial ray of the fin (MPEF-PV 1488#4b, 1469#9, 3934a). The ventral lobe of the caudal fin is limited by hypaxial rays (Fig. 11). Ventral to the last principal ray, there are four or five segmented procurrent rays, the length of which decreases anteriorly; they are in contact with the tips of the hemal spines of the preural centra (MPEF-PV 1469#9, 1476#11, 3195a). Between these segmented procurrent rays and the ventral scute, which is anterior to these elements, there are two to five sigmoid, unsegmented rays. The latter decrease in size rostrally and have no contact with the endoskeletal elements.

In addition, the caudal fin is composed of 19 principal rays, the length of which decreases from the margins to the middle portion of the fin. Ten principal rays participate in the formation of the dorsal lobe of the caudal fin, whereas the remaining nine are part of the ventral lobe (Fig. 11). The first principal ray (dorsal-most or principal ray 1) and the last one (ventral-most or principal ray 19) are the longest elements; they are segmented but unbranched. All principal rays have a 'Z' or step-like segmentation and a long first segment, whereas the succeeding segments are shorter than the latter, and of equal length. Branching occurs in the 17 internal principal rays only, taking place proximally in the inner rays and distally in the outer rays, at least three times in each ray. In the dorsal lobe, the first seven principal rays form a quite compact fascicle oblique to the dorsal hypurals. With the exception of principal rays 10 and 11, which exhibit a fan-like, expanded base and a crenulated anterior border, all the principal rays have pointed bases. In particular, a short dorsal process occurs at the bases of principal rays 8 and 9 (MPEF-PV 1476#11, 3186, 3425; Fig. 11). Usually, the last principal ray articulates with the hemal spine of the second preural centrum, although occasionally this last ray articulates with the hemal spines of both second and third preural centra, or with the hemal spine of the second ural centrum and parhypural, or with the hemal spine of the third preural centrum only (e.g., MACN 14430, MPEF-PV 1488#4b, 1487#4a, 3946, 3937).

Finally, there are two 'urodermal' ossifications located lateral to the basal segments of the most dorsal principal rays (i.e., PR 1–3). The 'urodermals' are elongate and small and are oriented anteroventrally to posterodorsally (e.g., MPEF-PV 1492#3, 1558#4, 3200b, 3937).

Dorsal Fin—The dorsal fin is located approximately at the midpoint of the total length of the fish, opposite to the distance between the pelvic and anal fins, and closer to the pelvic fins

(e.g., MPEF-PV 1354, 1475#5a; Supplementary Data, Table S3; Figs. 2A, 10). The endoskeleton of the dorsal fin is composed of 11 or 12 proximal pterygiophores (exceptionally 13 in MPEF-PV 3097, 3986) and an uncertain, but undoubtedly fewer, number of median and distal pterygiophores. Each proximal pterygiophore is a styliform, distally tapering bone that proximally bears an articulation area for the median pterygiophores, or directly for the principal dorsal rays in the anterior portion of the fin. Each element has membranous overgrowths on both sides of its main axis, which decrease in size distally (e.g., MPEF-PV 1389, 1483, 3936). Generally, the anterior proximal pterygiophores are longer than the posterior ones, and except for the first proximal pterygiophore (i.e., rostral-most), which is rather subhorizontal, all of these elements are oriented at approximately 75° with respect to the main axis of the fin. The first proximal pterygiophore usually bears three or four spine-like elements that are joined together by a membranous lamella (e.g., MACN 13036 [3], 13061 [4], MPEF-PV 3851 [3], 3932 [4]). Median pterygiophores are short, rod-shaped ossifications, whereas distal pterygiophores are small, round bones.

The dorsal fin has a triangular outline. The anterior rays are longer than the rest, which become progressively shorter posteriorly (e.g., MPEF-PV 1389). The fin is formed by one to three procurrent rays and 11 or 12 dorsal rays (Fig. 10). The first or first and second procurrent rays are rather short, but the most posterior one is long (about 2/3 the length of the first dorsal ray) and usually segmented. All the procurrent rays articulate with the first proximal pterygiophore (e.g., MPEF-PV 3936). The 11 or 12 dorsal rays are segmented along the distal half of each ray, and the first segment of each ray is always the longest. Except for the first dorsal ray, which is unbranched, the rays branch distally at least twice (e.g., MPEF-PV 3873).

Anal Fin—The anal fin is located closer to the pelvic fins than to the caudal fin (Supplementary Data, Table S3). Its origin is always posterior to the last pterygiophore of the dorsal fin (e.g., MPEF-PV 3936; Fig. 10). There are nine (sometimes 10) proximal pterygiophores in the anal fin and a fewer but undetermined number of median and distal pterygiophores. In general, the most anterior proximal pterygiophore is considerably broader and longer than the rest. It is sometimes placed between the last abdominal vertebra and the first caudal vertebra or often between the first and second caudal vertebrae. The remaining proximal pterygiophores are shorter and of equal length. Median and distal pterygiophores are usually preserved in the middle portion of the fin. Usually, the anal fin has 10 anal rays and two procurrent rays. Procurrent rays are short, unsegmented rays that, together with the first anal ray, articulate with the first proximal pterygiophore. The anterior anal rays are the longest of the series and branch at least two times rather distally, whereas the posterior elements branch more proximally and are gradually shorter in length. Besides, all the rays are segmented, having a long first segment.

Squamation—The body is covered with thin cycloid scales, which are approximately circular and have a well-defined anterior field. The anterior field extends for about 3/4 of the total surface of each scale and is ornamented with narrowly separated concentric circles that occur from the center of the scale to its margin. Unlike the anterior field, the posterior field bears few circles and radial striae. The scales have no radii.

Sensory Canals and Lateral Line—The cephalic sensory canal system is composed of relatively few and simple tubules, supraorbital, infraorbital, temporal, posttemporal, preopercular, and mandibular canals, anterior and middle pit lines, and ethmoidal and supratemporal commissures (Fig. 4).

The anterior portion of the supraorbital sensory canal extends through the nasal bones, from which it continues in a superficial bony crest borne by the frontal bones. In the frontals, this canal is parallel to the lateral margin of the bone; it describes a sigmoid curve at the level of the orbit and then curves medially reaching the posterior border of the frontal. Along its course, the supraorbital canal gives off four or five simple, short tubules; two or three of these tubules are medially directed and occur above the orbit, whereas the remaining one or two are laterally directed and occur posterior to the orbit (MPEF-PV 3959, 3415, 3851, MACN 13044). Each of these tubules ends in a pore that is clearly evident in the surface of the frontals. The supraorbital sensory canal ends in the parietal bone, where it is enclosed in a bony crest and reaches about the midlength of the bone. In the parietals, this sensory canal emits no tubule but it extends posteriorly in a short anterior pit line groove. There are also middle pit line grooves on both parietal and pterotic bones (e.g., MPEF-PV 3419; Figs. 4, 5).

The infraorbital sensory canal pierces the antorbital bone, infraorbitals 1–5, and the dermosphenotic bone. There is no trace of an ethmoidal commissure in the rostral portion of the skull. The infraorbital canal extends close to the dorsal margin of the antorbital bone (e.g., MPEF-PV 3192a, 3941b) and then continues in the infraorbital bones, where it gives off three to four simple and short tubules in the first infraorbital, which are ventrally directed (e.g., MACN 13068 [3], MPEF-PV 1476#3 [4], 3887 [4], 3417 [3]). The canal pierces the second infraorbital without giving off any tubule and extends close to the dorsal margin of the third infraorbital where it emits one perpendicular tubule, the length of which is nearly one-half of the length of the bone. In both fourth and fifth infraorbitals, the infraorbital canal extends close to the anterior margin, giving off two short and divergent tubules in each bone. Finally, the infraorbital canal is close to the anterior margin of the dermosphenotic bone, where it gives off two short tubules. One of these tubules is directed anteriorly and culminates within the dermosphenotic, whereas the other tubule is directed caudally and is in contact with the temporal sensory canal in the pterotic bone (e.g., MPEF-PV 1388). There is no direct evidence for a connection between supraorbital and infraorbital canals; this connection was either absent or was included in the skin; therefore, it is not preserved in the fossils.

The otic, or temporal, canal pierces close to the lateral margin of the pterotic bone and is connected anteriorly with the infraorbital canal, ventrally with the preopercular canal, posteromedially with the supratemporal commissure, and posteriorly with the posttemporal canal. In the pterotic, the temporal canal emits a medially directed tubule. Close to the posterior margin of the pterotic bone, this canal curves medially and relates to the supratemporal commissure. The supratemporal commissure pierces the extrascapular bones in a lateromedial direction and gives off two or three short and posteriorly directed tubules (MPEF-PV 3415, 3959, 3977a). The two halves of the supratemporal commissure are connected to each other at the level of the supraoccipital bone, where they leave no trace. Posteriorly, the posttemporal canal extends laterally through the posttemporal, giving off one or two short, medially directed tubules before reaching the posterior margin of this bone. The posttemporal canal perforates the dorsal portion of the supracleithrum without giving off any tubule and connects caudally with the lateral line canal that extends close and parallel to the vertebral column up to the caudal fin.

The preopercular canal extends through the mid-portion of both vertical and subhorizontal limbs of the preopercle (Figs. 3, 4) and gives off one or two short, posteriorly directed tubules in the ventral limb, one tubule in the zone or angle between the two limbs, and seven to eight ventrally directed tubules in the subhorizontal limb (exceptionally six; MPEF-PV 1472#1, 3426). The latter seven or eight tubules do not reach the ventral margin of the preopercle and frequently have different lengths and widths. There are specimens in which the tubules are elongate and narrow (e.g., MACN 13069, 14431, MPEF-PV 1481b, 1768,

3936), other specimens in which the tubules are short and wide (e.g., MPEF-PV 1769, 3887, 3959), and others where an intermediate condition is observed (e.g., MPEF-PV 3421a, 3969). Also, the tubules of the subhorizontal limb of the preopercle can occur parallel to each other (MPEF-PV 3936) or oriented at slightly different angles (e.g., MPEF-PV 1481b).

The anterior portion of the mandibular canal pierces the lateroventral border of the dentary, always enclosed in bone, and leaves this element through three or four laterally located pores. Posterior to the dentary, this canal extends ventrolaterally in the anguloarticular bone, giving off one or two pores and exits this bone through a laterally directed pore located near the postarticular process. The mandibular canal is not branched, and caudally it is connected to the anterior portion of the preopercular canal.

DISCUSSION

The Teleosts of the Almada Fish Fauna

The teleosts from Puesto Almada (see type locality) were discovered by Piatnitzky and first identified by Angel Cabrera (MLP) in Piatnitzky (1936) as †*Diplomystus longicostatus* Cope, 1887, a clupeomorph known from the Lower Cretaceous of the Araripe Basin in Brazil. Three decades later, Bocchino (1967) restudied the single specimen studied by Cabrera (MLP 35-III-1-4; Fig. 2B) and referred it to a new genus and species, †*Luisiella inexcutata*, which she included in the clupeiform family Dussumieriidae.

Independently, Bordas (1942) studied other teleost specimens from the same locality where Piatnitzky had collected the material studied by Cabrera. Bordas (1942) referred these specimens to a new species †*Tharrhias feruglioi* that he placed in the family †Leptolepididae within the order Clupeiformes. Subsequently, Bocchino (1978) restudied this material and referred it to the genus †*Leptolepis* Agassiz, 1832, without making any reference to her previous work on the single specimen described as †*Luisiella inexcutata*. For decades, and mainly due to its poor definition, the genus †*Leptolepis* gathered almost all the small- to medium-sized Jurassic and Cretaceous teleosts with a generalized morphology (Lehman, 1966; Taverne, 2001). In 1974, Nybelin gave a restricted diagnosis for this genus, and on this basis, other authors (e.g., Patterson and Rosen, 1977) considered that the genus should be regarded as monospecific, including only its type species, †*Leptolepis coryphaenoides* (Bronn).

In a general revision of the Jurassic fishes from Argentina, Cione and Pereira (1987) confirmed that †'*Tharrhias*' *feruglioi* Bordas represents a distinct species but indicated that it is not referable to †*Tharrhias*, a genus that includes a very different fish, †*Tharrhias araripis* Jordan and Branner, 1908, now placed within the gonorhynchiforms ostariophysans and endemic to the Araripe Basin of Brazil (Santana and Crato formations, Early Cretaceous; Brito and Yabumoto, 2011). Cione and Pereira (1987) commented on the doubtful validity of †*Luisiella inexcutata* Bocchino but tentatively considered both species as Teleostei incertae sedis.

After a thorough analysis of the anatomy and morphology (morphometric measurements provided in Supplementary Data) of the type specimens of †'*Tharrhias*' *feruglioi* Bordas, 1942, and †*Luisiella inexcutata* Bocchino, 1967, we conclude that they represent the same species, for which the new combination †*Luisiella feruglioi* is the appropriate name according the principle of priority (Art. 23; International Commission on Zoological Nomenclature (ICZN), 2000). These fishes are anatomically and morphometrically indistinguishable from one another (Figs. 2A, B, 13). The diagnostic features of †*L. feruglioi* enumerated above occur in the type specimens of both nominal species (e.g., abdominal neural arches expanded and hourglass-shaped, with neural spine

originating from the middle portion of the posterior border of each half of the neural arch). Similarly, with the exception of some badly preserved specimens, all the other teleosts from the Cañadón Calcáreo Formation that we examined (see Supplementary Data) represent the species †*Luisiella feruglioi*, new combination. The referral of those specimens is based on the diagnosis and a morphometric analysis that shows a variability that falls well within the range of variation expected for a single species according to the variation ranges described for other Jurassic teleosts by Nybelin (1974) and Bean (2006) (see discussion below). The referred material was collected from Puesto Almada (type locality) and from three other localities (see Distribution; Fig. 1) where a main fish-bearing bed can be followed laterally and is well correlated with the type horizon (see López-Arbarello et al., 2013). Also, the fish association is remarkably uniform in all of these localities.

Apart from the synonymy discussed above, two other nominal species have been proposed for teleosts from outcrops of the Cañadón Calcáreo Formation: †*Tharrias shamani* Dolgopol de Sáez, 1949, and †*Leptolepis leanzai* Dolgopol de Sáez, 1949. Each of these two species is represented by a single specimen and, according to the collection labels, the former comes from Paso de Shaman, southwestern Chubut Province, close to the international boundary with Chile, and the latter from Cerro Mirador, northwestern Chubut Province. Notwithstanding, Cione and Pereira (1987) pointed out that the fish-bearing rocks are identical to the laminated limestones of the basal lacustrine section of the Cañadón Calcáreo Formation and concluded that these specimens were probably collected in the area of Cerro Cóndor. The type specimens of †*Tharrias shamani* (MLP 48-VIII-1-3) and †*Leptolepis leanzai* (MLP 48-I-1-2) have a general resemblance to †*Luisiella feruglioi* (Bordas). However, no diagnostic feature of †*L. feruglioi* could be assessed in any of these two specimens, nor could any feature of the latter could be distinguished as characterizing a different taxon. Therefore, †*Tharrias shamani* Dolgopol de Sáez and †*Leptolepis leanzai* Dolgopol de Sáez are regarded as nomina dubia (Art. 75.5; ICZN, 2000).

Intraspecific Variation—Examination of the numerous specimens from the Cañadón Calcáreo Formation revealed morphological variation, which can be explained as intraspecific variability. According to Grande (2004), there are two types of intraspecific variability, namely, ontogenetic variability and an individual variability, which includes anomalies, sexual dimorphisms, and polymorphisms (either within the same individual or between individuals). Both types of intraspecific variability have been identified in †*Luisiella feruglioi*, which is represented by nearly 250 specimens, including juveniles and adults.

The comparison of juveniles and adults showed the presence of several osteological characters that vary during development. In juveniles, the dermal bones of the skull have a feeble ossification that contrasts with their strong ossification in adults; also, the orbital diameter is larger than in adults. In addition, the vertebral centra of juveniles are deeper and shorter than those of adults and, particularly, the midcaudal vertebrae are ring-like, lack well-developed autocentra, and the notochord is barely constricted, whereas these vertebrae are hourglass-shaped and have a well-developed autocentra that strongly constrict the notochord in adults. Another feature that varies with developmental stage is the separation between consecutive vertebrae, which is larger in juveniles than in adults. These juvenile features of †*Luisiella* have also been reported as such in other Jurassic teleost taxa (e.g., †*Todiltia schoewei* (Dunkle, 1942), †*Anaethalion* White, 1938, †*Orthogonikleithrus* Arratia, 1997; Schaeffer and Patterson, 1984; Arratia, 1997). In addition, Arratia (2008b) also considered the increase in the number of dorsal and anal procurrent rays and the low number of caudal basal fulcra as traits that
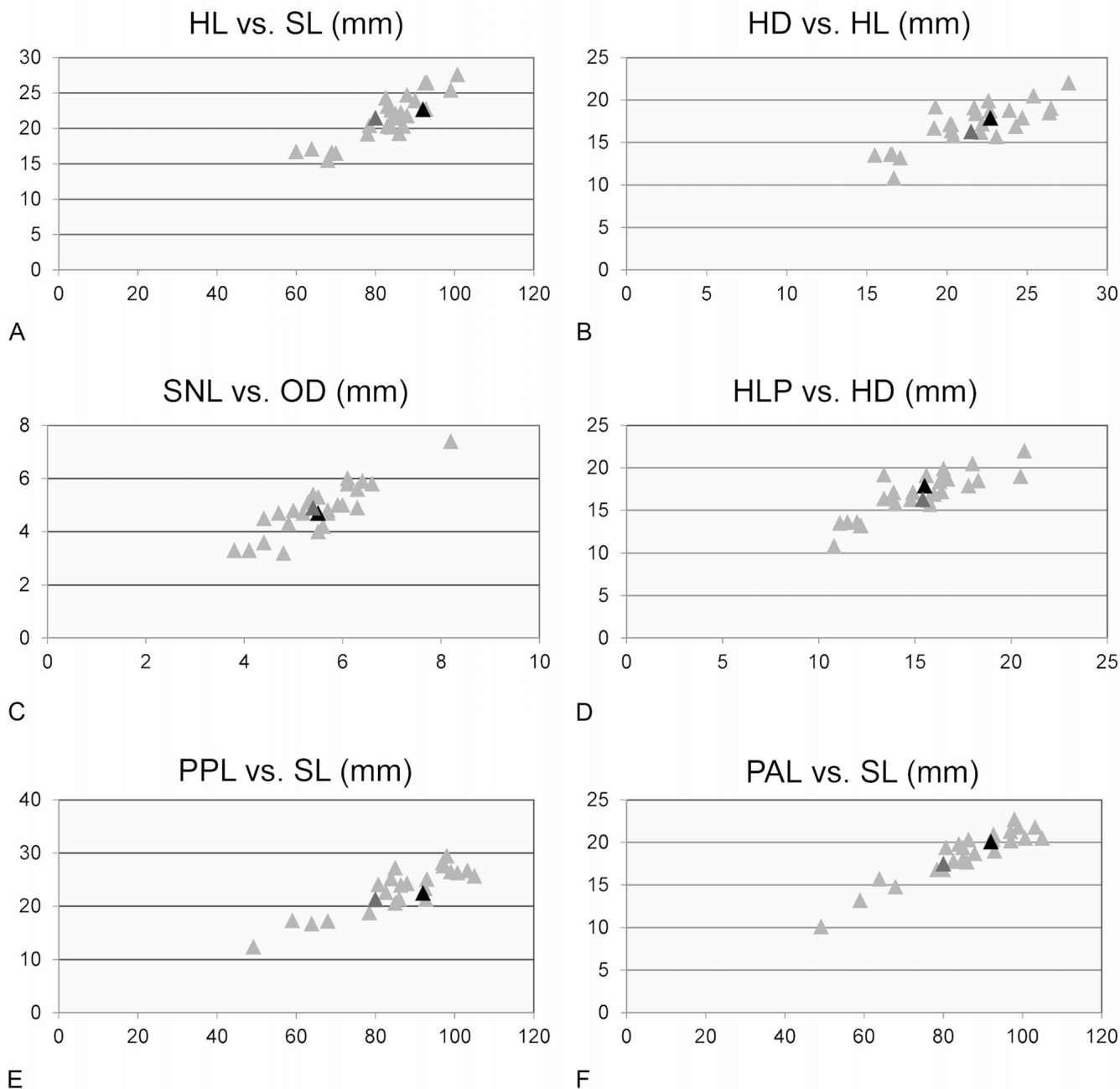
FIGURE 13. Bivariate plots. **A**, HL versus SL bivariate plot; **B**, HD versus HL bivariate plot; **C**, SNL versus OD bivariate plot; **D**, HLP versus HD bivariate plot; **E**, PPL versus SL bivariate plot; **F**, PAL versus SL bivariate plot. **A–D** are based on data from 28 specimens of †*L. feruglioi* provided in Supplementary Data, Table S1. **E**, **F** are based on data from 26 specimens of †*L. feruglioi* provided in Supplementary Data, Table S3. The lectotype of †'*Tharrhias*' *feruglioi* (MACN 13068-9) and the holotype of †*Luisiella inexcutata* (MLP 35-III-1-4) are indicated in black and dark gray, respectively.

characterize juveniles and may change during the ontogeny. However, due to the poor preservation of these elements in particular, these traits could not be assessed in †*Luisiella feruglioi*.

Nybelin (1974) suggested that the difference in the amount of tubules of the preopercular canal in the Jurassic teleosts †*Leptolepis normandica* Nybelin, 1974, and †*Leptolepis coryphaenoides* was also subject to ontogenetic variability. According to this author, there are fewer preopercular tubules in the preopercular canal of juveniles of both species than in the adults.

Although a similar pattern was observed in some juveniles of †*L. feruglioi* (only five tubules are present in the subhorizontal limb of the preopercular bone in the juvenile MPEF-PV 3199, whereas adults usually have seven or eight tubules in this limb), some adults have only six tubules (see description of preopercular canal). Thus, the available evidence does not permit us to discern whether this variation is actually individual variation.

The study of fully grown specimens has also revealed morphological variability. Usually in fossil assemblages, it is not easy to

discriminate between interspecific variability of closely related taxa and intraspecific variability. Grande (2004) proposed that in order to distinguish between individual variation (intraspecific) and taxonomic variation (interspecific), it is necessary to maximize the sample size to identify the 'typical' condition (more abundant) for each variable feature. Considering that a large number of adult specimens (more than a hundred) was available for this study, it was possible to evaluate the presence (or absence) of these 'typical' conditions in our teleost sample. The anatomical and morphometric analyses indicated variability in mosaic pattern for some features; that is, we did not find correlated variation that might indicate that more than one taxon was represented (Fig. 13). Hence, we regarded this variation as polymorphisms. Examples of these polymorphisms in †*L. feruglioi* are mentioned in the above description, including the shape and ornamentation of supramaxillary bones (i.e., supramaxilla 1 with a rounded or bilobate posterior margin; supramaxilla 2 with or without superficial striae; Fig. 14), the overall shape of frontals and parietal bones, the length and orientation of the preopercular canal tubules in the subhorizontal limb of the preopercle, the number of tubules of the supraorbital canal, the number of endoskeletal elements of the unpaired fins, and the number of dorsal and anal fin rays.

Intraspecific variation in other Jurassic teleosts was discussed by Patterson and Rosen (1977), Arratia (1997), and Bean (2006) for some anatomical features of the freshwater teleost †*Cavenderichthys talbragarensis* (Woodward, 1895) (e.g., length of the preopercular tubules, shape of supramaxillary bones, number of anal and dorsal fin rays). In addition, Nybelin (1974) showed variation in the arrangement of the tubules of the preopercular canal in the same individual (i.e., right and left elements), as well as between individuals of the Late Jurassic marine teleost †*Tharsis dubius* (Blainville, 1818). Thus, even though a reference to individual intraspecific variation is not abundant in fossil fish literature, the individual variability observed in adults of †*L. feruglioi* agrees with the intraspecific individual variability described for other Jurassic basal teleosts.

Morphology and Affinities of †*Luisiella feruglioi*

According to Arratia (1997), basal teleosts are those teleost taxa that are not part of an extant lineage (stem group), whereas the name Teleocephala was coined by De Pinna (1996) for the least inclusive clade that includes the most recent common ancestor of the living groups of teleosts (i.e., osteoglossomorphs, elopomorphs, and clupeocephalans) and all of its descendants (crown group).

The overall morphology of †*Luisiella feruglioi* agrees with the general morphology of most of the well-known Jurassic teleosts. As it usually occurs with these Jurassic species, unique diagnostic characters are difficult to find, but, instead, these taxa can be diagnosed by a combination of some features. †*L. feruglioi* has expanded, hourglass-shaped abdominal neural arches in lateral view, with neural spines originating from the middle portion of the posterior border of each half of the neural arch. This feature occurs rarely among teleosts and has been described only in some Jurassic–Cretaceous crossognathiforms (Arratia, 2008a), the Jurassic †*Ascalabos* von Münster, 1839, and †*Domeykos* Arratia and Schultze, 1985, and in a few fossil and extant euteleosts (e.g., †*Orthogonikleithrus, Thymallus* Linck, 1790; Arratia, 1997). However, †*L. feruglioi* differs from †*Ascalabos*, the varasichthyid †*Domeykos*, and euteleosts in the absence of epipleural bones, intermuscular bones associated with the ribs, which were considered a derived teleost feature by Patterson and Johnson (1995). Also, †*L. feruglioi* differs from crossognathiforms and varasichthyids in having a preopercle lacking a posteroventral expansion and bearing a preopercular canal with tubules that does not reach the ventral margin of the bone. In contrast, crossognathiforms (except †*Chongichthys* Arratia, 1982, and †*Bavarichthys* Arratia and Tischlinger, 2010) and varasichthyids have a posteroventrally expanded preopercle and the tubules of the preopercular canal reach the ventral margin of the bone (Arratia, 2008a; Arratia and Tischlinger, 2010).

The present study of †*Luisiella feruglioi* has led to the identification of several features of possible phylogenetic importance, which include plesiomorphic features also present in other basal teleosts and derived characters shared with some teleocephalan groups (i.e., Clupeocephala). As in basal teleosts (e.g., †*Leptolepis coryphaenoides*, †*Tharsis dubius*, †Ichthyodectiformes, †Varasichthyidae; Nybelin, 1974; Patterson and Rosen, 1977; Arratia and Tischlinger, 2010), †*L. feruglioi* has the plesiomorphic state of several characters that according to recent analyses occur in the derived state in teleocephalans (Arratia, 2008a; Arratia and Tischlinger, 2010). A median gular plate is present in †*L. feruglioi*. Arratia (1999) pointed out that at least one gular plate is usually found in the skull of primitive actinopterygians, and one median gular plate is the condition present in basal teleosts. In contrast, the occurrence of a gular plate is rare among teleocephalans, having been noted only in elopiforms (Forey, 1973) and in basal osteoglossomorphs (i.e., Lycopteriformes; Greenwood, 1970). The presence of fringing fulcra in the caudal fin, which are absent in teleocephalans (except for the fossil elopomorph †*Anaethalion* and the living elopomorph *Megalops* Valenciennes, 1847; Arratia, 1987, 1997), is another plesiomorphic feature present in †*L.*
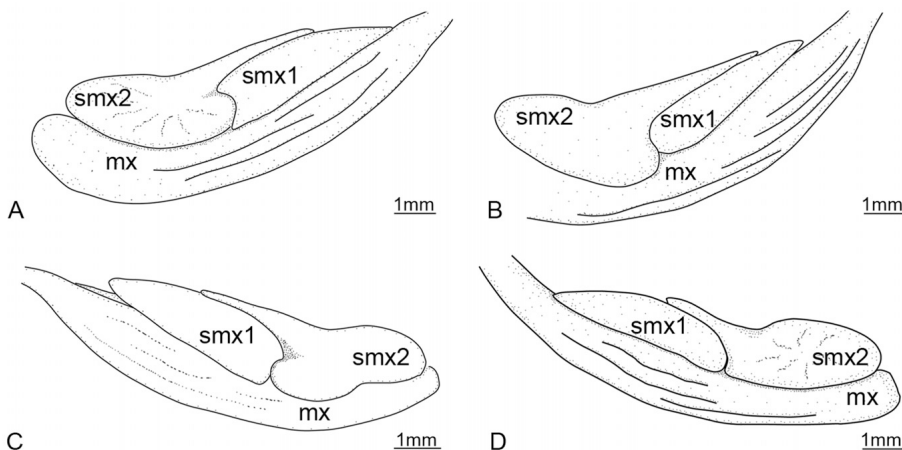

FIGURE 14. †*Luisiella feruglioi*, new combination. Schematic drawing showing intraspecific variation in the shape of the supramaxillae (polymorphism). **A**, right maxilla and supramaxillae (MPEF-PV 3420); **B**, right maxilla and supramaxillae (MPEF-PV 1477#1); **C**, left maxilla and supramaxillae (MPEF-PV 3415); **D**, left maxilla and supramaxillae (MPEF-PV 1476#3).

feruglioi and putative members of the stem of Teleocephala. Also, †*L. feruglioi* shows a feature that occurs commonly in non-teleostean neopterygians but is not frequent among teleosts, namely, a middle pit line groove on the parietal and pterotic bones. This feature has been considered part of the 'primitive' pit line plan of teleosts by Nelson (1972), and it has been described only for a few basal teleosts (i.e., †*Dorsetichthys bechei*, †*Leptolepis coryphaenoides*, †*Varasichthys ariasi* Arratia, 1981, †*Protoclupea chilensis* Arratia et al., 1975; Nybelin, 1974; Arratia, 1994; Grande and Bemis, 1998) and for the extinct euteleost †*Leptolepides haertesi* Arratia, 1997. In addition, †*L. feruglioi* has one feature that has been traditionally considered as a synapomorphy of the basal teleost family †Leptolepididae (e.g., †*Leptolepis coryphaenoides*): the presence of a well-developed preopercular process on the hyomandibular bone (Nybelin, 1974). This feature, although not widely distributed, is also present in some non-leptolepidid basal teleosts, such as †*Tharsis dubius*, †*Cavenderichthys talbragarensis*, and the icthyodectiform †*Allothrissops mesogaster* (Agassiz, 1832) (Patterson and Rosen, 1977; Bean, 2006; E.S., pers. observ.). Consequently, Patterson and Rosen (1977) suggested that the presence of a preopercular process in the hyomandibular bone should not be considered as unique to leptolepidids. Unlike leptolepidids, †*L. feruglioi* lacks a 'leptolepid' notch on the ascendant margin of the dentary, a feature also traditionally thought to be unique of Leptolepididae, although it is also present in some non-leptolepidid teleosts, such as the basal teleosts †*Ascalabos*, †*Protoclupea chilensis*, and †*Varasichthys ariasi*, and in some teleocephalans, such as the gonorynchiforms †*Gordichthys* Poyato-Ariza, 1994, and *Chanos* Lacépède, 1803 (Poyato-Ariza, 1996; Arratia, 1997). Recently, Arratia and Hikuroa (2010) published a revised diagnosis for the family †Leptolepididae sensu stricto, excluding the two features because they considered that Nybelin's diagnosis was based only on primitive features widely distributed in basal teleosts. Additionally, based on features of the vertebral centra, Arratia and Hikuroa (2010) have suggested that †*L. feruglioi* (as †*L. inexcutata* in the publication) is not a leptolepidid because it possesses features more derived than those present in leptolepidids (i.e., hourglass-shaped centra, thick and sculptured autocentra, autocentra and cordacentra strongly constricting the notochord, contrary to ring-like centra, thin and smooth autocentra, autocentra and cordacentra not constricting the notochord).

†*Luisiella feruglioi* shows an intriguing resemblance to the Late Jurassic basal teleost †*Cavenderichthys talbragarensis* (Arratia, 1997; Bean, 2006). These species share a combination of features, some of which are primitive even among basal teleosts, whereas others are typical of Teleocephala. Among the primitive features is the condition of the parypural and the hemal arches of the preural vertebrae, which remain separated from their corresponding vertebral centra in adult specimens of †*Luisiella* and †*Cavenderichthys*. This condition is present in teleosteomorphs and non-teleostean neopterygians but is otherwise known only in the basal †*Dorsetichthys bechei*, †*Siemensichthys macrocephalus* (Agassiz, 1844), and †*Eurycormus* speciosus Wagner, 1863, among teleosts (Arratia, 1991, 1999, 2000, 2013). A preopercular process on the hyomandibular bone and a deep coronoid process on the lower jaw, which also lacks a 'leptolepid' notch on the ascendant margin of the dentary, are other features shared by †*Luisiella* and †*Cavenderichthys* (E.S., pers. observ.). These features occur occasionally in basal teleosts and are not common in teleocephalans. Also, the two Gondwanan genera have features that are frequent among teleocephalans but not in known basal teleosts, namely, the first uroneural anteriorly reaching the second preural centrum (not reaching the third preural vertebrae) present in †*Pachythrissops propterus* (Wagner, 1863) and †*Paraclupavus caheni* (Saint-Seine and Casier, 1962) among basal teleosts, and in elopomorphs and Jurassic euteleosts such as †*Leptolepides haertesi*, among teleocephalans. Finally, both taxa share some derived teleocephalan features, such as a

preopercular canal with few simple tubules. It should be noted that like †*L. feruglioi*, †*C. talbragarensis* has been included in the leptolepidids for decades until Nybelin excluded this species from the family in 1974. Nybelin's proposal was subsequently supported by Patterson and Rosen (1977) and Arratia (1997) but opposed by Bean (2006). Although †*C. talbragarensis* shows some leptolepidid attributes (i.e., preopercular process in the hyomandibular bone), it differs from leptolepidids in that the notochord is slightly constricted at midlength of each vertebral centrum, the autocentra are comparatively thicker, and the lateral walls of the midcaudal vertebrae may be weakly ornamented with longitudinal grooves and ridges (Bean, 2006; Arratia and Hikuroa, 2010). At present, this taxon is regarded as a Teleostei incertae sedis. However, †*C. talbragarensis* and †*Paraclupavus caheni* show the connection between supraorbital and infraorbital or otic cephalic sensory canals (Cavender, 1970: fig. 1C; Taverne, 2001; Bean, 2006: fig. 1) that is absent in †*L. feruglioi* and leptolepids (Nybelin, 1974). As described above, the connection between those sensory canals in †*L. feruglioi* may have occurred, but it is not preserved.

In sum, the absence of several teleocephalan synapomorphies suggests that †*L. feruglioi* lies outside the node that supports Teleocephala. Also, this species shows some anatomical similarities with †*C. talbragarensis* (see above), and both taxa lack the attributes that characterize crossognathiforms, varasicthyds, ichthyodectiforms, and leptolepidids. The unambiguous resolution of the taxonomic position and phylogenetic relationships of †*Luisiella* and †*Cavenderichthys* through a parsimony analysis based on the available evidence will be addressed in a forthcoming paper, although preliminary cladistic analyses have suggested their close phylogenetic relationship (Sferco and López-Arbarello, 2010).

Recently, López-Arbarello et al. (2013) discussed the taxonomic composition of the Patagonian Almada Fauna and compared it with other well-known Jurassic freshwater fish faunas from Gondwana such as the Early to Middle Jurassic Kota Formation of India (Prasad et al., 2004; López-Arbarello et al., 2008), the continental deposits of the Late Jurassic to Early Cretaceous Stanleyville Group of the Democratic Republic of Congo (Saint-Seine and Casier, 1962; Myers et al., 2011; Taverne 2011a, 2011b), the Late Jurassic to Early Cretaceous Tacuarembó Formation of Uruguay (Soto and Perea, 2010; Soto et al., 2012), and the Late Jurassic Talbragar fauna of Australia (Woodward, 1895). The Almada Fauna is composed of one abundant species of teleost, †*Luisiella feruglioi*, the chondrostean †*Condorlepis groeberi* (Bordas, 1942), and poorly preserved basal actinopterygians of uncertain relationships. However, in addition to teleosts and coccolepidids, all other known Jurassic freshwater fish assemblages are characterized by abundant coelacanths and basal non-teleostean neopterygians, most of them also including dipnoans and hybodontid sharks. Interestingly, and as López-Arbarello et al. (2013) discussed in their revision of the chondrosteans of the Almada Fauna, the taxonomic composition of this Patagonian fish fauna is remarkably similar to that of the Late Jurassic freshwater Talbragar fauna, although the latter fauna is more diverse. In the Talbragar fauna, the most abundant taxon is the single teleost present, †*Cavenderichthys talbragarensis*, although the fauna also includes a single chondrostean, †*Coccolepis australis* (Woodward, 1895), four teleosteomorph ('pholidophoriformes') aphnelepid species (†*Aphnelepis australis* Woodward, 1895, †*Aetheolepis mirabilis* Woodward, 1895, †*Archaeomaene tenuis* Woodward, 1895, and †*Madariscus robustus* Wade, 1941), and a coelacanth represented by one fragmentary specimen. According to López-Arbarello et al. (2013), †*Condorlepis groeberi* and †*Coccolepis australis* are members of the same chondrostean family †Coccolepididae, but this family is distributed worldwide and the relationships between these two species within the family are still unknown. In

this regard, if the anatomical resemblance shown by †*L. feruglioi* and †*C. talbragarensis* is confirmed as resulting from common ancestry, as suggested by preliminary analyses (Sferco and López-Arbarello, 2010), it might indicate the presence of a distinct southern Gondwanan fish fauna. However, as López-Arbarello et al. (2013) observed, new discoveries and detailed studies of Jurassic freshwater fish faunas are extremely important to elucidate whether this resemblance might only be due to palaeoenvironment.

CONCLUSIONS

The detailed anatomical and morphometric study of the available material from the Jurassic Almada Fauna of central Chubut, Patagonia, revealed that only one teleost species is represented. Previously, two teleost species have been described from this fish fauna: †'*Tharrhias*' *feruglioi* and †*Luisiella inexcutata*, although their taxonomic status has remained ambiguous. We conclude that †*L. inexcutata* is a junior synonym of †'*T.*' *feruglioi*, and because the generic assignation is taxonomically erroneous, the new combination †*Luisiella feruglioi* is proposed herein. This species shows the plesiomorphic condition of many features that have been described almost exclusively in basal teleosts within Teleostei and occur rarely in teleocephalans. Examples of these features are the occurrence of a median gular plate and the presence of a middle pit line in the parietal and pterotic bones in the skull of †*L. feruglioi*, as well as the presence of fringing fulcra in the caudal fin and the absence of epipleural bones in the column. †*L. feruglioi* bears a distinct resemblance to the Late Jurassic freshwater teleost †*Cavenderichthys talbragarensis* in the presence of parypural and hemal arches of the preural vertebrae separated from their corresponding vertebral centra, hyomandibular bone with preopercular process, lower jaw with deep coronoid process and lacking a 'leptolepid' notch in the dentary, first uroneural anteriorly reaching the second preural centrum (but not the third preural centrum), and a preopercular canal with few simple tubules. Also, like the latter species, †*L. feruglioi* lacks features that characterize the known clades of basal teleosts, namely, crossognathiforms, varasichthyids, ichthyodectiforms, and leptolepidids; therefore, it should be regarded as a Teleostei incertae sedis

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