

A NEW HUMP-BACKED GINGLYMODIAN FISH (NEOPTERYGII, SEMIONOTIFORMES) FROM THE UPPER TRIASSIC CHINLE FORMATION OF SOUTHEASTERN UTAH

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ABSTRACT—A new species of hump-backed semionotiform fish, *Lophionotus sanjuanensis*, gen et sp. nov., is described based on specimens recently and previously collected from the Upper Triassic Church Rock Member of the Chinle Formation of southeastern Utah. It is characterized by a deep body with a large postcranial hump, and dense tuberculation on the posterodorsal margin of the skull that continues into the dorsal ridge and dorsolateral flank scales. The vertical preoperculum bears a short and broad paddle-like ventral process. The infraorbital series expands ventral to the suborbital and contacts the anterior ramus of the preoperculum, although this character has also been observed in other deep-bodied semionotiform taxa. This taxon represents the first newly described semionotiform fish species from the western United States in over 45 years, and adds to knowledge of Triassic fishes biodiversity.

INTRODUCTION

Semionotiforms are a diverse group of extinct neopterygian fishes known worldwide from both marine and freshwater deposits (e.g., Woodward, 1890; McCune, 1986; López-Arbarelo, 2004; McCune, 2004; Cavin and Suteethorn, 2006), and range in age from the Middle Triassic to the Late Cretaceous (Gardiner, 1993).

The majority of described semionotiform diversity in the United States comes from the Upper Triassic–Lower Jurassic Newark Supergroup deposits of the eastern United States (e.g., Newberry, 1888; McCune, 1987), including the well-described species *Semionotus elegans* (Olsen and McCune, 1991). Biodiversity of semionotiform taxa in the western United States is largely unknown, as few specimens have been described despite their presence being well documented (e.g., Eastman, 1905, 1917; Schaeffer, 1967; Huber et al., 1993; Johnson et al., 2002; Milner and Kirkland, 2006; Milner et al., 2006b) from Triassic and Jurassic localities. Schaeffer and Dunkle (1950) described a semionotid fish, *Semionotus kanabensis*, which is currently the only described species of *Semionotus* from the western United States. Specimens of *S. kanabensis* are known from the Lower Jurassic Moenave Formation of southern Utah (Schaeffer and Dunkle, 1950). *Semionotus kanabensis* is a small semionotid (average SL is 68 mm), with a fusiform body; a gently sloping dorsal border; smooth dorsal ridge scales (lacking tuberculation); a narrow preoperculum with a narrow ventral branch that is of about equal length to, and slightly wider than, the dorsal branch; and deep infraorbitals (Schaeffer and Dunkle, 1950). In overall body morphology *S. kanabensis* is similar to other species of *Semionotus*, but the skull differs from species such as *S. bergeri* (the type species) and *S. elegans*, particularly in having deep infraorbitals that contact the preoperculum.

Recent field work in the Upper Triassic Chinle Formation of Lisbon Valley, Utah, recovered numerous specimens of fossil fishes that remain presently undescribed. Schaeffer (1967) first described a number of Mesozoic actinopterygian fishes from southeastern Utah and southwestern Colorado, including redfieldiid palaeonsiciforms, a perleidiform (*Tanaocrossus kalliokoskii* Schaeffer, 1967), and a species of semionotiform fish

(*Hemicalypterus weiri* Schaeffer, 1967). Schaeffer's (1967) work briefly documented semionotid diversity and morphology from the Chinle Formation, with comments on differences in size and body shape among specimens, but did not describe any new species of *Semionotus* (citing the need for future work on this material and locality).

The taxonomic composition of the family Semionotidae has a complicated history (e.g., Olsen and McCune, 1991; Wenz, 1999). The genus *Semionotus* was first described by Agassiz (1836) and the family Semionotidae was erected by Woodward (1895). *Semionotus* possesses lepidosteoid ganoid scales (Goodrich, 1907), and one of the defining characteristics of semionotids is the presence of prominent dorsal ridge scales (Agassiz, 1836; McCune, 1986; Olsen and McCune, 1991).

The family Semionotidae sensu Wenz (1999) includes the genera *Semionotus*, *Lepidotes*, *Paralepidotes*, *Araripelepidotes*, and *Pliodetes*. Wenz (1999) examined morphological characters from previous studies (e.g., Patterson, 1975; Thies, 1989; Olsen and McCune, 1991; Gardiner et al., 1996), but did not perform any character-based phylogenetic analyses, or provide a diagnosis for the family itself. Subsequent parsimony-based studies of Semionotiformes (Cavin and Suteethorn, 2006; Cavin, 2010) recovered a largely unresolved clade that includes semionotiform and lepisosteiform taxa. However, the family Semionotidae sensu Olsen and McCune (1991), including *Semionotus* and *Lepidotes*, was recovered as monophyletic when taxon sampling was limited to extinct species with the least amount of missing character data (Cavin and Suteethorn, 2006).

Recently, Grande (2010), in his work on lepisosteids and holostean evolutionary relationships, indicated that the order Semionotiformes is the sister group to Lepisosteiformes. However, his taxonomic sampling of the order Semionotiformes was restricted to just *Semionotus*, and within that genus Grande (2010) only considered two species (*S. bergeri* and *S. elegans* as described by Olsen and McCune, 1991) that had substantial material and complete descriptions. Specifically, *S. elegans* was used as the representative for the family and genus, and Grande (2010) indicated that *S. elegans* is arguably the most well-preserved species within the order, such that its comprehensive morphological description minimizes the amount of missing

data for inclusion in a phylogenetic analysis. Grande (2010) suggested that until other species of *Semionotus* and *Lepidotes* are redescribed thoroughly and reanalyzed within a phylogenetic framework, he would only consider species that provide the most informative characters for establishing sound relationships. This highlighted the need for thorough morphological redescrptions of known semionotid species, descriptions of new species, and a comprehensive taxonomic revision of the Semionotiformes. This sentiment has also been discussed by many previous studies on semionotiform taxonomy and evolutionary relationships (e.g., McCune, 1987; Olsen and McCune, 1991; Wenz, 1999; López-Arbarello, 2008).

Recent investigations into the relationships of Ginglymodi include the parsimony-based phylogenetic study of Xu and Wu (2012), which focused on neopterygian relationships in order to identify the phylogenetic position of their newly described taxon *Kyphosichthys grandei*. Their analysis supported Grande (2010) in the resurrection of Holostei to include the Ginglymodi and Halecomorphi within Neopterygii. Their analysis, however, was limited to 15 taxa, and did not provide a robust hypothesis of relationships of taxa within Semionotiformes from a dense sampling of semionotiform taxa.

At present, López-Arbarello (2012) is the most taxonomically comprehensive phylogenetic hypothesis of semionotiform relationships to date. Her analysis of 37 taxa (including outgroups) and 90 characters recovered a monophyletic Semionotiformes based on five unambiguous synapomorphies, and restricted the family Semionotidae to the genus *Semionotus*. López-Arbarello (2012) identified several species that were traditionally placed in the genus *Lepidotes* as two new genera: *Callipurbeckia* and *Scheenstia*. Some species of *Lepidotes* have yet to be thoroughly evaluated and are designated as '*Lepidotes*' until further analysis can be performed. Many genera that had been placed in Semionotidae were placed in a new family Callipurbeckiidae: *Semiolepis*, *Macrosemimimus*, *Callipurbeckia*, *Paralepidotus*, and *Tlayuamichin*. Other genera, such as *Araripelepidotes*, *Pliodetes*, *Lepidotes*, *Scheenstia*, and *Isanichthys*, were placed in the order Lepisosteiformes. The placement of the genus *Neosemionotus* within Ginglymodi remains unresolved (López-Arbarello, 2012).

The purpose of this study is to describe a new semionotiform genus from specimens recently and previously collected from the Chinle Formation in the Lisbon Valley area of San Juan County, Utah. Several of the specimens described herein were originally figured in Schaeffer (1967) and identified as *Semionotus* sp., but were not named or described in that work. Additional specimens include recently collected material from field expeditions in 2004 and 2005, which are now housed at the Natural History Museum of Utah (UMNH). This new genus and species possesses a unique combination of morphological characters that is not observed in other described genera of semionotiform fishes. The addition of this new genus and species provides key morphological information that is essential to furthering the understanding of semionotiform biodiversity, and will allow for the inclusion of this new taxon in future phylogenetic studies of semionotiform taxa.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **FMNH**, Field Museum of Natural History, Chicago; **NMMNHS**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **SGDS**, St. George Dinosaur Discovery Site at Johnson Farm, St. George, Utah; **UMNH**, Natural History Museum of Utah, Salt Lake City, Utah.

Anatomical Abbreviations—**a.io**, anterior infraorbital (lacrimal); **ang**, angular; **ar**, articular; **bchst**, branchiostegal; **bf**, basal fulcrum; **b.pr**, branched principal ray; **ch**, ceratohyal; **cl**, cleithrum; **d**, dentary; **dpt**, dermopterotic; **d.scu**, dorsal scutes; **dsph**, dermosphenotic; **ecp**, ectopterygoid; **enp**, endopterygoid; **ex**, extrascapular; **ff**, fringing fulcrum; **io**, infraorbital; **iop**, in-

teroperculum; **n**, nasal; **mx**, maxilla; **op**, operculum; **p.bf**, paired basal fulcrum; **p.ff**, paired fringing fulcrum; **p**, parietal (frontal); **pcl**, postcleithrum; **pmx**, premaxilla; **pop**, preoperculum; **pp**, postparietal (parietal); **pr**, principal ray; **psph**, parasphenoid; **ptt**, posttemporal; **qu**, quadrate; **scl**, supracleithrum; **so**, supraorbital; **sop**, suboperculum; **su**, suborbital.

Other Abbreviations—**HL**, head length; **MBD**, maximum body depth; **SL**, standard length.

GEOLOGIC SETTING

The specimens described herein were collected from several localities in the Upper Triassic Chinle Formation, Lisbon Valley (San Juan County), southeastern Utah (Fig. 1A). The Chinle Formation in Lisbon Valley can be separated into two major sections. The lower, gray, bentonitic beds (Fig. 1B) are the localized Kane Springs beds of Blakey and Gubitosa (1983). The Kane Springs beds contain numerous terrestrial and semiaquatic vertebrate remains, including phytosaurs, metoposaurs, dinosauromorphs, and other archosaurs (e.g., Milner et al., 2006a). The upper beds are currently recognized as the Church Rock Member of the Chinle Formation (Blakey and Gubitosa, 1983; Blakey, 1989), and comprise alternating layers of mudstone, siltstone, fine-grained sandstone, and conglomerate (Fig. 1B). The fish-bearing beds are within the Church Rock Member, in fine-grained, red and pale green sandstone layers that show cross-lamination (Fig. 1B).

Based on geology and lithostratigraphy, the Chinle Formation in Lisbon Valley represents a complex fluvial-deltaic-lacustrine system (e.g., Blakey and Gubitosa, 1983; Dubiel, 1987). The Triassic habitat of the Chinle Formation in Lisbon Valley has been interpreted by previous studies (e.g., Stewart et al., 1972; Blakey, 1989) as a freshwater system with a perennial, monsoonal climate (Dubiel, 1987), which transitioned from humid to increasingly arid over time (Blakey and Gubitosa, 1983). The fossil fish-bearing layers of the Church Rock Member (Chinle Formation, Lisbon Valley) are in isolated channel deposits of fine-grained sandstones and mudstones. These have been interpreted as small fluvial systems crossing a lacustrine or playa mudflat (Dubiel, 1987). Many undescribed specimens of semionotiform fishes have been recovered from this area (Schaeffer, 1967; Milner et al., 2006a, 2006b). A diverse group of Late Triassic taxa are also known from this locality, including coelacanthids, dipnoans, redfieldiids, palaeoniscoids, and hybodont sharks, as well as tetrapods (phytosaurs, metoposaurs, dinosauromorphs, and other archosaurs; e.g., Schaeffer, 1967; Milner et al., 2006a, 2006b).

MATERIALS AND METHODS

Specimens described in this study were collected by the American Museum of Natural History (AMNH) between 1958 and 1964; those with the AMNH prefix are a result of that field work and are housed at that institution. Additional specimens were collected in 2004–2005 by a team consisting of scientists from the Natural History Museum of Utah (UMNH) and the St. George Dinosaur Discovery Site at Johnson Farm (SGDS). Those specimens were prepared by the author and Andrew R. C. Milner while temporarily housed at SGDS, and then deposited at the UMNH. Specimens collected in 2004 and 2005 for this study were collected under Utah State Institutional Trust Lands Administration permits 02-334 and 05-347.

Specimens were mechanically prepared with the use of pneumatic tools and microjacks to remove excess matrix from within a few millimeters above the specimen. To avoid destruction of the specimen, the remainder of preparation was done with sharpened carbide needles. In instances where only a negative impression of the fossil is preserved, a latex peel was made to provide a positive 'cast' of the specimen. Several stereomicroscopes of varying

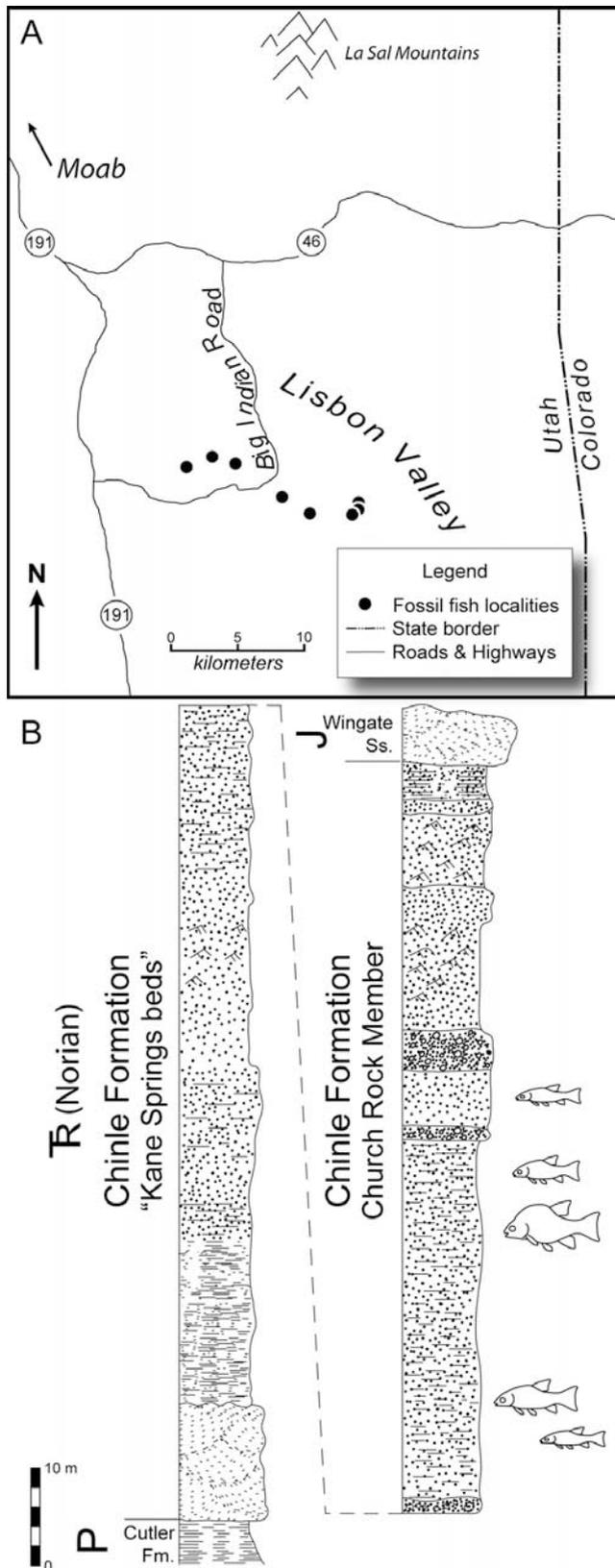


FIGURE 1. **A**, locality map of Lisbon Valley, Utah, with fossil fish localities indicated; **B**, generalized stratigraphic column for the Chinle Formation in Lisbon Valley, Utah, with fish-bearing layers indicated by generalized semionotid fish symbols on the right. **Abbreviations:** **P**, Permian Period; **TR**, Triassic Period; **J**, Jurassic Period. Modified from Milner et al. (2006b).

resolution power (Wild M4 and MZ8; USA Scopes SZ65) were used in this study. Photographs of the specimens were taken with a Canon EOS Rebel T1i digital SLR camera with a Canon EF 100 mm f/2.8L IS USM 1-to-1 macro lens and a Canon 18-55 mm IS II lens. Drawings of the specimens were done with a camera lucida arm attachment and a Wacom Intuos Duo tablet over high-resolution photographs.

Bone Terminology

The terminology used herein follows the osteological terminology outlined by Schultze (2008) and Wiley (2008). Postcranial morphology follows the terminology outlined in Arratia (2008). In instances where terminology has varied in the literature over the years, the traditional terminology will be presented in parentheses the first time that the bone is cited. This will aid in preventing problems with homology when using this descriptive work in later studies and phylogenetic analyses.

Materials Examined

- Araripelepidotes temnurus*: AMNH 19067 CP, 11813; FMNH PF 11835, PF 11849, PF 11852, PF 11853, PF 14043, PF 14349
Callipurbeckia notopterus: FMNH UF 539
Dapedium pholidotus: FMNH P 25056, UC 2056
Dapedium punctatus: FMNH PF 25433
Hemicalypterus weiri: AMNH 5709–5718
Lepidotes elvensis: FMNH P 25095
Lepidotes gigas: FMNH PF 5367
Lepidotes sp.: FMNH PF 12564, PF 15470
Semionotus capensis: AMNH 8828, 8829, 19702; FMNH P 25053–25056
Semionotus elegans: FMNH P 12751, UC 2060, UF 551; NMMNHS P-15501, P-15503, P-15504, P-15506, P-15536, P-15539, P-15546, P-15548, P-15554, P-15560, P-15563, P-15593, P-15595, P-15598, P-15600
Semionotus kanabensis: AMNH 8870 (Holotype), 8871
Semionotus fultus: FMNH UF 958
Semionotus micropterus: FMNH PF 13104, UC 2059, UF 37
Semionotus tenuiceps: FMNH P 12548, P 25049, PF 13105, PF 25050–25052, UF 431
Semionotus sp.: AMNH 5681–5683, 5686–5689, 5691–5696, 5698, 5699, 5702, 5703, 5705–5707, 18970–18972; FMNH PF 5732, PF 13106, PF 151567, UC 2006, UF 452–458, UF 957; NMMNHS P-4184, P-4185, P-17199, P-17254, P-17312, P-22055, P-22065, P-22066, P-22068, P-22069, P-22077, P-22087, P-22088, P-29043, P-32672, P-32673, P-32682, P-32683, P-32684, P-32687, P-32689, P-35423, P-35424, P-35429, P-35430, P-35431, P-44698; SGDS 886, 894, 1059, 1237, 1241, 1314; UMNH VP 19413–19418, VP 19422–19443
Tetragonolepis semicinctus: FMNH UF 36

SYSTEMATIC PALEONTOLOGY

OSTEICHTHYES Huxley, 1880
 NEOPTERYGII Regan, 1923
 GINGLYMODI Cope, 1872 (sensu Grande, 2010)
 SEMIONOTIFORMES Arambourg and Bertin, 1958
 (sensu López-Arbarello, 2012)
LOPHIONOTUS, gen. nov.

Type Species—*Lophionotus sanjuanensis*, gen. et sp. nov.
Etymology—Generic name is a combination of the Greek words 'Lophio' for 'ridge' and 'notus' for 'back.'

Diagnosis—As for the type and only species.

LOPHIONOTUS SANJUANENSIS, gen. et sp. nov.
 (Figs. 2–8)

Semionotus sp. Schaeffer, 1967:317, pls. 21–23.

Semionotus n. sp. Milner et al., 2006b:164, fig. 2.1.

Etymology—The specific name ‘*sanjuanensis*’ refers to San Juan County, Utah, where the specimens of this new species were recovered.

Holotype—AMNH 5680 (Figs. 2, 3).

Paratypes—AMNH 5679A, B (Figs. 4, 5); AMNH 5690 (Fig. 6); AMNH 5684 (Fig. 7).

Referred Specimens—UMNH VP 19419A, B; UMNH VP 19420A, B; UMNH VP 19421.

Type Locality—Lisbon Valley, San Juan County, Utah. AMNH specimens were collected in the area of Big Indian Wash (west of Big Indian Road), and near Big Indian Rock (east of Big Indian Road; Fig. 1A). UMNH specimens were collected from a locality named Walt’s Quarry on the east end of Little Valley within Lisbon Valley (Fig. 1A).

Type Horizon—Church Rock Member of the Chinle Formation (Upper Triassic: Norian).

Diagnosis—Medium-sized semionotiform fish; deep body with large postcranial hump; parietals (frontals) broad and short (approximately 2.5 times longer than wide); closed circumorbital ring; two supraorbitals; anterior supraorbital narrow and of equal greater length than posterior supraorbital; single, narrow anamestic suborbital; deep infraorbitals that expand below suborbital and contact the anterior ramus of the preoperculum; preoperculum with vertical, narrow dorsal process and short, broad, paddle-like ventral process; gape small; maxilla short and dentulous; styliform teeth on maxilla, premaxilla, and dentary; dense tuberculation on dorsal ridge scales in adult form; one to two rows of tubercles on the supraorbitals; tubercles on the extrascapulars; tubercles on the posttemporals; pterygial formula (scale count formula of Westoll, 1944):

$$\frac{D18 - 20}{P7A17 - 19C27} T31$$

Description

Specimens—The holotype (AMNH 5680A, B) is a nearly complete specimen of 84 mm SL (Figs. 2, 3). The specimen is in two parts and is best preserved in negative impression on the counterpart (AMNH 5680A; Figs. 2, 3). AMNH 5679A, B (SL 104 mm) is partially preserved in part and counterpart in right ventrolateral view with a complete skull, the majority of the body, and pectoral and pelvic fins preserved. The anal and dorsal fins of the specimen are partially preserved (although the distal parts are broken off and missing), and the caudal peduncle and tail are missing (Figs. 4, 5). AMNH 5690 (SL 80 mm) is a nearly complete specimen preserved in right dorsolateral view. Its skull is partially disarticulated and the flank is slightly distorted on the posterior end. The ventral portion of the body may be preserved under the matrix, but the caudal fin is likely not preserved (Fig. 6). AMNH 5684 (SL 75 mm) is a smaller, nearly complete specimen preserved in impression in left lateral view (Fig. 7). UMNH VP 19419 (field number LV05-78; SL 80 mm) is a partially preserved, articulated fish in part and counterpart on a slab with a *Hemicalypterus weiri* specimen. It is preserved in left lateral view, and is missing the caudal fin, pectoral fins, pelvic fins, and anal fin. UMNH VP 19420 (field number LV04-15; SL 84 mm) is a complete fish in right lateral view preserved in part and counterpart. The skull is partially disarticulated, the fins are poorly preserved, and the specimen is highly weathered. UMNH VP 19421 (field number LV05-131; SL 94 mm) is an articulated fish partially preserved in right lateral view, including portion of the flank, the dorsal fin, and posterior of skull.

Lophionotus sanjuanensis, gen. et sp. nov., is a deep-bodied fusiform fish that is distinguishable by its deeply curved dorsal border and gently curved ventral border. The standard length (SL) of AMNH 5680 (Fig. 2) is 84 mm. However, the largest specimen (AMNH 5679; Fig. 4) has a SL of 104 mm, indicating that

the species could reach a larger size than that of the holotype. The maximum body depth (MBD), measured from the crest of the dorsal margin to the ventral margin midway between the pectoral and pelvic fins, is 43 mm in the holotype. The skull is triangular, and deeper than long (Figs. 2–7). The average head length (HL) of the new species is 27 mm, approximately 32% of SL.

Skull Roof—The skull roof is preserved in six specimens. A pair of square parietals (frontals) and a pair of postparietals (parietals) are present (Figs. 2–6). The parietals constitute the bulk of the skull roof and are broad (at least two times longer than wide). They are widest at the posterior margin and constrict over the orbits. Anterior to the constriction the parietals broaden triangularly (the antorbital process), which then tapers anteriorly. Anteriorly, the parietals interdigitate with the ascending processes of the premaxillae (Figs. 4, 5). The suture between the parietals is smoothly digitate (Figs. 2, 3). The lateral borders of the parietals contact the supraorbital series and dermosphenotics, the posterior borders interdigitate with the postparietals, and the posterolateral corners of the parietals contact the anteromedial margins of the dermopterotics (Figs. 3, 5).

The postparietals are rectangular and are slightly longer than wide. The suture between the postparietals and the parietals, as well as the suture between the postparietals, is gently sinuous (Figs. 2–6). The postparietals articulate laterally with the medial borders of the dermopterotics (Figs. 3, 5). In the holotype (AMNH 5680A; Figs. 2, 3), a small triangular process at the anterolateral corner of the parietal extends between the posterolateral corner of the parietal and the medial border of the dermopterotic. The posterior border sutures with a single pair of extrascapulars (Figs. 3, 5).

The dermopterotic is an hourglass-shaped bone, longer than deep. It articulates anteriorly with the dermosphenotic, dorsally with the postparietal, posteriorly with the extrascapular, and ventrally with the suborbital, preoperculum, and operculum. It carries the temporal canal, as observed by two to three pores on the surface of AMNH 5679A (Fig. 5) and AMNH 5690 (Fig. 6).

Posterior to the postparietals is a pair of extrascapulars. The extrascapulars are trapezoidal in shape and deeper than long, and their anterior edges articulate with the posterior borders of the postparietals and dermopterotics (Figs. 2–5). Posterior to the extrascapulars are the posttemporals (Figs. 2–5), which are discussed below. The extrascapulars and posttemporals are covered to a varying degree by tubercles that continue onto the dorsal ridge scales.

In the nasal area, a single antorbital is preserved in the holotype (AMNH 5680A; Figs. 2, 3). It is a small, narrow bone, with a nearly 90° curve along its length. It is positioned posterior and dorsal to the premaxilla. The medial process of the antorbital lies perpendicular to the axis of the fish. The lateral process curves aborally and dorsad.

Circumorbital Series—*Lophionotus sanjuanensis* has a complete circumorbital ring. There are two anamestic supraorbitals above the orbit and adjacent to the lateral edge of the parietal (Figs. 2–6). They bear one to two linear rows of tubercles on their ventral sides, closest to the orbital cavity (Fig. 3). The anterior supraorbital is narrower and of equal or greater length than the posterior supraorbital, and articulates anterodorsally with the posteroventral margin of the antorbital process of the parietal. The dermosphenotic is triangular and forms the posterodorsal corner of the orbital ring. Its anterior margin articulates with the posterior supraorbital, and its posteroventral margin articulates with the infraorbital series. Posteriorly, it articulates with the dermopterotic, and dorsally it contacts the parietal. It carries the infraorbital canal from the infraorbitals to the dermopterotic. The dermosphenotic also bears a series of linear tubercles on its anteroventral surface, as seen in AMNH 5680A (Fig. 3).

There are five to seven infraorbitals constituting the posterior and ventral portions of the orbital ring (Figs. 2–5). Because

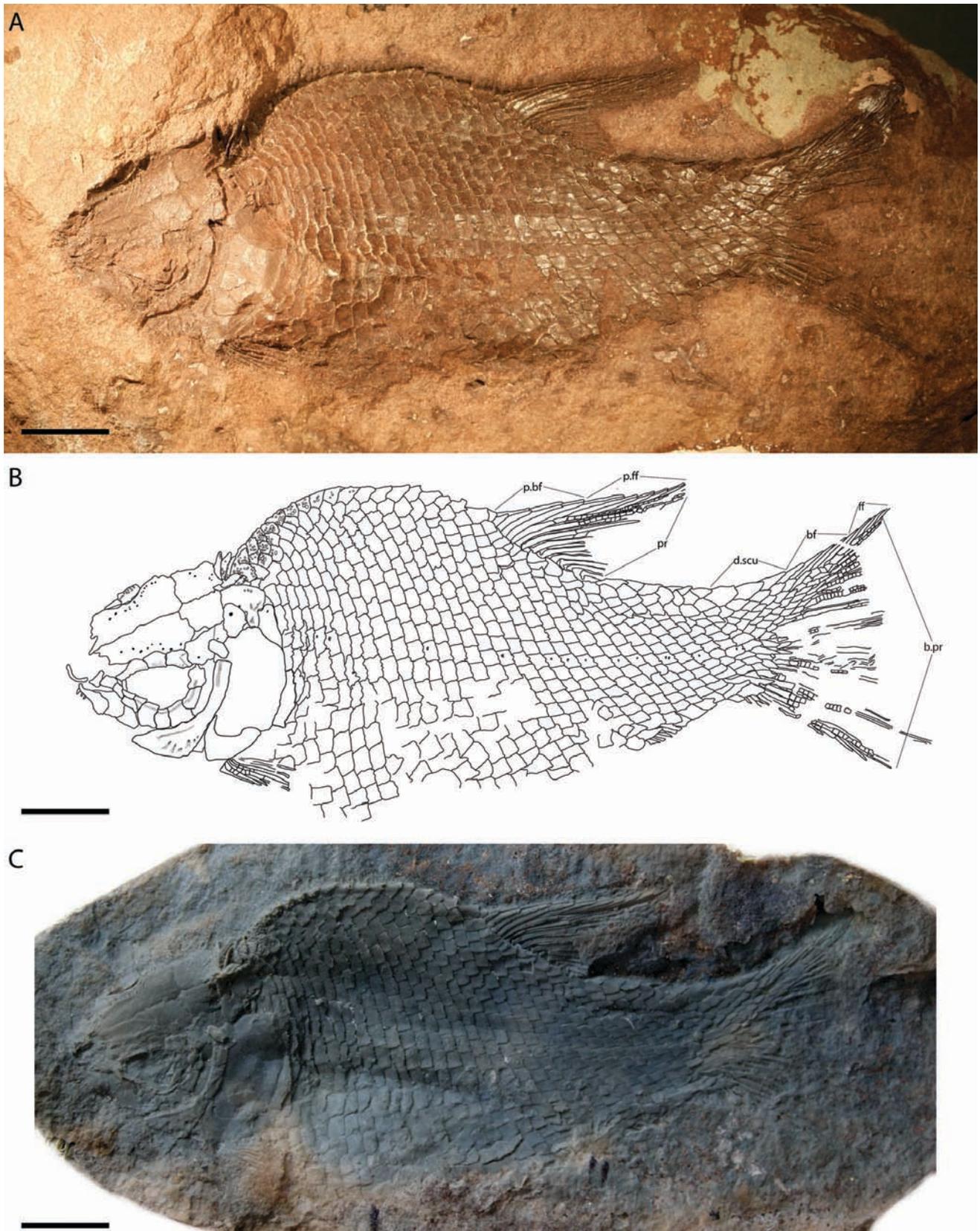


FIGURE 2. *Lophionotus sanjuanensis*, gen. et sp. nov., holotype (AMNH 5680A). **A**, overview of the specimen in left lateral view; **B**, line drawing of **A**; **C**, latex peel. Scale bars equal 1 cm. (Color figure available online.)

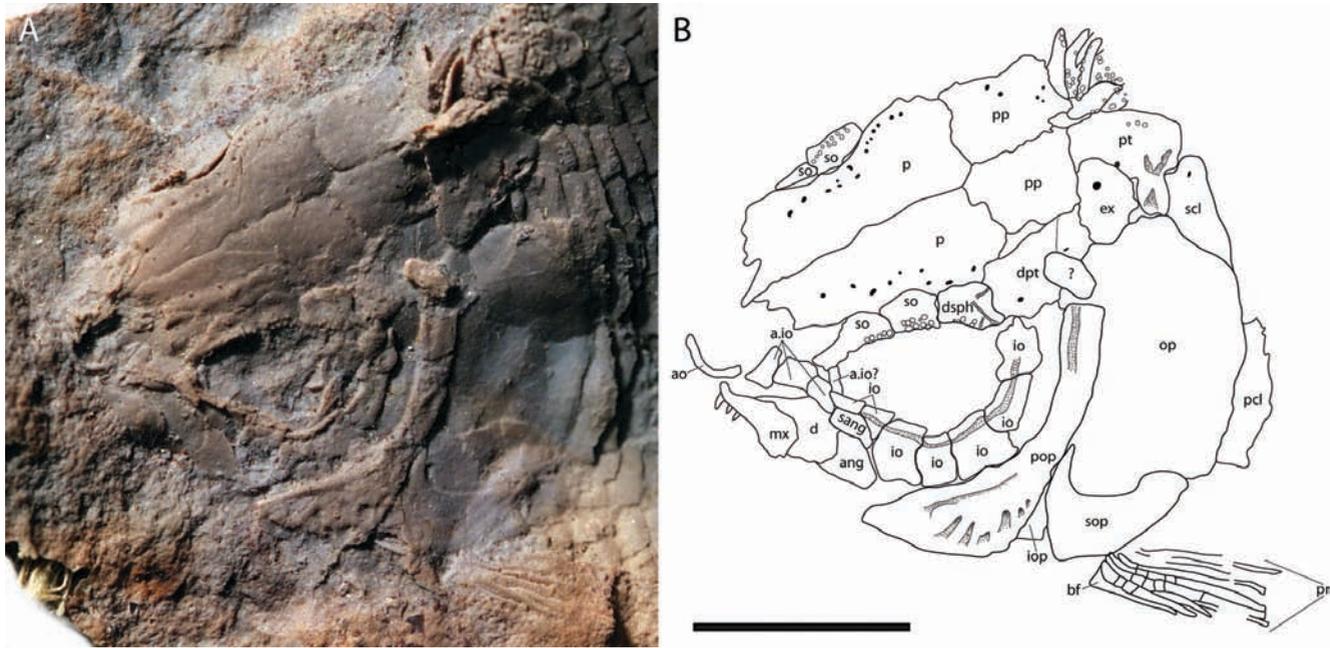


FIGURE 3. *Lophionotus sanjuanensis*, gen. et sp. nov. **A**, skull of holotype AMNH 5680A in left lateral view; **B**, line drawing of **A**. Scale bar equals 1 cm. (Color figure available online.)

establishing homology on the infraorbital bones is difficult to impossible (see Jollie, 1986), I will describe the infraorbitals by their position relative to the orbit, rather than assigning numbers to each, to avoid any problems of homology. There are two infraorbitals posterior to the orbit (seen in AMNH 5680A; Fig. 3), which are narrow and lie anterior to the suborbital (as seen in AMNH 5679; Figs. 4, 5). The infraorbitals ventral to the orbit, including its posteroventral corner, expand posteroventrally; they are at least one and a half times deeper than the posterior infraorbitals, and carry the infraorbital canal on the dorsal portion of the bone. The depth of the ventral infraorbitals fills the space below the suborbital between the circumorbital ring and the preoperculum (Figs. 3, 5).

The anterior infraorbitals (lacrimals or lachrymals) are poorly preserved in all specimens. In the holotype (AMNH 5680A; Fig. 3) and AMNH 5679 (Fig. 5), the anterior infraorbitals are present as a series of three to four small, narrow bones anterior to the orbital cavity. The anterior-most anterior infraorbital has a narrow, trapezoidal shape. The posterior-most anterior infraorbital appears to articulate with the supraorbital and infraorbital series.

Suborbital Bone—*L. sanjuanensis* has a single, anamestic suborbital. It lies anterior to the preoperculum (does not appear to overlap the preoperculum) and posterior to the posterior infraorbitals. It is deep and narrow (approximately two times deeper than wide). The suborbital is not preserved in the holotype, but is seen in AMNH 5679 (Figs. 4, 5), AMNH 5690 (Fig. 6), AMNH 5684 (Fig. 7), and UMNH VP 19419–19421.

Opercular Bones—*Lophionotus sanjuanensis* has the typical neopterygian arrangement and number of opercular bones. The preoperculum has a deep, vertical dorsal arm and a short, wide ventral process. The dorsal arm is more robust and rod-like than the ventral arm, which is robust on the anterior edge and thin on the posterior edge (Figs. 2–7). The preoperculum articulates with the deep infraorbital series anteroventrally and the suborbital anterodorsally. It articulates with the operculum, suboperculum, and interoperculum posteriorly. The dorsal edge of the preoperculum contacts the dermopterotic.

The operculum is the largest element of the skull (Figs. 2–7). It is rhomboidal in shape. The dorsal margin contacts the lateral edges of the extrascapular and posttemporal. It overlaps posteriorly the supracleithrum and dorsal postcleithrum. It also covers the dorsal part of the cleithrum (as seen in AMNH 5679B).

The suboperculum lies ventral to the operculum. Its dorsal border underlies the ventral edge of the operculum. It has a slightly convexly curved posteroventral margin. A narrow, vertical process of the suboperculum expands dorsally between the anterior margin of the operculum and the posterior margin of the preoperculum. This narrow process reaches less than halfway up the depth of the operculum and tapers to a point (Figs. 2–7).

The interoperculum lies anteroventral to the suboperculum and posterior to the preoperculum. It is a small, triangular bone (Figs. 2–7).

Jaws and Snout—The jaws of *Lophionotus sanjuanensis* are small. The lower jaw is best seen in AMNH 5679B, where both sides of the jaw are preserved as an impression. The dentary is broad and triangular, and tapers anteriorly, where a series of small, styliform teeth are preserved (at least 10–13 teeth are preserved in a single row in AMNH 5679B). The dentary articulates along its posterior edge with the angular.

The angular constitutes the posterior portion of the lower jaw. It is rectangular in shape, with a straight posterior border inclined anterodorsally. The anterior suture with the dentary is deeply sinuous (Fig. 3). The retroarticular is a small bone that articulates dorsally with the angular, and constitutes the posteroventral corner of the lower jaw. It is either not preserved or very poorly preserved in all of the specimens described here.

The surangular is best preserved in the holotype (AMNH 5680A; Fig. 3) and UMNH VP 19420. It is a small, dorsal process of the lower jaw, articulating along its ventral border with the dentary and angular.

The premaxilla of *Lophionotus sanjuanensis* is best preserved in AMNH 5679A (Figs. 4, 5), UMNH VP 19419B, and AMNH 5690 (Fig. 6). The premaxilla has a long, robust ascending process that is cupped inwards to accommodate the nasal cavity covered by the overlying antorbital (Fig. 3) and nasal bones;

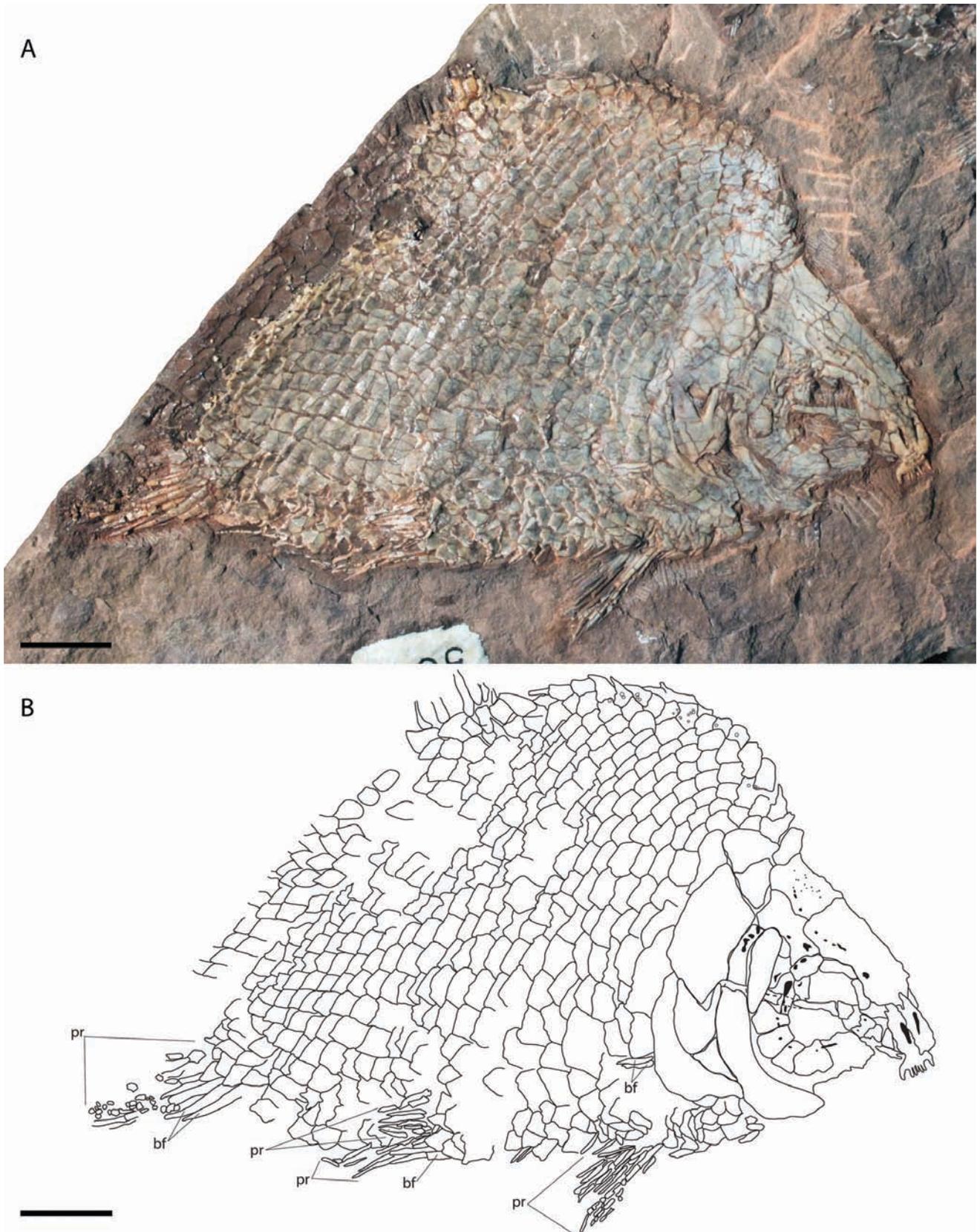


FIGURE 4. *Lophionotus sanjuanensis*, gen. et sp. nov., specimen AMNH 5679A. **A**, overview of the specimen in right lateral view; **B**, line drawing of **A**. Scale bars equal 1 cm. (Color figure available online.)

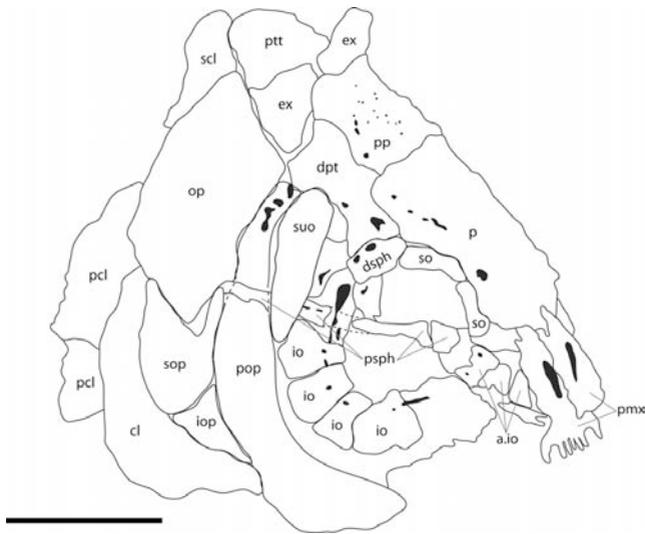


FIGURE 5. *Lophionotus sanjuanensis*, gen. et sp. nov. Line drawing of the skull of AMNH 5679A. Scale bar equals 1 cm.

however, the nasal bone is not preserved in any specimen. The posterior margin of the ascending process of the premaxilla is sutured to the anterior of the parietals on the skull roof (Figs. 4, 6A). The ascending process of each premaxilla bears a large opening (Figs. 4–6), which represents the foramen for the olfactory nerve. The median suture between the two ascending processes of the premaxillae is gently curved, with the dorsal right process extending slightly over the margin between the two bones. There are four to six stout, pointed teeth on each premaxilla.

The maxilla is relatively short, and ends posteriorly below the anterior infraorbitals (Figs. 2, 3). Each maxilla narrows anteriorly to a short, small process. Although lateral compression has flattened the maxilla in *Lophionotus sanjuanensis*, it is possible that, prior to fossilization, the anterior process of the maxilla curved medially to articulate in a hinge-like manner between the premaxilla, the dermopalatine, and the vomer, as seen in *Amia*. This is the condition seen in the three-dimensionally preserved specimens of *Semionotus kanabensis* Schaeffer and Dunkle (1950). The maxilla ends posteriorly with a vertical edge. The maxilla bears a single row of peg-like styliform teeth along the ventral margin. The supramaxilla may be present, as in other semionotiforms, but it is not visible in any specimens described here. Either it is not preserved or it is not present in *Lophionotus sanjuanensis*; this will require further investigation.

Neurocranial and Palatal Elements—The neurocranium is not visible in any of the specimens. The ectopterygoid is poorly preserved in AMNH 5690, and is a narrow and slightly curved bone that tapers anteriorly. Its lateral surface is smooth (Fig. 6). The parasphenoid can be seen in AMNH 5679 in the orbit medially as a long, slender, horizontal bone passing from the anterior of the skull posteriorly (Figs. 4, 5).

Hyoid Arch and Branchiostegal Rays—Most elements of the hyoid arch are not seen in any specimen. The ceratohyal is observed in AMNH 5679B. It lies at the ventral margin of the skull and is a long, narrow bone that constricts at the center of its length and widens at its anterior and posterior ends. The posterior end expands more than the anterior end, and then tapers slightly posteriorly. The posterior end has a flat posterior border. The complete series of branchiostegals is not preserved in any of the specimens, although two branchiostegals can be seen in AMNH 5679B.

Sensory Canals of the Head—The cephalic sensory canals are best preserved in AMNH 5680A (Figs. 2, 3), AMNH 5679A (Figs. 4, 5), and AMNH 5690 (Fig. 6). The supraorbital canal is seen as a distinct row of pores that extends on the lateral edge of the parietals, above the supraorbital bones (Figs. 3, 5, 6). It continues posteriorly onto the postparietals; a juncture between the supraorbital canal and the infraorbital and temporal canals is not directly observed in any specimen.

The preopercular sensory canal is best observed in AMNH 5680A (Figs. 2, 3) and AMNH 5690 (Fig. 6), where it is seen as a deep groove penetrating the length of the anterior margin of the preoperculum (Figs. 3, 6B). The preopercular bone bears a series of ventrally directed pores, which are the exits of branches of the preopercular sensory canal. The exits of the sensory canal branches are seen in the form of three to five openings along the paddle-like ventral process of the preoperculum (Figs. 3, 6, 7). The disarticulated preoperculum of AMNH 5690 shows the actual connection of the branches to the canal (Fig. 6). The preopercular canal exits anteriorly through the ventral process and continues as the mandibular canal in the angular and dentary. The mandibular canal is not well preserved in any of the specimens, and can be only be recognized by two visible pores in the mandible of UMNH VP 19419B.

The infraorbital canal is located in the infraorbital bones. In each infraorbital, the canal runs along the side closest to the orbit (i.e., in the dorsal portion of the infraorbitals below the orbit, and continues into the anterior portion of the infraorbitals posterior to the orbit. In AMNH 5680A (Figs. 2, 3), the canal is seen clearly as a groove running through the infraorbital series and continuing onto the dermosphenotic, where it connects to the temporal canal. The infraorbital canal is also preserved in the infraorbital bones of AMNH 5679A and recognizable by series of pores (Figs. 4, 5).

The temporal canal begins in the dermopterotic and continues posteriorly to the lateral borders of the extrascapular bone, posttemporal, and supracleithrum, where it connects with the lateral line canal system of the body and the occipital commissure (Figs. 4–6).

Pectoral Girdle—Only the postcleithra, supracleithrum, posttemporal, and cleithrum were observed in any of the specimens. The postcleithra sit posterior to the operculum, and articulate directly with the cleithrum anteriorly (seen in AMNH 5679A, B; Figs. 4, 5). The dorsal postcleithrum is narrow, tapering dorsad (Figs. 2–5, 7). The ventral postcleithrum is a rectangular element (Figs. 2, 4, 5, 7). The supracleithrum is dorsal to the dorsal postcleithrum and also lies posterodorsal to the operculum and cleithrum. It is deep and short anteroposteriorly, and tapers ventrad (Figs. 2–4, 5, 7).

The posttemporal bone is preserved in AMNH 5680 (Fig. 3) and AMNH 5679A (Fig. 5). The posttemporal is trapezoidal, tapering dorsally. In the holotype (AMNH 5680A; Fig. 3), the posttemporal has an anteroventral process somewhat similar to the posttemporal of *Scheenstia* described in López-Arbarello and Sferco (2011). This anteroventral process is robust and carries a series of pores, representing the temporal canal. The posterior margin articulates with the concave surface of the supracleithrum. The ventral tip of the anteroventral process of the posttemporal articulates with the dorsal margin of the operculum. Anteriorly, the posttemporal articulates with the extrascapular. In AMNH 5679A, this anteroventral process is not observed, and the trapezoidal posttemporal articulates with the supracleithrum directly.

The cleithrum is preserved in lateral aspect. It is a large, long, crescent-shaped bone, and maintains a nearly consistent width throughout its length, with the exception of the tapering ends (Figs. 4, 5, 7).

Fins—All fins of *Lophionotus sanjuanensis* are preceded by well-developed basal fulcra. Fringing fulcra originate on the first

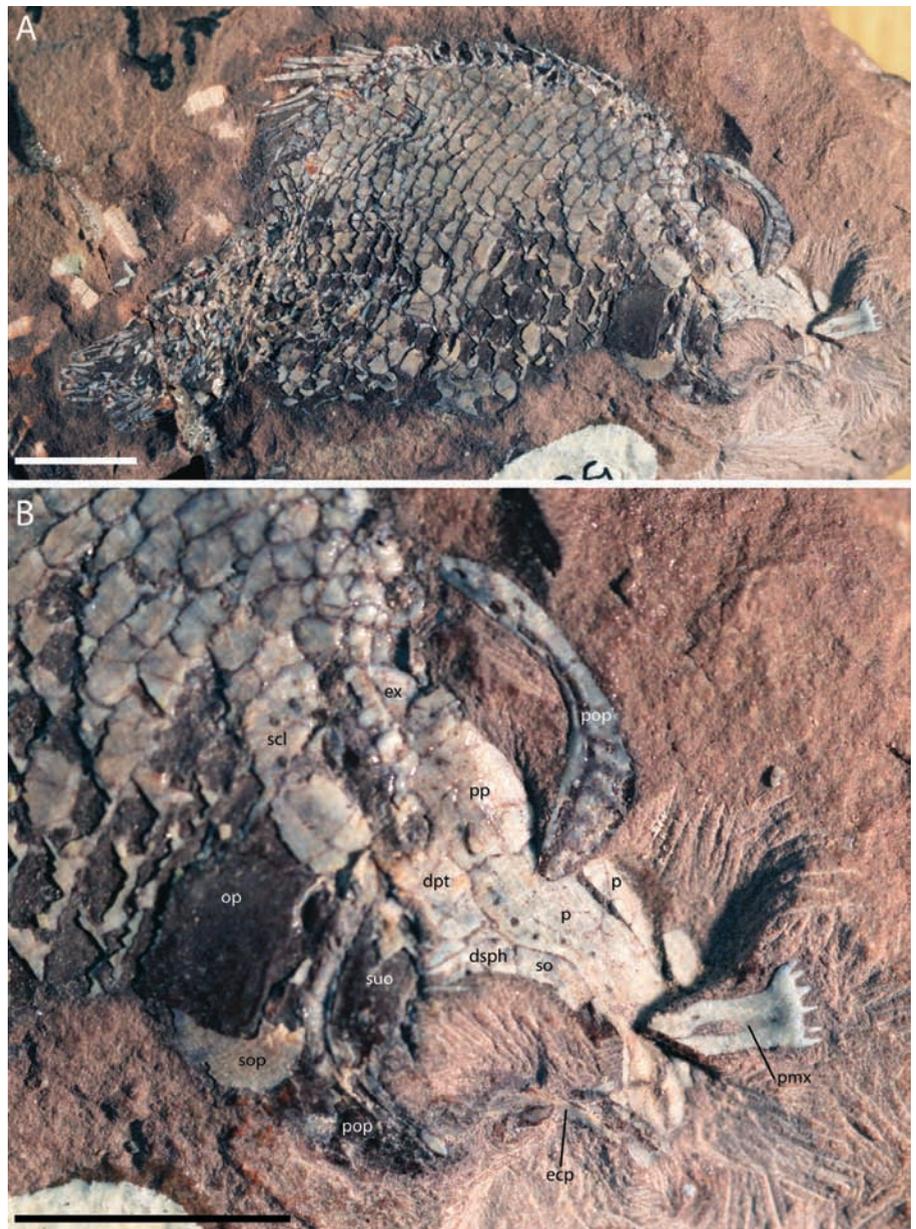


FIGURE 6. *Lophionotus sanjuanensis*, gen. et sp. nov. (AMNH 5690). **A**, complete specimen in right lateral view; **B**, close-up of skull region. Scale bars equal 1 cm. (Color figure available online.)

lepidotrichium. Due to incomplete preservation and/or missing portions of some specimens, the exact number of lepidotrichia is not known for any fin. The numbers provided here are estimates of the number of lepidotrichia for each fin.

The pectoral fins are preserved in the holotype (AMNH 5680A; Figs. 2, 3), AMNH 5679 (Fig. 4), and AMNH 5684 (Fig. 7). They are best preserved in AMNH 5679 (Fig. 4). In AMNH 5679B, both left and right pectoral fins are preserved. Each pectoral fin of this specimen has approximately nine lepidotrichia, with three fringing fulcra on the first lepidotrichium. The basal fulcra are partially preserved in AMNH 5679B and AMNH 5680A (Figs. 2, 3), and indicate that three basal fulcra were present in each specimen.

The pelvic fins are preserved in the holotype (AMNH 5680B) and AMNH 5679 (Fig. 4). The pelvic fin is a small fin that originates approximately mid-flank, on the ventral border of the fish. The pelvic fins of AMNH 5680B are poorly preserved, but display three basal fulcra and eight lepidotrichia. The proximal segment

of each lepidotrichium is approximately one-third of the total length of the ray and longer than the distal segments of each lepidotrichium. Both left and right pelvic fins are present in AMNH 5679 (Fig. 4), although they are not completely preserved.

The dorsal fin is preserved in the holotype (AMNH 5680; Fig. 2), AMNH 5679 (Fig. 4), AMNH 5684 (Fig. 7), and AMNH 5690 (Fig. 6); and in UMNH VP 19419–19421. The dorsal fin in AMNH 5680A (Fig. 2) originates approximately midway between the positions of the pelvic and anal fins. The fin originates beneath the highest point (the ‘crest’) of the postcranial hump (Figs. 2, 4, 6, 7). The dorsal ridge scales lead into the dorsal fin, but the paired basal fulcra are differentiated from the single dorsal ridge scales in their attenuated shape, which tapers distally. The dorsal fin has four to seven paired basal fulcra, and comprises approximately 14–16 lepidotrichia and five to seven fringing fulcra (Fig. 2).

The anal fin is preserved in the holotype (AMNH 5680B), AMNH 5679 (Fig. 4), and AMNH 5684 (Fig. 7). The anal

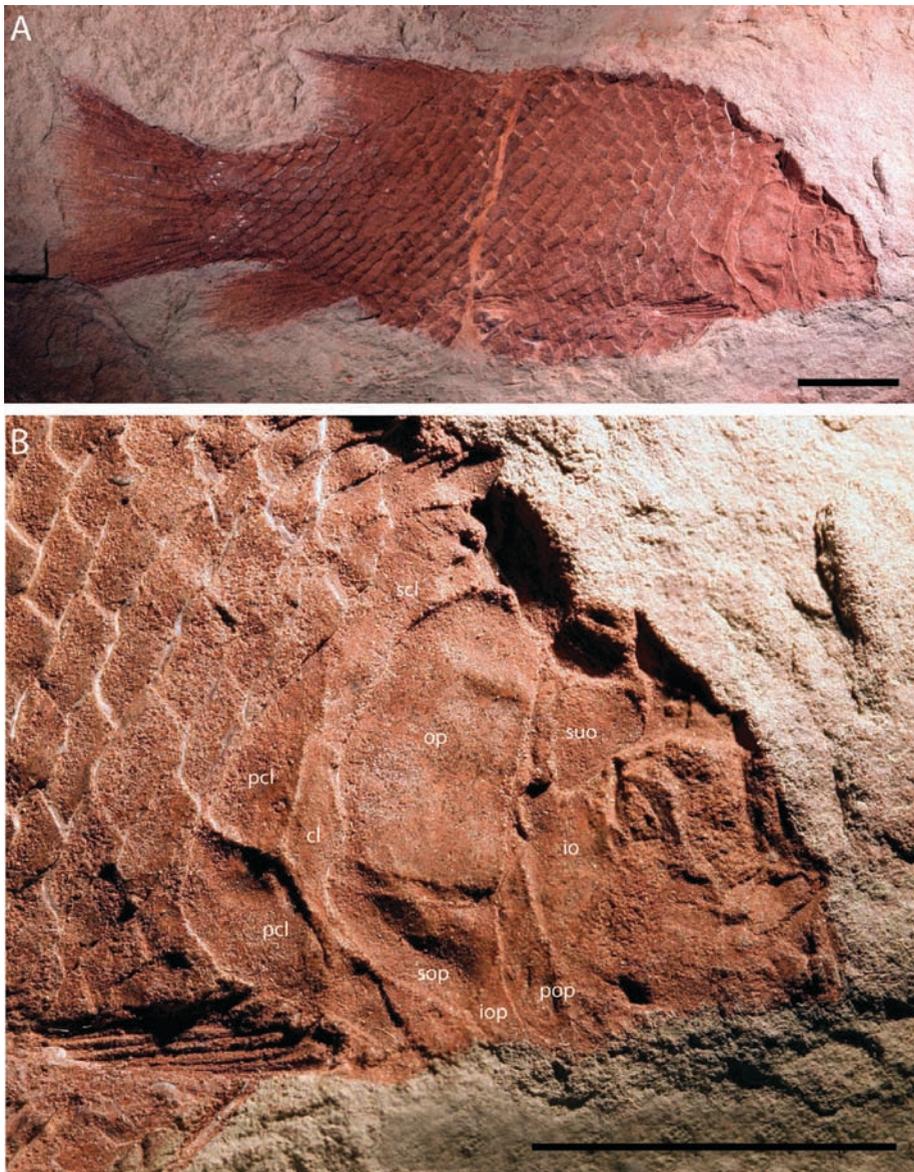


FIGURE 7. *Lophionotus sanjuanensis*, gen. et sp. nov., juvenile specimen (AMNH 5684). **A**, right lateral view; **B**, close-up of skull region. Scale bars equal 1 cm. (Color figure available online.)

fin is comparable in size to the dorsal fin and originates immediately behind its posterior border (Figs. 2, 4, 7). The anal fin comprises two to three basal fulcra and seven lepidotrichia. The first lepidotrichium supports approximately three to four fringing fulcra.

The caudal fin is preserved in the holotype (AMNH 5680A; Fig. 2), AMNH 5690 (Fig. 6), AMNH 5684 (Fig. 7), and UMNH VP 19420. The caudal fin is of the abbreviated heterocercal (hemiheterocercal) type. In the holotype (AMNH 5680A), the caudal fin is relatively complete, lacking only a few lepidotrichia (Fig. 2) that are not completely preserved. Almost all other specimens are lacking the caudal fin, due to incomplete preservation. The caudal fin is completely preserved in AMNH 5684 (Fig. 7), which is a juvenile (see below).

The dorsal lobe of the caudal fin has seven basal fulcra and at least four fringing fulcra (the entire extent of the fin is not preserved). The fulcra of the ventral lobe of the tail are incompletely preserved, but have at least three basal fulcra (Fig. 2).

The caudal fin rays are finely segmented distally (with the exception of the proximal segment of the ray, which is about six times as long as the following segments). Not all fin rays are pre-

served, and some are only preserved as fine impressions (Fig. 2B). In the dorsal lobe of the caudal fin at least seven rays are preserved, which branch posteriorly. The ventral lobe of the tail preserves at least eight rays (seen in AMNH 5680A and AMNH 5684; Figs. 2, 7).

Squamation—The body is covered by thick, rhombic scales. The pattern of squamation is best preserved in the holotype AMNH 5680A (Fig. 2), in which there are approximately 30 scales along the lateral line. The surface of the scales is smooth and unornamented, although the posterior borders of some scales have serrations, especially in the anterodorsal part of the flank in the area of the hump. This is well observed in AMNH 5680A (Fig. 2), AMNH 5679 (Fig. 4), and UMNH VP 19419.

Scales are quadrangular on the flank, and show the typical vertical peg-and-socket articulation of ganoid fish scales. The scales possess an anterodorsal process, anterior to the dorsal peg on the scale, similar to the scales of *Semionotus bergeri* or *Callipurbeckia minor* (López-Arbarelló 2012:fig. 15). There appears to be no anteroventral process on the scales. Flank scales are deeper anteriorly, and become less deep posteriorly (Figs. 2, 4, 6, 7). Scales of the caudal peduncle and caudal fin have a more

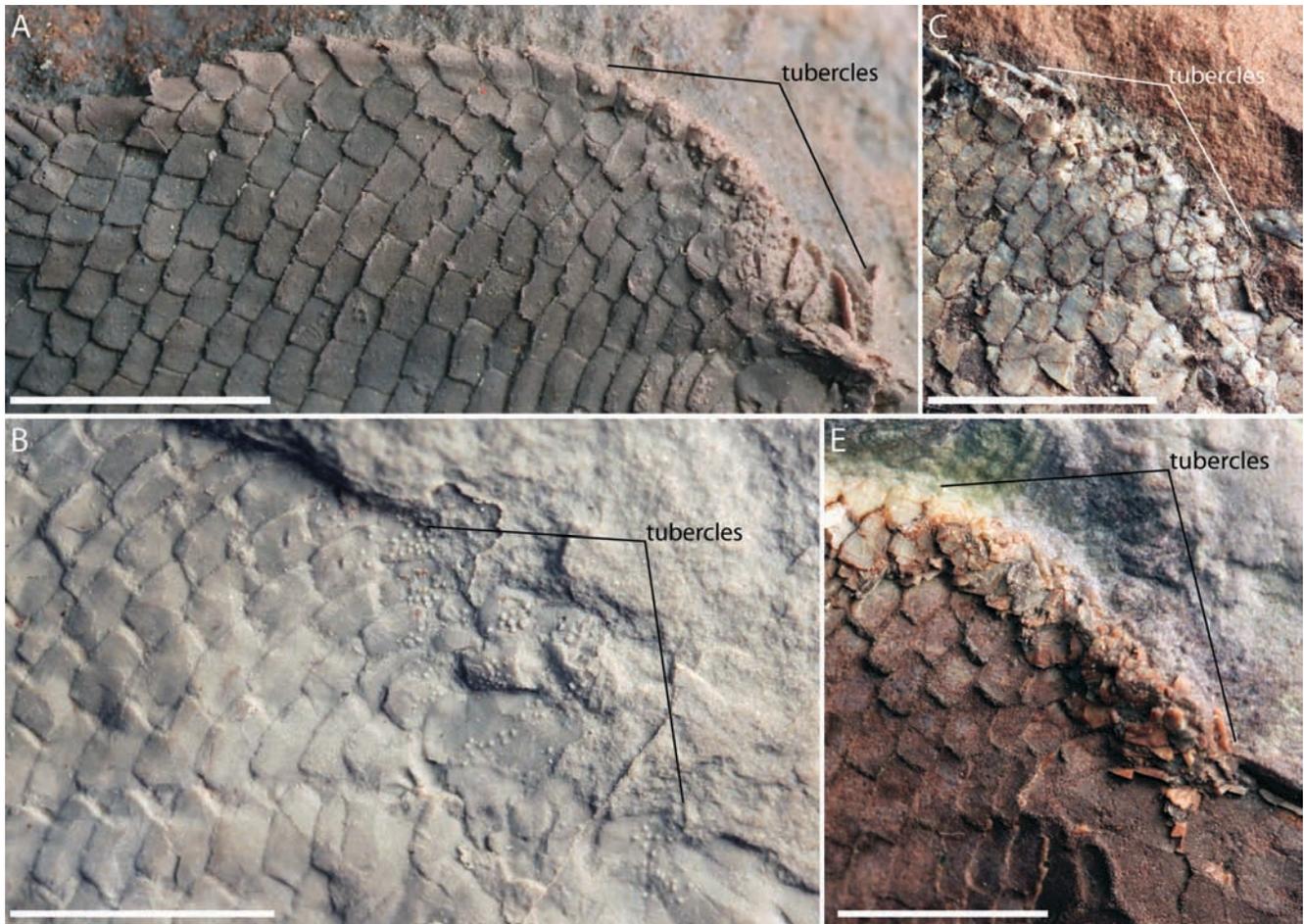


FIGURE 8. Dense tuberculation on the dorsal ridge scales of *Lophionotus sanjuanensis*, gen. et sp. nov. **A**, holotype (AMNH 5680A), peel; **B**, AMNH 5679B, peel; **C**, UMNH VP 19419; **D**, UMNH VP 19421. All images in right lateral view. Scale bars equal 1 cm. (Color figure available online.)

rhomboidal shape and lack a peg-and-socket articulation (Schultze, 1966).

Scales of the lateral line preserve small pits in the centers of the scales, and are best observed in holotype (AMNH 5680A; Fig. 2). These pits represent the pit organs (Schultze, 1966). The lateral line scales are notched posteriorly, allowing for the openings of the lateral line organ to the outside (Figs. 2, 4, 6).

Scales at the ventral margin are modified belly scales. They are larger, and their morphology ranges from nearly pentagonal to star-shaped. Some, especially those in the area of the pectoral fin, have slight serrations on the posterior border (as seen in AMNH 5679B).

The dorsal scales and scutes between the posterior border of the dorsal fin and the anterior border of the caudal fin are larger than the flank scales, and straddle the dorsal margin in a single row rather than being paired. This is best observed in the holotype (AMNH 5680A; Fig. 2) and in UMNH VP 19421.

The dorsal ridge scales are conspicuous. These scales form a single row along the dorsal margin, beginning at the back of the skull and continuing to the origin of the dorsal fin. Each dorsal ridge scale has a posteriorly directed process that originates on the posterodorsal corner of the scale and extends posteriad (Figs. 2, 4, 6, 7, 8). These processes are short and erect near the skull, and longer and more horizontally oriented posteriad (Fig. 8A). The dorsal ridge scales of *Lophionotus sanjuanensis*

are covered with tubercles that begin immediately posterior to the skull and continue posteriad (Fig. 8). These tubercles are also present on some flank scales adjacent to the dorsal ridge scales and posterior to the skull (Figs. 2, 4, 6, 8).

COMPARISONS AND DISCUSSION

Lophionotus sanjuanensis, gen. et sp. nov., was originally identified as *Semionotus* sp. by Schaeffer (1967). It shares many features with *Semionotus*, such as the closed circumorbital ring, conspicuous dorsal ridge scales, and single suborbital. However, these characters are found in several semionotiform taxa and are not exclusive to *Semionotus*, so attributing these specimens to *Semionotus* is problematic from these characters alone. In comparison with the type species for *Semionotus*, *S. bergeri* from the Upper Triassic of Germany, *L. sanjuanensis* differs in many respects. The skull bones of *Semionotus bergeri* are slender and delicate in comparison with the broad, robust snout and skull-roof bones of *L. sanjuanensis*. The preoperculum is a single ossification in *L. sanjuanensis*, whereas *S. bergeri* has two distinct ossifications in the preoperculum. The most obvious difference between *S. bergeri* and *L. sanjuanensis* is found in the infraorbital series. Species of *Semionotus*, such as *S. elegans* (Olsen and McCune, 1991:fig. 4) and *S. bergeri* (López-Arbarelo, 2008:fig. 4), have a narrow infraorbital series whose ventral

edge does not articulate with any other bones in the cheek. This arrangement leaves an 'open' cheek region, exposing endochondral elements such as the metapterygoid and endopterygoid. *L. sanjuanensis* has pronounced expanded infraorbitals that fill that 'open' cheek region.

An expanded infraorbital series, a feature of *Lophionotus sanjuanensis*, gen. et sp. nov., is also observed in other ginglymodian taxa, although the distinct morphology varies. A posteroventrally expanded infraorbital series occurs in *Araripelepidotes temnurus* (Santos, 1990), *Kyphosichthys grandei* (Xu and Wu, 2012), '*Lepidotes*' *microrhis* (Wenz, 2003), *Neosemionotus puntanus* (López-Arbarello and Codorníu, 2007), *Paralepidotus ornatus* (Tintori, 1996), *Sangiorgioichthys aldae* (Tintori and Lombardo, 2007), *Sangiorgioichthys sui* (López-Arbarello et al., 2011), and *Semiolepis bremanus* (Lombardo and Tintori, 2008). This character varies among these taxa in that the ventral margin of the infraorbital series may reach the anterior margin of the preoperculum, as in *L. sanjuanensis*, *Araripelepidotes temnurus*, '*Lepidotes*' *microrhis*, *Kyphosichthys grandei*, and *Semiolepis bremanus*, or it may not be fully expanded to the anterior margin of the preoperculum, as in *Neosemionotus puntanus* and *Paralepidotus ornatus*. In *Sangiorgioichthys aldae*, the expansion of the posteroventral infraorbital is extreme, but a variable mosaic of suborbital bones fills the gap between the infraorbital series and the preoperculum.

The expanded infraorbital is also observed in *Semionotus kanabensis* from the Lower Jurassic Moenave Formation of southwestern Utah (Schaeffer and Dunkle, 1950), which is the only described semionotid taxon from the western United States. *Lophionotus sanjuanensis* is larger and deeper-bodied, with a postcranial hump that *S. kanabensis* lacks (whereas *S. kanabensis* is a generally slender fish). *S. kanabensis* also lacks the dense tuberculation that is seen in almost all specimens of *L. sanjuanensis* (Fig. 8) on the supraorbitals, extrascapulae, posttemporals, and dorsal ridge scales. Overall, the skull of *L. sanjuanensis* has a much deeper and shorter appearance than that of *S. kanabensis*, due to the deeper body of the former. In *L. sanjuanensis*, the preoperculum has a vertically orientated dorsal process and shorter and broader ventral process than the respective portions of the preoperculum in *S. kanabensis*. The preoperculum of *S. kanabensis* has a longer, narrower ventral process, almost equal in length and width to the dorsal process. Further investigation into the morphology of *S. kanabensis* is needed to identify whether *S. kanabensis* belongs in the genus *Lophionotus* or *Semionotus*.

As with the expanded infraorbital series, presence of a deep-bodied morphology is common across extinct holostean lineages. A newly described, deep-bodied ginglymodian fish, *Kyphosichthys grandei* from the Middle Triassic in the Yunnan Province, China (Xu and Wu, 2012), shares many characters with *Lophionotus sanjuanensis*, such as the deep body, pronounced postcranial hump (though more extreme in *K. grandei*), deep skull, small gape, narrow infraorbitals posterior to the orbit, and a ventrally expanded infraorbital series ventral to the orbit (though much deeper in *K. grandei*). However, it is distinctly different morphologically from *Lophionotus sanjuanensis*. *K. grandei* has two suborbital bones and a nearly straight preoperculum, and lacks supraorbital bones (it has an open circumorbital ring). In general, the snout of *K. grandei* is more blunt than in *L. sanjuanensis*, and the overall body shape is distinct, with *K. grandei* possessing a body shape that is almost as deep as it is long as a result of its more pronounced dorsal hump.

Neosemionotus puntanus from the Lower Cretaceous Lagarcito Formation of Argentina (Bocchino, 1973; López-Arbarello and Codorníu, 2007) shares some similarities with *Lophionotus sanjuanensis*. It has expanded posteroventral infraorbitals, although they do not reach the preoperculum as in *L. sanjuanensis*. *Neosemionotus puntanus* has broader, relatively shorter parietals (about 2.5–3 times longer than wide), and robust ascending processes on the premaxillae. The maxilla in both

L. sanjuanensis and *N. puntanus* carries a single row of small styli-form teeth, but the maxilla in *N. puntanus* is longer, reaching below the orbit, rather than ending anterior to the orbit as in *L. sanjuanensis*. Both taxa have a closed circumorbital ring, but differ in the number and shape of the infraorbital and anterior infraorbital bones. Other differences between the two taxa include the number of suborbitals (three suborbitals in *N. puntanus* versus one single narrow suborbital in *L. sanjuanensis*); the shape of preoperculum (narrow ventral process in *N. puntanus* versus broad, paddle-like ventral process in *L. sanjuanensis*); presence of fringing fulcra on the dorsal and anal fins in *L. sanjuanensis* (absent in *N. puntanus*); and presence of a massive fifth basal fulcum in the dorsal fin of *N. puntanus* (whereas basal fulcra in *L. sanjuanensis* are of approximately equal width).

Another deep-bodied semionotid fish, *Semiolepis bremanus* from the Upper Triassic of Italy (Lombardo and Tintori, 2008), possesses a large dorsal hump similar to *Lophionotus sanjuanensis*. *Semiolepis bremanus* also possesses a single narrow suborbital and expanded infraorbital series. However, beyond these similarities, *Semiolepis bremanus* varies greatly from *L. sanjuanensis* in the following important features: number and organization of infraorbital and supraorbital bones (five supraorbital bones in *Semiolepis bremanus*); length of the snout; presence of long, delicate, slender parietals; the shape of the preoperculum (*Semiolepis bremanus* has a very narrow, long, delicate preoperculum); presence of seven extrascapulars; and patterns of squamation in the caudal fin.

Paralepidotus ornatus from the Upper Triassic of Italy (Tintori, 1996) is a deep-bodied (hump-backed) semionotiform possessing an expanded posteroventral infraorbital, although it does not reach the anterior edge of the preoperculum as in *Lophionotus*. *Paralepidotus ornatus* also possesses a single suborbital, but beyond this the two taxa share very little resemblance. For example, *P. ornatus* has crushing dentition; a mandible with a much more robust coronoid process; a stout anterior ceratohyal; an open circumorbital ring; long, more slender parietals; an edentulous maxilla; a conspicuous, elongate dorsal fin; and inconspicuous dorsal ridge scales (Tintori, 1996). However, Tintori (1996) describes ontogenetic stages of *P. ornatus* that are similar to what is observed in *L. sanjuanensis* (see below).

Lophionotus sanjuanensis shares very few characteristics with taxa belonging to a monophyletic clade in the newly erected family Callipurbeckiidae (López-Arbarello, 2012), including the genera *Tlayuamichin* from the Early Cretaceous of Mexico (López-Arbarello and Alvarado-Ortega, 2011), *Macrosemimimus* from the Late Jurassic of Germany, England, and France (Schröder et al., 2012), and *Callipurbeckia* ('*Lepidotes*' *minor*, '*Lepidotes*' *notopterus*, '*Lepidotes*' *tendaguruensis*) from the Late Jurassic of Germany, England, and Tanzania (Agassiz, 1833; Arratia and Schultze, 1999; López-Arbarello, 2012). López-Arbarello (2012) placed *Semiolepis* and *Paralepidotus* in this family, but they are stem taxa and are not part of the clade represented by *Macrosemimimus*, *Callipurbeckia*, and *Tlayuamichin*. This clade possesses small postparietals (length less than one-third the length of the parietals), whereas *L. sanjuanensis* has postparietals that are greater than one-third the length of the parietals. *L. sanjuanensis* does not possess an orbital sensory canal, 'open' cheek, long parietals and long snout, two or more suborbital bones, an open circumorbital ring, or tritoral teeth. Characteristics shared by *L. sanjuanensis* and this clade within Callipurbeckiidae include conspicuous dorsal ridge scales.

Sangiorgioichthys (Tintori and Lombardo, 2007; López-Arbarello et al., 2011) is placed within Semionotiformes incertae sedis (López-Arbarello, 2012). As discussed before, both *Sangiorgioichthys* and *Lophionotus* have expanded infraorbitals, as well as a closed circumorbital ring, and two supraorbitals with the anterior supraorbital being very elongate. Between the two species of *Sangiorgioichthys*, *Lophionotus sanjuanensis* more

superficially resembles *Sangiorgioichthys sui* from the Middle Triassic Guanling Formation of China (López-Arbarello et al., 2011), particularly in regards to the broad parietals; the parietal-postparietal size ratio; short snout; maxilla with a row of small, conical teeth; and presence of fine serrations on some flank scales. *L. sanjuanensis* bears very little resemblance to *Sangiorgioichthys aldae* from the Middle Triassic of Switzerland and Italy (Tintori and Lombardo, 2007), the latter having a long snout with long, slender parietals; slender jaw bones; and an exaggerated large infraorbital in the posteroventral corner; creating a very distinct disposition of bones in the skull. Both species of *Sangiorgioichthys* have a linear mosaic of suborbital bones, possessing anywhere from two to nine suborbitals in the region between the infraorbitals and the preoperculum, in comparison with the single, narrow suborbital of *L. sanjuanensis*.

Remarks on Juvenile Characters and Tuberculation

AMNH 5684 (Fig. 7) is the smallest of the specimens examined (SL 74 mm, MBD 24 mm) and is similar in size to *Semionotus kanabensis* (Schaeffer and Dunkle, 1950), but it is distinct from the latter species morphologically and shares diagnostic characters with *L. sanjuanensis*, gen. et sp. nov. Its body is not as deep as in the other specimens of *L. sanjuanensis*, but it clearly exhibits a postcranial hump. Although the postcranial hump is not as pronounced as in the adult form, it is distinctly different from the gently sloped dorsal margin of *S. kanabensis*. The skull of the juvenile specimen of *L. sanjuanensis* is deep and the preoperculum is vertical with a short, broad expansion on the ventral arm (Fig. 7B), which is also not observed in *S. kanabensis*. The infraorbitals are expanded and contact the anterior ramus of the preoperculum. AMNH 5684 lacks the dense tuberculation seen in the other specimens (Fig. 8), which are interpreted here as adult forms. This specimen is interpreted as a juvenile, and the absence of tuberculation is potentially a consequence of ontogeny.

Placement of *Lophionotus sanjuanensis*, gen. et sp. nov., in Semionotiformes

In following López-Arbarello's (2012) reclassification of Ginglymodi, *Lophionotus sanjuanensis* is placed in the order Semionotiformes based on possessing the following synapomorphies: conspicuous dorsal ridge scales, narrow infraorbital bones forming the posterior border of the orbit; one or two rows of elongated scales at the posteroventral margin of the body lobe of the tail; and small supraorbital bones. In regard to the family Callipurbeckiidae, *Lophionotus sanjuanensis* shares some characteristics with stem taxa *Semiolepis* and *Paralepidotus* (as discussed above), but it is likely *L. sanjuanensis* does not belong to the monophyletic clade of *Callipurbeckia*, *Tlayuamichin*, and *Macrosemimimus*. *Lophionotus sanjuanensis* also possesses many characteristics of Semionotidae, such as large basal fulcra in the dorsal and anal fins, and closed circumorbital ring. At present, *L. sanjuanensis* is placed as incertae sedis within Semionotiformes, until further taxonomic and phylogenetic work is conducted to investigate the evolutionary relationships of *L. sanjuanensis* to other semionotiform taxa.

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