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

EMILIA SFERCO,1,2,3 ADRIANA LÓPEZ-ARBARELLO,2,3 and ANA MARÍA BÁEZ3

1Laboratorio de Paleontología Evolutiva de Vertebrales, Departamento de Geología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, 1428 Buenos Aires, Argentina, emiliasferco@gmail.com; baez@gl.fcen.uba.ar;
2SNSB–Bayerische Staatsammlung für Paläontologie und Geologie, Richard-Wagner-Strasse 10, D-80333 Munich, Germany, a.Lopez-Arbarello@lrz.uni-muenchen.de;
3Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Argentina

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 †Lusiiella 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 †Lusiiella 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 urodeural anteriorly reaching the second pracial 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 (Bonn, 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 †Hengniania 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 Canadón 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 †Lusiiella inexecutata 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.

*Corresponding author.
1Current address: CICTERRA, CONICET–Universidad Nacional de Córdoba. Av. Velez Sarsfield 1611, X0516GCA Córdoba, Argentina.
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; asp, axial process; ber.fur, beryciform foramen; bpt, basipterygium; br, r, branchiostegal rays; cl, cleithrum; d, dentary; d.hyp, dorsal hypohyal; dr, dorsal rays; dsct, 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; hsp, hemal spine; hy, hyomandibular bone; ihm, infrahemal spine; io1–5, infraorbital bones 1–5; ioc, infraorbital canal; iop, interopercle; m.c, mandibular canal; mpl, 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; na, 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; pel, postcleithrum; pectr, 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, procurent rays; psph, paraphenoid; pt, pterygiophores; pto, pterotic bone (fused autop- and dermopterotics); ptt, posttemporal bone; ptt.c, posttemporal sensory canal; Pu1–5, preural centra 1–5; q, quadrate; r, ribs; s, co, supraterminal commissure; sc, supracleithrum; smx1–2, supramaxillae 1–2; sn, supraneural bone; so, supraorbital bone; soc, supraorbital sensory canal; soc, supraoccipital bone; sop, subopercle; sr, sclerotic ring; t.e, temporal sensory canal; U1–2, ural centra 1–2; u.n.sp, unpaired neural spines; un, unornearals; 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

NEOPTERYGIID Regan, 1923

Order and family indet.

| LUSIELLA | Bocchino, 1967 |

Type Species—Lusielia inexcucata Bocchino, 1967.

Diagnosis—same as for the type and only known species.

| LUSIELLA FERUGLIOI (Bordas, 1942), new combination | Figs. 2–12 |

| Diplomystus longicostatus Cope, 1887: Piatnitzky, 1936:105 (referred). |
†Tharrhis 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 Condor 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 2.** †Luisiella feruglioi, new combination. **A**, lectotype (MACN 13069); **B**, holotype of †Luisiella inexcutata (MLP 35-III-1-4).

**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 3419, 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 14882b, 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 14882a, 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.
dermosphenotics, and anterolateral to the extrascapular bones, forming the posteroventral 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 posteroventral 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). 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 anteroventral projections. In dorsal view, the mesethmoid has two symmetrical, well-ossified anteroventral 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 posteroventral projections of the vomer in MPEF-PV 1654.

The autosphenotics are paired bones located at the anterodorsal 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 dorsoventral portion of the most posterior region of the neurocranium (MPEF-PV 488#2b, 3871h, 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-PV 3421, 10534). Each circumorbital series includes an antorbital, infraorbital 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 lancelolate 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
a long side in contact with the preopercle and a short side delimiting the posterior, or sometimes the posterodorsal, 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. Anteriondorsally, the bone bears a small condyle for the articulation with the lower jaw (e.g., MPEF-PV 3909). Immediately behind this condyle, the anterodorsal rim of

---

**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).

**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 posteroverentral process, which originates near the anterovelar 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 posteroverentral 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 anteroverental 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 endopterygoid 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 doroventrally 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 anteroverentially, with the preopercle posteroverentlich, 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 posteriordirected 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 ephial) 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 hypothals and posteriorly with the posterior ceratohyal. Ventrally, it articulates with the acincliform 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 fenestra (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 arc. They are posteriory 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, Stiasny, 1986). The supramaxillae are in contact with one another through a high and sinusuous 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 3369, 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 symphysis 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...
posteroventrally 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 expanded posterodorsal 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 posterodorsally 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 posterodorsal 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 portion and a triangular ventral portion. Ventrally, the opercle is ornamented with fine concentric lines. In addition, the opercle is orna-
mented with fine concentric lines. The opercle is ornamented with fine concentric lines (Supplementary Data, Table S2). The anterior margin is 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), 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 orna-
mented 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 ante-
rior ceratohyal. The remaining seven to eight branchiostegal rays are spathiform (paddle-like) and articulate with the poste-
rior 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 branchioste-
gal 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 poste-
rior 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 posteri-
orly 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),
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 anteromedially. 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 3907).

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 354, 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

![Diagram of caudal skeleton](image-url)
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
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 epurals (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 paired, lanceolate 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 minute, 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#89, 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 ‘urodernals’ 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.
is parallel to the lateral margin of the bone; it describes a sigmoid
through the nasal bones, from which it continues in a superficial
and supratemporal commissures (Fig. 4).

mandibular canals, anterior and middle pit lines, and ethmoidal
bital, infraorbital, temporal, posttemporal, preopercular, and
system is composed of relatively few and simple tubules, supraor-
circles and radial striae. The scales have no radii.

margin. Unlike the anterior field, the posterior field bears few
shorter in length. Besides, all the rays are segmented, having a
procurrent rays. Procurrent rays are short, unsegmented rays
portion of the fin. Usually, the anal fin has 10 anal rays and two
and distal pterygiophores are usually preserved in the middle
or was included in the skin; therefore, it is not preserved
of the pterotic bone and is connected anteriorly with the infraor-
the antorbital bone (e.g., MPEF-PV 3192a, 3941b) and then con-
the infraorbital canal in the pterotic bone (e.g., MPEF-PV
3936). There is no direct evidence for a connection between
infraorbital 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 infraor-
ventrally with the preopercular canal, posterome-
dialy 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 supra-
temporal 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 commis-
sure are connected to each other at the level of the supraocci-
tal bone, where they leave no trace. Posteriorly, the posttemporal
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) proxim-
ally 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 prox-
imal 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 ante-
rior field. The anterior field extends for about 3/4 of the total sur-
face 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, supraor-
bital, 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 supraor-
bital 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 3595, 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 poste-
riorly 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 con-
tinues in the infraorbital bones, where it gives off three to four
simple and short tubules in the first infraorbital, which are ven-
trally 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 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
infraorbital 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 infraor-
bital canal, ventrally with the preopercular canal, posterome-
dially 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 supra-
temporal 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 commis-
sure are connected to each other at the level of the supraocci-
tal 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 pos-
terior 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 caud-
al 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 from 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 Ararip 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 Leptoplepis Agassiz, 1832, without making any reference to her previous work based on the single specimen described as Luisiella inexcutata. For decades, and mainly due to its poor definition, the genus Leptoplepis 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, Leptoplepis coryphaenoides (Broom). 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 Bannen, 1908, now placed within the gonorhynchiforms ostariophysans and endemic to the Ararip 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 to 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 Canadón 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 Canadón Calcáreo Formation: Tharrhias shamani Dolgo pol de Sáez, 1949, and Leptolepis leanzai Dolgo pol 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 Shamen, 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 Canadón Calcáreo Formation and concluded that these specimens were probably collected in the area of Cerro Cóndor. The type specimens of Tharrhias shamani (MLP 48-VIII-1-3) and Leptolepis leanzai (MLP 48-1-1-2) 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, Tharrhias shamani Dolgo pol de Sáez and Leptolepis leanzai Dolgo pol de Sáez are regarded as nomina dubia (Art. 75.5; ICZN, 2000).

Intraspecific Variation—Examination of the numerous specimens from the Canadón 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 midcudal vertebrae are ring-like, lack well-developed autozona, and the notochord is barely constricted, whereas these vertebrae are hourglass-shaped and have a well-developed autozona that strongly constrict the notochord in adults. Another feature that varies with developmental stage is the separation between successive 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., Todilith schoeweii (Dunkle, 1942), Anuathony 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...
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 polyphyletic variation that might indicate that more than one taxon was involved.

The number of adult specimens (more than a hundred) was available for each variable feature. Considering that a large number of adult specimens (more than a hundred) was available for each variable feature. 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 crossopterygians (Arratia, 2008a), the Jurassic \(Ascalabos\) von Münster, 1839, and \(Domeykos\) Arratia and Schultz, 1985, and in a few fossil and extant euteleosts (e.g., \(Orthognathichthys\), \(Thymallus\) Linck, 1790; Arratia, 1997). However, \(L. feruglioi\) differs from \(Ascalabos\), the varasichthyid \(Domeykos\), and euteleosts in the absence of epipleural bones, intermuscular bones associated to the ribs, which were considered a derived teleost feature by Patterson and Johnson (1995). Also, \(L. feruglioi\) differs from crossopterygians 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, crossopterygians (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 \(Anarthron\) and the living elopomorph \(Megalops\) Valenciennes, 1847; Arratia, 1987, 1997), is another plesiomorphic feature present in \(L. feruglioi\).

**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 crossopterygians (Arratia, 2008a), the Jurassic \(Ascalabos\) von Münster, 1839, and \(Domeykos\) Arratia and Schultz, 1985, and in a few fossil and extant euteleosts (e.g., \(Orthognathichthys\), \(Thymallus\) Linck, 1790; Arratia, 1997). However, \(L. feruglioi\) differs from \(Ascalabos\), the varasichthyid \(Domeykos\), and euteleosts in the absence of epipleural bones, intermuscular bones associated to the ribs, which were considered a derived teleost feature by Patterson and Johnson (1995). Also, \(L. feruglioi\) differs from crossopterygians 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, crossopterygians (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 \(Anarthron\) and the living elopomorph \(Megalops\) Valenciennes, 1847; Arratia, 1987, 1997), is another plesiomorphic feature present in \(L. feruglioi\).
feruglioi and putative members of the stem Teleostei. 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., Dorsettichthys bechei, Leptolepis coryphaenoides, Varasichthys ariasi Arratia, 1981, Protolepis chilensis Arratia et al., 1975; Nybelin, 1974; Arratia, 1994; Grande and Bemis, 1998) and for the extinct euteleost Leptolepis haertesi Arratia, 1997. In addition, L. feruglioi has one feature that has been traditionally considered as a synapomorphy of the basal teleost family Leptolepidae (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-leptolepid basal teleosts, such as Tharis dubius, Cavenderichthys talbragarensis, and the ichthyodectiform 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 leptolepids. Unlike leptolepids, L. feruglioi lacks a ‘leptolepid’ notch on the ascendant margin of the dentary, a feature also traditionally thought to be unique of Leptolepidae, although it is also present in some non-leptolepid teleosts, such as the basal teleosts Ascalabos, Protolepis chilensis, and Varasichthys ariasi, and in some teleosts, such as the gonorynchiforms Gordichthys Poyato-Arzia, 1994, and Chanos Lacépede, 1803 (Poyato-Arzia, 1996; Arratia, 1997). Recently, Arratia and Hikuroa (2010) published a revised diagnosis for the family Leptolepidae 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 leptolepid because it possesses features more derived than those present in leptolepids (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 base teleost Cavenderichthys talbragarensis (Arratia, 1997; Bean, 2006). These species share a combination of features, some of which are primitive euteleosts and others are typical of Teleosteia. Among the primitive features is the condition of the papyral 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 Dorsettichthys bechei, Siemimenschichthys 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 teleosteomorphs. Also, the two Gondwanan genera have features that are frequent among teleosteomorphs but not in known basal teleosts, namely, the first uroneural anteriorly reaching the second preural centrum (not reaching the third preural vertebrae) present in Pachythrisops propertus (Wagner, 1863) and Paracolupavus caheni (Saint-Seine and Casier, 1962) among basal teleosts, and in elopomorphs and Jurassic euteleosts such as Leptolepides haertesi, among teleosteomorphs. Finally, both taxa share some derived teleosteomorph features, such as a preopercular canal with few simple tubules. It should be noted that L. feruglioi, C. talbragarensis has been included in the leptolepids 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 leptolepid attributes (i.e., preopercular process in the hyomandibular bone), it differs from leptolepids in that the notochord is slightly constricted at midlength of each vertebral centrum, the autocentra are comparatively thicker, and the lateral wings of the midaudal 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 Varacolupavus 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 teleosteomorph synapomorphies suggests that L. feruglioi lies outside the node that supports Teleostea. Also, this species shows some anatomical similarities with C. talbragarensis (see above), and both taxa lack the attributes that characterize crossognathiforms, varasichthyids, ichthyodectiforms, and leptolepids. 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 (Bordin, 1942), and poorly preserved basal actinopterygians of uncertain relationships. However, in addition to teleosts and coccopelids, all other known Jurassic freshwater fish assemblages are characterized by abundant coelancaths 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 chondrostean assemblage 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, Coccoludepis australis (Woodward, 1895), four teleosteomorphs (pholidophoriformes) aphanlepid species (Aphlepsi australis Woodward, 1895, Aetheolepis mirabilis Woodward, 1895, Archeoamaeae 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 Coccoludepis australis are members of the same chondrostean family Coccoluididae, 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 (Sfetcu 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: \( \text{†Tharrrias} \) feruglioi and \( \text{†Lusiella} \) inexcucata, although their taxonomic status has remained ambiguous. We conclude that \( L. \) inexcucata is a junior synonym of \( T. \) feruglioi, and because the generic assignment is taxonomically erroneous, the new combination \( \text{†Lusiella} \) feruglioi is proposed herein. This species shows the pleiosomorphic 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 \( \text{†Cavenderichthys talbragarensis} \) 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 urocentral anteriorly reaching the second preural centrum (but not the third preural centre), 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, crossagnosthiforms, varasichthiids, ichthyodectiforms, and leptolepidids; therefore, it should be regarded as a Teleostei incertae sedis

ACKNOWLEDGMENTS

This research constitutes part of the Ph.D. dissertation of E.S. The authors thank O. M. W. Rauhut (BSPG), E. Ruig (MACYN), and M. Reguero (MLP) for providing access to collections under their care. They are also thankful to J. Alvarado-Ortega, J. Casciotta, M. Ramírez, M. Friedman, and two anonymous reviewers for their helpful suggestions and comments. Thanks are extended to M. Köbl-Ebert, F. Witzman, Z. Johanson, M. Richter, and H. Tischlinger. We thank R. Liebreich (BSPG) and L. Rainer, P. Puerta, L. Canessa, N. Pfeiffer, and S. Bessone (MEF) for preparing the fossils. The CONICET (PIP 948/2011), the DAAD (A/07/72315), and the German Research Foundation (DFG LO1405/3-1 and RA1012/9-1) supported this research. Also, E.S. received support from the SYNTHESYS Project (http://www.synthesys.info/), which is financed by European Community Research Infrastructure Action under the FP7 Integrating Activities Programme.

LITERATURE CITED

Agassiz, L. 1832. Untersuchungen über die fossilen Fische der Lia–Formation. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 3:139–149.

Agassiz, L. 1833–1844. Recherches sur les Poissons Fossiles. 5 volumes.

Pettie, Pierre, Neuchâtel and Soleure, 1798 pp.

Arratia, G. 1981. Varasichthys ariasii n. gen. et sp. from the Upper Jurassic of Chile (Pisces, Teleostei, Varasichthyidae). PalaeonograPhica Abt. A 175:107–139.

Arratia, G. 1982. Chongichthys dentatus, a new genus and species from the Late Jurassic of Chile (Pisces: Teleostei: Chongichthyidae, New Family). Journal of Vertebrate Paleontology 2:133–149.

Arratia, G. 1987. Anathalodon and similar teleosts (Actinopterygii, Pisces) from the Late Jurassic (Tithonian) of southern Germany and their relationships. PalaeonograPhica Abt. A 200:1–44.

Arratia, G. 1991. The caudal skeleton of Jurassic teleosts: a phylogenetic analysis; pp. 249–340 in M.-M. Chang, Y. H. Liu, and G. R. Zhang (eds.), Early Vertebrates and Related Problems in Evolutionary Biology. Beijing Science Press, Beijing, China.

Arratia, G. 1994. Phylogenetic and palaeogeographic relationships of the varasichthyid group (Teleostei) from the Late Jurassic of Central and South America. Revista Geológica de Chile 21:119–165.

Arratia, G. 1997. Basil teleosts and teleostean phylogeny. PalaeoIchthyologica 7:1–166.

Arratia, G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements; pp. 265–334 in G. Arratia and H.-P. Schultz (eds.), Mesozoic Fishes 2. Systematics and Fossil Record. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Arratia, G. 2000. New teleostean fishes from the Jurassic of southern Germany and the systematics problems concerning the ‘pholidophoriforms’”. Palaeontologische Zeitschrift 74:113–143.

Arratia, G. 2004. Mesozoic teleost osteomes and the early radiation of teleosts; pp. 279–315 in G. Arratia and A. Tintori (eds.), Mesozoic Fishes 3. Systematics, Palaeoenvironments and Biodiversity. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Arratia, G. 2008a. The varasichthyid and other crossoagnostiform fishes, and the break-up of Pangaea; pp. 71–92 in L. Cavin, A. Longbottom, and M. Richter (eds.), Fishes and the Break-up of Pangaea. Geological Society of London: Special Publication 295, London.

Arratia, G. 2008b. Actinopterygian postcranial skeleton with special reference to the diversity of fin ray elements, and the problem of identifying homologies; pp. 49–101 in G. Arratia, H.-P. Schultz, and M. V. H. Wilson (eds.), Mesozoic Fishes 4. Homology and Phylogeny. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Arratia, G. 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). Journal of Vertebrate Paleontology 33:sup1, 1–138.

Arratia, G., and D. C. H. Hikuroa. 2010. Jurassic fishes from the Latady Group, Antarctic Peninsula, and the oldest teleosts from Antarctica. Journal of Vertebrate Paleontology 30:1331–1342.

Arratia, G., and H.-P. Schultz. 1985. Late Jurassic teleosts (Actinopterygii, Pisces) from northern Chile and Cuba. PalaeonograPhica Abteilung A 189:29–61.

Arratia, G., and H. Tischlinger. 2010. The first record of Late Jurassic crossoagnostiform fishes from Europe and their phylogenetic importance for teleostean phylogeny. Fossil Record 13:317–341.

Berrigan, A. G., and Chong, 1975. Sobre un pez fósil del Jurásico de Chile y sus probables relaciones con clupeidos sudamericanos vivientes. Revista Geológica de Chile 21:10–21.

Bean, L. B. 2006. The leptolepid fish Cavenderichthys talbragarensis (Woodward, 1895) from the Talbragar Fish Bed (Late Jurassic) near Gilgong, New South Wales. Records of the Australian Museum 23:43–76.

Blainville, H. D. dc. 1818. Poissons fossiles. Nouvelle Dictionnaire d’Histoire naturelle. Nouvelle édition 27:334–361.

Bocchino, A. 1967. Lusiella inexcucata gen. et sp. nov. (Pisces, Clupeiformes, Dussumieridae) del Jurásico Superior de la Provincia de Chubut, Argentina. Ameghiniana 4:91–100.

Bocchino, A. 1975. Revision de los Ostichthyas fósiles de la República Argentina. I. Identidad de Tharrias feruglioi Bordas 1943 y Oligopleurus groberi Bordas 1943. Ameghiniana 15:301–320.

Bordas, A. F. 1942. Peces del Cretácico del Río Chubut (Patagonia). Physis XIX 53:313–318.

Brito, P., and Y. Yabumoto. 2011. An updated review of the fish faunas from the Crato and Santana formations in Brazil, a close relationship to the Tethys fauna. Bulletin of the Kitakyushu Museum of Natural History, Series A 9:107–136.

Bromn, H. 1830. Über zwei fossile fischarten: Cyprinus corphynoides und Tetragonolepis semicinctus aus dem Gryphitenkalke bei Donaueschingen. Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde 1:14–30.
Taverne, L. 2011b. Ostéologie et relations phylogénétiques de *Catervar-iolus* (Teleostei, “Pholidophoriformes”) du Jurassique moyen de Kisangani en République Démocratique du Congo. Bulletin de l’Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 81:175–212.

Turner, S., L. B. Bean, M. Dettmann, J. McKellar, S. McLoughlin, and T. Thulborn. 2009. Australian Jurassic sedimentary and fossil successions: current work and future prospects for marine and non-marine correlation. GFF 131:49–70.

Valenciennes, A. 1847. Histoire naturelle des poissons. Tome dix-neuvième. Suite du livre dix-neuvième. Brochets ou Lucioïdes. Livre vingtième. De quelques familles de Malacoptérygiens, intermédiaires entre les Brochets et les Clupes 9:1–544.

Wade, R. T. 1941. The Jurassic fishes of New South Wales. Journal and Proceedings of the Royal Society of New South Wales 75:71–84.

Wagner, J. A. 1863. Monographie der fossilen Fische aus den lithographischen Schiefern Bayerns. Zweite Abtheilung. Abhandlungen der mathematisch-naturwissenschaftlichen Abtheilung der königlichen bayerischen Akademie der Wissenschaften 9:611–748.

Wang, N.-Ch. 1977. Les poissons jurassiques du Hunan, Chine. Première partie. Vertebrata PalAsiatica, 15:177–183. [Chinese]

White, E. I. 1938. The generic name *Aethalion*. The Annals and Magazine of Natural History 11:319.

Woodward, A. S. 1895. The fossil fishes of the Talbragar Beds (Jurassic?). Memoirs 50 of the Geological Survey of New South Wales, Palaeontology 9:1–27.

Submitted November 9, 2013; revisions received April 28, 2014; accepted May 12, 2014.

Handling editor: Martha Richter.

Citation for this article: Sferco, E., A. López-Arbarello, and A. María Baez. 2015. Anatomical description and taxonomy of *Luisella feruglioi* (Bordas), new combination, a freshwater teleost (Actinopterygii, Teleosteoi) from the Upper Jurassic of Patagonia. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2014.924958.