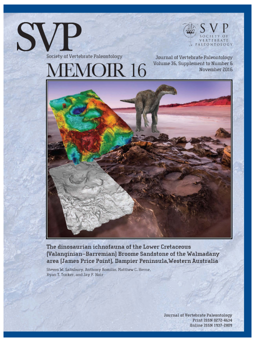

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# A new species of *Lasalichthys* (Actinopterygii, Redfieldiiformes) from the Upper Triassic Dockum Group of Howard County, Texas, with revisions to the genera *Lasalichthys* and *Synorichthys*

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ARTICLE

# A NEW SPECIES OF *LASALICHTHYS* (ACTINOPTERYGII, REDFIELDIIFORMES) FROM THE UPPER TRIASSIC DOCKUM GROUP OF HOWARD COUNTY, TEXAS, WITH REVISIONS TO THE GENERA *LASALICHTHYS* AND *SYNORICHTHYS*

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ABSTRACT—A new species of redfieldiiform fishes, *Lasalichthys otischalkensis*, sp. nov., is described based on new, three-dimensionally preserved specimens from the Upper Triassic Dockum Group of Howard County, western Texas. *Lasalichthys otischalkensis* is diagnosed by a combination of unique traits found in the skull, including shape of maxilla, shape of preoperculum and associated cheek bones, pattern and articulation of bones in the snout, and patterns of sensory line canals in the dermal skull bones. Specimens of this new species display novel patterns in the sensory line canals of the skull that have never been observed in any other redfieldiiform. Examination and comparison of specimens of *Lasalichthys* and *Synorichthys* from the Upper Triassic Chinle Formation and Dockum Group indicates that these taxa are only distinguishable at the species level, and *Synorichthys* is placed into synonymy with *Lasalichthys*, based on comparison of diagnostic morphological characters. *Lasalichthys otischalkensis* represents one of the oldest redfieldiiform taxa in North America.

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## INTRODUCTION

Actinopterygii (ray-finned fishes), the most abundant group of vertebrates on the planet today (e.g., Nelson et al., 2016), have a long and complex history (e.g., Long, 2010), with notable examples such as *Cheirolepis* Agassiz, 1835, representing one of the oldest (middle to late Devonian) unequivocally actinopterygian, articulated specimens (e.g., Arratia and Cloutier, 1996; Giles et al., 2015). During the early Mesozoic, several radiations of stem actinopterygian fishes were present globally in freshwater and marine deposits. One such lineage is the order Redfieldiiformes (ca. 17 genera and 23 species), with representatives recovered globally in Triassic and Early Jurassic deposits in Africa (e.g., Brough, 1931; Haughton, 1934; Lehman et al., 1959; Hutchinson, 1973, 1978; Martin, 1980), Australia (e.g., Wade, 1935; Hutchinson, 1973), Europe (e.g., Lombardo, 2013); North America (e.g., Schaeffer, 1967; Schaeffer and McDonald, 1978), and South America (e.g., López-Arbarello, 2004; Gouric-Cavalli et al., 2017).

Redfieldiiforms possessed fusiform bodies, thick enameled (ganoin) scales covering the entire body, and a vertebral column extending into the dorsal lobe of the caudal fin, although the extension of the body lobe is reduced compared with other stem actinopterygians, in which the body lobe reaches the tip (heterocercal tail). Redfieldiiforms possessed fixed maxillae (maxillae firmly attached to the preopercula), with a more upright jaw suspensorium that is hypothesized to allow for more efficient feeding by allowing the gape to expand further without compromising breathing capacity (Schaeffer and Rosen, 1961). These characteristics are observed in many generalized stem actinopterygians of the Paleozoic and the Mesozoic. However, more indicative of Redfieldiifomes, the snouts of redfieldiiforms were prominent, and many species of redfieldiiforms possessed heavily tuberculated or denticulated rostral bones extending anterior to the gape. The skull profile created by a prominent snout and almost subterminal gape has been hypothesized by previous authors (e.g., Hutchinson, 1973; Schaeffer, 1984) to contribute to a possible benthic feeding lifestyle for redfieldiiforms, with the tuberculated snout possibly supporting a prominent fleshy lip.

In North America, the order Redfieldiiformes is represented by specimens from the Triassic–Jurassic Newark Supergroup of the eastern coast (e.g., *Dictyopyge macrurus*, *Redfieldius gracilis*, *Synorichthys* sp.; Schaeffer and Mangus, 1970; Schaeffer and McDonald, 1978), from the Upper Triassic Chinle Formation in Arizona, Colorado, and Utah, and from the Dockum Group of eastern New Mexico and western Texas (Schaeffer, 1967).

Within the Chinle Formation, Schaeffer (1967) described three species (*Cionichthys dunklei*, *Lasalichthys hillsi*, and *Synorichthys stewarti*) from sites in Lisbon Valley, San Juan County, Utah, and contemporaneous sites in nearby Dolores Formation (= Chinle Formation) of Colorado (Fig. 1). Schaeffer (1967) also described several additional new bony fishes from the Chinle and Dolores formations, including a new coelacanth, *Chinlea sorenseni*, the actinopterygians *Tanaocrossus kalliokoskii* and *Turseodus dolorensis*, and the deep-bodied neopterygian *Hemicalypterus weiri*. The relationship of *Tanaocrossus kalliokoskii* to other actinopterygians has varied in recent years, with placement within Perleidiformes (e.g., Milner et al., 2008) or Scanilepiformes (e.g., Xu and Gao,

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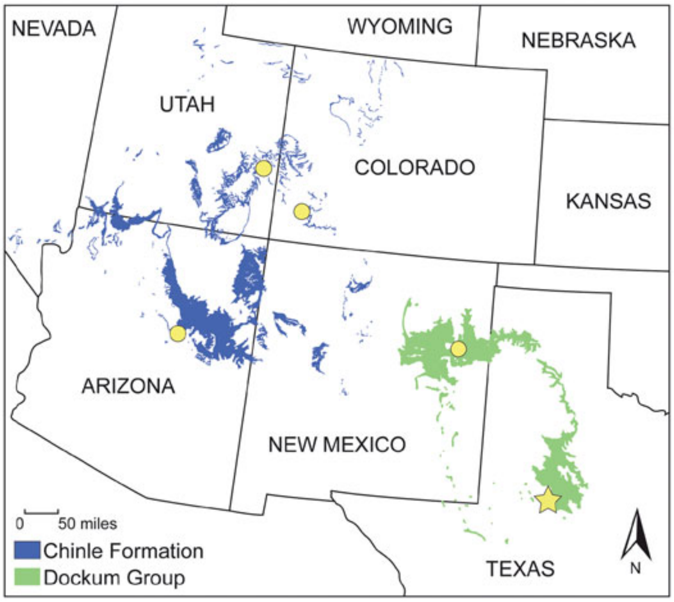

FIGURE 1. Map of the Upper Triassic geologic outcrops in southwestern U.S.A. (modified from Stewart et al., 1972; Lehman, 1994; and Martz, 2008). Circles indicate sites that produce articulated fish fossils; star indicates the Otis Chalk fish locality where the specimens described herein were recovered.

2011; Xu et al., 2014); Scanilepiformes was recently recovered as a stem polypterid (e.g., Giles et al., 2017). The deep-bodied fish *Hemicalypterus* was redescribed by Gibson (2015, 2016) and placed within the order Dapediiformes. Gibson (2013a, 2013b) additionally described two new species of holostean semionotid fishes from the Chinle Formation of Lisbon Valley: *Lophionotus chinleana* and *L. sanjuanensis.*

The highly productive Dockum Group of western Texas has yielded fossil vertebrates from the Late Triassic, beginning with discoveries made by Cope at the end of the 19th century (Cope, 1892). A large push to collect tetrapods in the 1920s was undertaken by E. C. Case from the University of Michigan and J. W. Stovall from the University of Oklahoma; their recovery efforts provided fossilized remains of large tetrapods, particularly phytosaurs (e.g., Case, 1929; Lucas et al., 1993). A considerable collecting effort was conducted under the Works Progress Administration (WPA) from 1939 to 1941, resulting in the discovery and descriptions of significant Triassic taxa, including the aetosaur *Typothorax meadei* (Sawin, 1947) and the metoposaur *Buettneria* '*howardensis*' (= *perfecta*) (Sawin, 1945, 1947; Hunt and Lucas, 1990; Hunt, 1993). Gregory (1945) also described the reptile *Trilophosaurus* based on a significant amount of material collected from sites near Otis Chalk, Howard County, Texas.

Collection of identifiable fossil fishes in this horizon has, however, been lower compared with the collection of tetrapods, due to the predominantly fragmentary nature of fishes in the Dockum Group (Schaeffer, 1967). Lungfishes were first reported in the Dockum Group by Case (1921), who described a new species of *Ceratodus*, *C. dorotheae.* Warthin (1928) described a second species, *C. crosbiensis*, based on a tooth plate recovered in 1925 by E. C. Case and others from the University of Michigan. Martin (1979) erected a new genus, *Arganodus*, and later placed the *C. dorotheae* from the Dockum Group in this new genus (Martin, 1982), with subsequent workers following the new combination *Arganodus dorotheae* (e.g., Schultze, 1992; Hunt, 1994; Heckert, 2004). Murry (1986) synonymized *Ceratodus crosbiensis* with *Arganodus dorotheae*, noting that '*C. crosbiensis*' likely represented an ontogenetic stage for *A. dorotheae.*

Ray-finned fishes were first recognized in the Dockum Group near the quarry producing *Trilophosaurus* fossils (Gregory, 1945). In 1954, Bobb Schaeffer of the American Museum of Natural History and F. Earl Green of Texas Technological College (now University) discovered a locality near Otis Chalk, a ghost town in Howard County, Texas (Fig. 1), that represented an isolated pond deposit replete with dissociated fish remains, in particular ganoid scales, and isolated dermal elements (Schaeffer, 1967). They returned to the site in 1963, at which time they collected a complete, partially compressed redfieldiiform skull that Schaeffer (1967) described and named as *Cionichthys greeni.*

Among the other fish remains recovered from the Dockum Group, Schaeffer (1967) described and figured three partial skulls collected from the Otis Chalk locality in the Dockum Group (Schaeffer, 1967:fig. 16, pl. 30). These specimens, collectively given the specimen number AMNH 5662, were not identified or diagnosed by Schaeffer, but he noted the similarity of the jaws of these specimens to those of perleidiform fishes, such as *Meidiichthys* Brough, 1931. The general morphology of dermal bones of the skulls of AMNH 5662 shares some similarities with that of perleidiforms from Bekker's Kraal, Upper Triassic of South Africa (e.g., Hutchinson, 1973), such as a maxilla with a low postorbital expansion that articulates with an embayment along the anteroventral margin of a broad, vertically inclined preoperculum; a preoperculum that possesses a shallow process that extends anteriad between the maxilla and an infraorbital series; and four small, quadrangular, anamestic suborbitals that separate the preoperculum from the infraorbital series (Schaeffer, 1967:fig. 16, pl. 30.3).

Schaeffer (1967) also noted a partial redfieldiiform skull preserved in three dimensions. Although well preserved and figured (Schaeffer, 1967:pl. 19), the specimen was never described due to its incompleteness. Schaeffer (1967) reported being unable to find any additional material as well preserved as the partial redfieldiiform skull, and the specimen was deposited at what is now the Texas Memorial Museum as TMM 31098-44. Additional partial skull and skull fragments, body fragments, and scales were attributed to *Lasalichthys* or *Synorichthys* (AMNH 5722), although the similarity between the two genera and lack of diagnostic characters prevented a specific diagnosis.

Additional fish fossil specimens from the Schaeffer fish quarry near Otis Chalk were collected by New Mexico Museum of Natural History and Science in 1990 (Lucas et al., 1993); this material was left unprepared and unsorted for over two decades. A thorough search through this bulk material by the author in February 2016 yielded high-quality, three-dimensionally preserved specimens of a redfieldiiform fish that display conspicuous similarities to the partial, three-dimensional redfieldiiform skull originally mentioned by Schaeffer (1967). The material available represents a new species of redfieldiiform and warrants a thorough morphological description and diagnosis that is provided herein.

The purpose of this study is to describe a new species of redfieldiiform based on the specimens collected from the Dockum Group, Howard County, Texas. Based on examination of these specimens, which have been previously attributed to both *Lasalichthys* and *Synorichthys*, it is clear that these two genera are largely identical in their anatomy and morphology and that their separation at the generic level is unjustifiable, and *Synorichthys* is placed into synonymy with *Lasalichthys*; a new diagnosis for the genus *Lasalichthys* is provided. The new species of *Lasalichthys* from the Dockum Group, along with *Cionichthys greeni*, is the oldest representative of

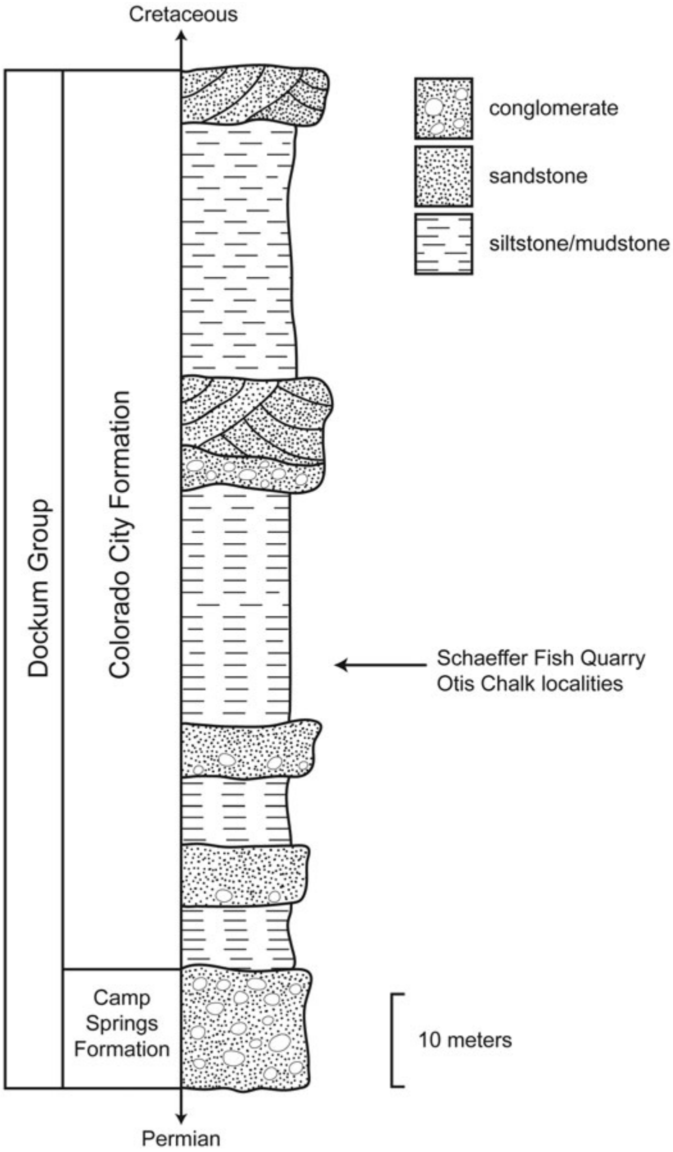

FIGURE 2. Generalized stratigraphic column for the Dockum Group in Howard County, Texas (modified after Lucas et al., 1993; and Sarigül, 2016). Schaeffer's fish quarry is indicated.

Redfieldiiformes in North America. In addition, the new species of *Lasalichthys* described herein possesses novel morphological features that are not described in other redfieldiiform fishes.

**Institutional Abbreviations**—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **DMNH**, Denver Museum of Nature and Science, Denver, Colorado, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, Natural History Museum, London, U.K.; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **NMNH**, Smithsonian National Museum of Natural History, Washington, D.C., U.S.A.; **TMM**, Texas Memorial Museum, Austin, Texas, U.S.A.; **UMNH**, Natural History Museum of Utah, Salt Lake City, Utah, U.S.A.

## GEOLOGIC SETTING

The Dockum Group has been the subject of several geologic, stratigraphic, and paleontological studies concerning its age, correlation to the Chinle Formation, and relation to 'faunachrons' used by certain authors to distinguish biostratigraphic distribution and age of organisms. Much of this discussion is outside of the scope of this study; however, a summary of the generally agreed-upon geology and stratigraphy regarding the fish fossil sites near Otis Chalk, Howard County, Texas, is provided here.

Most authors have considered the Otis Chalk localities to be the stratigraphically lowest in the Chinle/Dockum basins (A. Heckert, pers. comm.). The stratigraphic nomenclature has been highly contested (e.g., Lehman, 1994; Lucas et al., 1994), but more recent studies (Heckert, 2004; Martz, 2008) agree that these deposits fall within the Colorado City Formation (Carnian) of the Dockum Group.

The Otis Chalk fish fossil localities were recognized by Lucas et al. (1993) as belonging within an 80-m-thick bed of reddish brown to grayish red smectitic mudstone, intercalated with pale orange to yellowish brown cross-bedded, subarkosic sandstone (Fig. 2). This section of strata was identified originally as the Iatan Member of the Dockum Group by Lucas et al. (1993) and Lucas and Anderson (1994), although this name was preoccupied. Lucas et al. (1994) emended this by renaming it the Colorado City Member. Lucas et al. (1994) refers to the Dockum Formation rather than Group, and so the Colorado City unit was established initially as a member of the Dockum Formation. Because most researchers in this area follow the stratigraphic nomenclature of the Dockum Group, most recent authors (e.g., Sarigül, 2016; Heckert et al., 2017) refer to the Colorado City Formation rather than as a member.

The Otis Chalk fossil sites occur between two sandstone beds in the lower half of the Colorado City Formation (Fig. 2). Lehman (1994) and Lehman and Chatterjee (2005) have argued that the Colorado City Formation is correlative with the Cooper Canyon Formation. Martz (2008) outlined and discussed the many correlative problems argued in Lucas and Anderson (1993a, 1993b, 1994), Lehman (1994), Lucas et al. (1994), and others.

Specimens described in this study are from a site known colloquially as the 'Schaeffer Fish Quarry' (Murry, 1987; Lucas et al., 1993). It represents a small, isolated, dark red siltstone lens filled with dissociated fish remains (Schaeffer, 1967). Inferring from the taphonomy of the site, the deposit likely represents an ephemeral pond or small lake that filled during a previous advance of water on a floodplain and then dried up during a period of aridity, as is indicated by the dark red, oxidized color of the deposits (Lehman and Chatterjee, 2005). The fishes that lived in this ephemeral pond died during a period of desiccation and were dissociated and macerated (Schaeffer, 1967), possibly by scavengers, indicated by high irregularity of bones and little or no association between fragments (Elder and Smith, 1988).

## MATERIALS AND METHODS

The specimens described herein are the result of the collecting trips described above. Specimens collected in the 1950s by Bobb Schaeffer and crew were deposited at the American Museum of Natural History (AMNH) and the Texas Memorial Museum (TMM). Specimens from the New Mexico Museum of Natural History and Science (NMMNH) were collected by Spencer Lucas and crew in 1990 from private land (locality L-3099), with permission of the landowner. Three bags of unprepared material were given a single catalog number

(NMMNH P-25801); these bags of material contain hundreds of isolated skull and body fragments, scales, and partially articulated sections of fishes; they were sorted by the author in February of 2016. Preparation of a subsample of this material has yielded a new species of redfieldiiform that is described herein. Fossils were exposed from the hard, fine sandstone matrix with careful use of a pneumatic microjack tool (PaleoTools Microjack 1) and sharpened carbine needles. Minimal adhesive was used as needed (Paleobond penetrant stabilizer). Specimens were prepared and examined under normal light using Leica and Bausch and Lomb stereomicroscopes with varying resolution power. Photographs of each specimen were taken under normal lighting with a Canon digital SLR camera (partial mode) with an APS-C sensor with macro-style lenses (65 and 100 mm). Specimens were also examined and photographed under fluorescence using a Leica stereomicroscope fitted with GFP-LP and GFP3 filters. Due to the three-dimensional nature of the material, photography under both normal and fluorescent lighting conditions was conducted using a z-stacking method, where photographs were taken at multiple focal planes and merged using a stacking software program (HeliconFocus); the end results are fully focused images of the specimens. Drawings of the specimens were done using a digital drawing tablet over high-resolution photographs.

### Bone Terminology

In order to maintain consistency and transparency regarding bone identification and interpretation, bone terminology will follow the osteological terminology outlined by Schultze (2008) and Wiley (2008), which is based on comprehensive examinations of anatomical structures and homologies of bony fishes. Snout bone terminology follows Mickle (2015). In instances where traditional terminology deviates from the above studies, the traditional terminology will be indicated in parentheses the first time the bone is described. This will aid in interpreting homologous structures for future studies involving this material. See Appendix 1 for full list of materials examined.

**Anatomical Abbreviations**—**ang**, angular bone; **d**, dentary; **dhy**, dermohyal; **dpt**, dermopterotic; **dsph**, dermosphenotic; **enp**, entopterygoid; **ex**, extrascapular bone; **io**, infraorbital; **mx**, maxilla; **n**, nasal; **op**, operculum; **p**, parietal (frontal); **pmx-ao**, premaxillo-antorbital; **pop**, preoperculum; **pp**, postparietal (parietal); **pro**, postrostral; **pscl**, presupracleithrum; **ptt**, posttemporal; **ro**, rostral bone; **sc**, scale; **scl**, supracleithrum; **so**, supraorbital (adnasal); **sop**, suboperculum; **suo**, suborbital.

## SYSTEMATIC PALEONTOLOGY

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Cope, 1871

REDFIELDIIFORMES Berg, 1940 (sensu Schaeffer, 1984)

REDFIELDIIDAE Berg, 1940 (sensu Hutchinson, 1973)

Genus *LASALICHTHYS* Schaeffer, 1967

**Type Species**—*Lasalichthys hillsi* Schaeffer, 1967.

**Revised Generic Diagnosis**—*Lasalichthys* is diagnosed among Redfieldiidae by the unique combination of the following characters: medium-sized redfieldiid fishes; dermal skull bones covered in prominent rugose ridges and tubercles; snout bones heavily denticulated; nasal bones meet at midline; postrostral either reduced and separated from rostral, or absent; parietals (frontals) slender with smooth medial articulation; one pair of postparietals (parietals), triangular in shape with pointed anterolateral processes; single pair of large extrascapular bones that taper mediad; 'T'-shaped premaxillo-antorbitals forming anterior of orbital rim; large, triangular- to trapezoid-shaped single supraorbitals with reduced participation in orbital rims; dermosphenotics large and broad and form posterodorsal rim of the orbit; dermopterotics large and broad with broad pointed dorsomedial process; maxillae and mandibles short, not extending anteriad below snout; single row of pores in nasals and mandibles; duplicated, parallel rows of pores along cranial sensory canals of parietals, postparietals, extrascapula, posterior infraorbitals, and preopercula; and supraorbital canals extend posteriad through entire postparietals to join supratemporal commissure in extrascapular bones.

*LASALICHTHYS STEWARTI*, comb. nov.

(Schaeffer, 1967)

(Fig. 3)

*Synorichthys stewarti*: Schaeffer, 1967:312, figs. 10, 11; pls. 17, 18 (original description).

*Synorichthys* Schaeffer: Schaeffer, 1984:4, figs. 2O, 3O.

**Horizon and Locality**—Upper Triassic Chinle Formation, San Juan County, Utah, U.S.A.

**Revised Specific Diagnosis**—*Lasalichthys stewarti*, comb. nov., is distinguished from other species of *Lasalichthys* by the unique combination of the following characters: postrostral bone fully absent; nasal bones enlarged, rectangular, and meet completely along midline; triangular supraorbital (adnasal) bones abut dermosphenotics and participate minimally in orbital rim; single row of denticles along anteroventral margin of dermosphenotic along orbital rim; suborbitals do not articulate ventrally with dorsal margins of posteroventral infraorbitals; preopercula vertical ventral process and broad, triangular-shaped dorsal process; presupracleithra absent; sensory canal pores of skull present as single row or double rows only; preopercular canals present as single row of pores that terminate in middle of the preopercula and do not continue through suborbitals; and scales on belly and posterior part of body narrow, about one-half depth of flank scales.

**Remarks**—Little morphological evidence separates the genera *Lasalichthys* and *Synorichthys*, as was done by Schaeffer (1967). Even Schaeffer (1967) noted that the only difference separating *Lasalichthys* from *Synorichthys* is the presence/absence of the postrostral bone. Most redfieldiiforms have a large postrostral that articulates with the rostral bone and separates the nasal bones medially. *Lasalichthys* possesses a postrostral, but it is highly reduced and remote from the rostral, allowing enlarged nasal bones to meet at the midline. The postrostral is absent in *Synorichthys stewarti*, as well as in an unnamed species of '*Synorichthys*,' '*S.*' sp., from the Lockatong Formation, Newark Supergroup of New Jersey (Schaeffer and Mangus, 1970). In instances where specimens are missing the snout, it is difficult to determine if the specimen represents *Lasalichthys hillsi* or *Synorichthys stewarti*.

Other features seemed to distinguish *Lasalichthys* and *Synorichthys*, but upon closer examination they lend support to the synonomy of the genera. In *L. hillsi*, the preopercular canal traverses the entire length of the preoperculum and continues through the ventral portion of the suborbital, whereas in *L. stewarti* and '*S.*' sp. the preopercular canal terminates mid-bone.

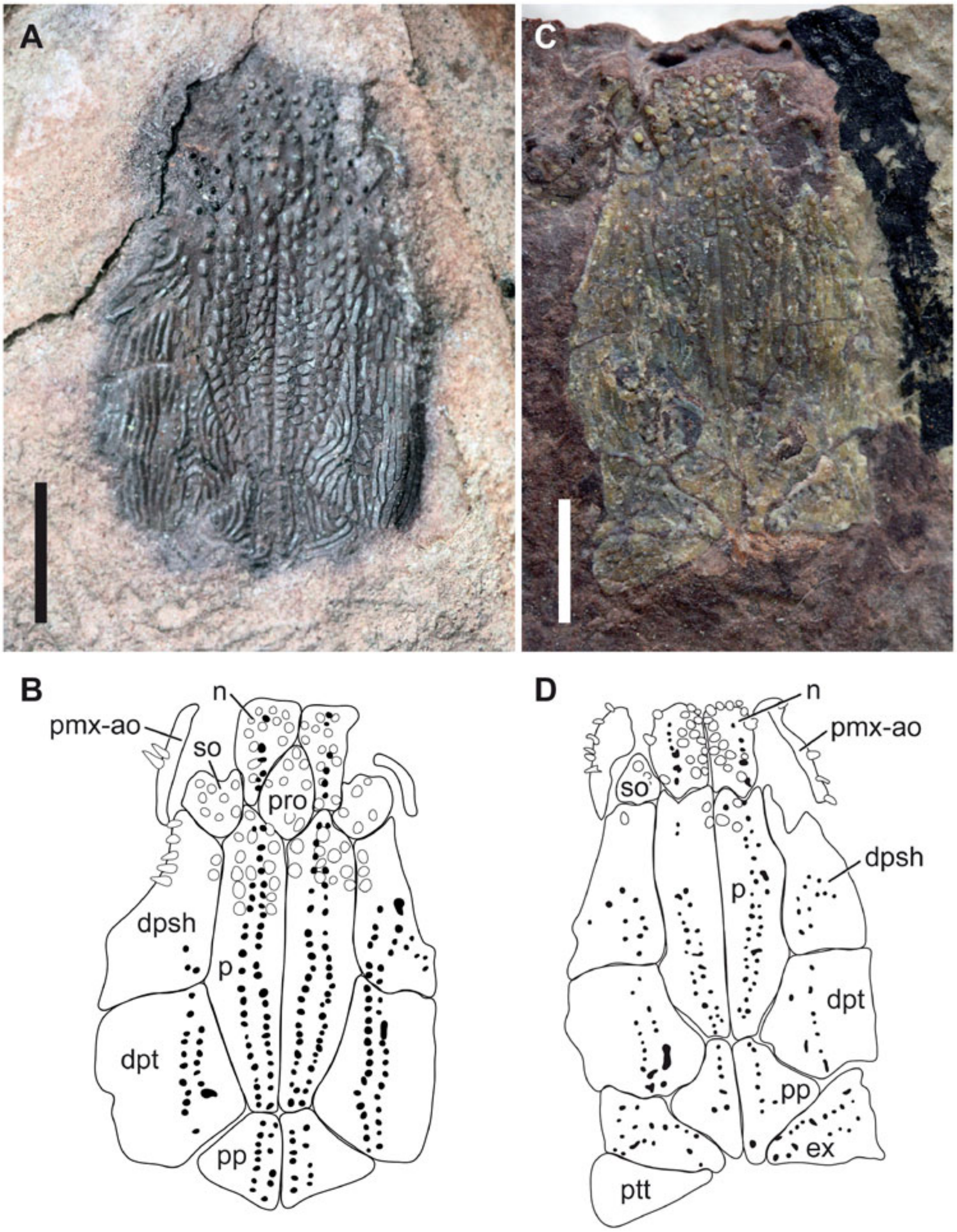

FIGURE 3. Skull-roof bones of *Lasalichthys hillsi* Schaeffer, 1967, and *Lasalichthys stewartii*, comb. nov. **A**, holotype of *L. hillsi*, AMNH 5636, in dorsal view. **B**, drawing interpretation of **A**. **C**, *Lasalichthys stewarti*, AMNH 5677, skull, in dorsal view. **D**, drawing interpretation of **C**. Scale bars equal 5 mm.

The presupracleithrum is present in '*S.*' sp. and the new species described below but is absent in *L. hillsi* and *L. stewarti.*

Comparison of specimens of these taxa indicates that, aside from the postrostral condition, presupracleithrum condition, and preopercular canal path, the taxa share almost all other synapomorphic characters aside from independent variation in bone size in individuals (Fig. 3). These features are important to note because the new species described below possesses a mosaic of characters found in *L. hillsi*, *L. stewarti*, and '*S.*' sp. Given the mosaic of derived characters between these taxa and the near-indistinguishable nature of all other features, the differences between the taxa are more indicative of species differences, not generic differences. The presence of a reduced postrostral is thus likely autapomorphic for *Lasalichthys hillsi* and is not enough evidence to separate it at the generic level from *Synorichthys*. The termination of the preopercular canal in the mid-preoperculum is shared between *L. stewarti* and '*S.*' sp.; the continuation of the preopercular canal through the suborbital is shared between *L. hillsi* and the new species described below. The presence of the presupracleithrum is shared between the new species described herein and '*S.*' sp., whereas the absence of the presupracleithrum is shared between *L. hillsi* and *L. stewarti*.

Because the genera *Lasalichthys* and *Synorichthys* were established at the same genus-group level at the same time in the same publication (Schaeffer, 1967), *Lasalichthys* is selected as the senior synonym over *Synorichthys*, with the type species being *Lasalichthys hillsi* (Fig. 3A, B). *Synorichthys stewarti* will thus be recognized under the new combination *Lasalichthys stewarti*, comb. nov.

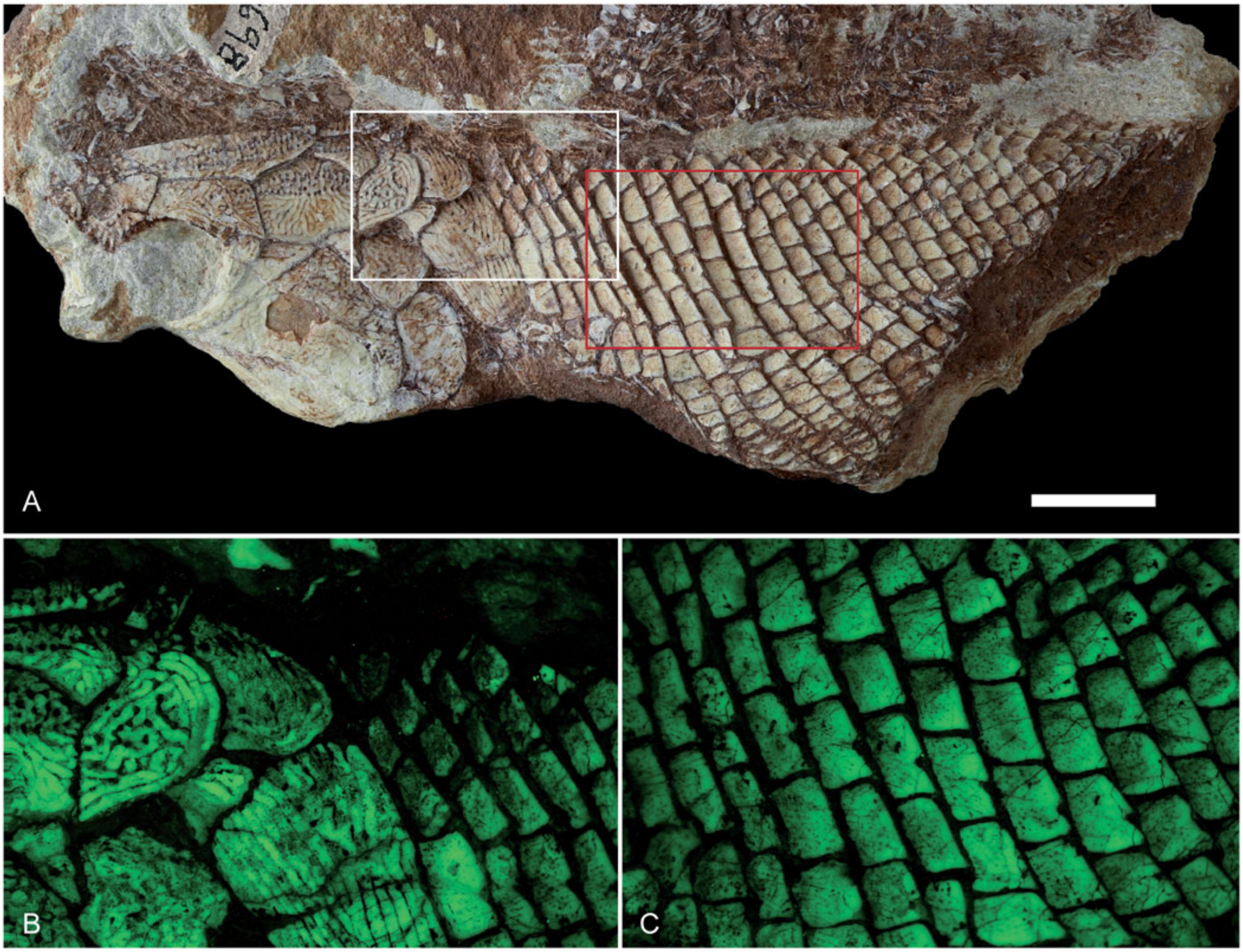

FIGURE 4. *Lasalichthys otischalkensis*, sp. nov., NMMNH P-44698, holotype. **A**, skull and anterior portion of body, preserved in left lateral view under normal lighting. **B**, close-up of posterior portion of skull and anterodorsal flank scales as indicated by white inset box in **A**, fluorescent lighting. **C**, close-up of midflank scales as indicated by red inset box in **A**, fluorescent lighting. Scale bar equals 5 mm.

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### *LASALICHTHYS OTISCHALKENSIS*, sp. nov.

(Figs. 4–8)

cf. *Lasalichthys* or *Synorichthys*: Schaeffer, 1967:315, pl. 19.
*Lasalichthys*/*Synorichthys*: Murry, 1986:115.
*Lasalichthys* or *Synorichthys*: Murry, 1987:76.
*Lasalichthys hillsi*: Lucas et al., 1993:243.
*Sinorichthys* [sic] *stewarti*: Lucas et al., 1993:243.

**Holotype**—NMMNH P-44698, a nearly complete skull and partial body preserved in left lateral aspect, lacking all fins and posterior portion of body (Figs. 4, 5).

**Paratypes**—TMM 31098-44 (Schaeffer, 1967:pl. 19), a partial skull, three-dimensionally preserved, displaying part of the dermal skull roof and neurocranial elements; NMMNH P-78661 (Figs. 6–7), a partially complete, three-dimensionally preserved skull, missing posterior-most bones of the skull and various dermal elements

**Referred Specimens**—NMMNH P-78662, body fragment with flank scales and pelvic fin (Fig. 8); NMMNH P-78663, isolated cleithrum preserved in left lateral view (Fig. 8); NMMNH P-78664, partial cleithrum preserved in left lateral view (Fig. 8); NMMNH P-78665, partial cleithrum preserved in right lateral view (Fig. 8); NMMNH P-78666, partial cleithrum preserved in right lateral view (Fig. 8); NMMNH P-78667, complete supracleithrum preserved in left lateral view (Fig. 8); NMMNH P-78668, partial cleithrum preserved in left lateral view (Fig. 8); NMMNH P-78669, partial supracleithrum preserved in right lateral view (Fig. 8); NMMNH P-78670, partial supracleithrum preserved in left lateral view (Fig. 8); NMMNH P-78671, complete left dermopterotic preserved in dorsal view (Fig. 8).

**Diagnosis**—The species is diagnosed from other members of this genus by the following unique combination of characters: absence of postrostral bone; nasal bones quadrangular and fully articulating along the midline; supraorbital (adnasal) bone not participating in the orbital rim; posterodorsal margin of premaxillo-antorbital articulating with anterior margin of the dermosphenotic; dermosphenotic lacking denticles along orbital rim; suborbital articulating ventrally with dorsal margin of infraorbital at posteroventral corner of orbital rim; preoperculum more anteriorly inclined than other species of *Lasalichthys*; concave embayment on posteroventral margin of dermopterotic for articulation with dermohyal; small knob-like process on posteroventral corner of maxilla; large teeth on distal end of dentary; multiple parallel rows (2–4 parallel rows of pores) along parietal (frontal), postparietal (parietal), dermosphenotic, dermopterotic, extrascapular, preoperculum, and supracleithrum; preopercular sensory canal extending anteriorly along entire length of preoperculum and through suborbital; supraorbital canal passing through entire length of postparietal bone and likely connecting to supratemporal commissure; and presence of single presupracleithrum; scales lacking ornamentation.

**Etymology**—The specific epithet refers to Otis Chalk, a ghost town located in Howard County, Texas, near where the new specimens described below were recovered.

## Description

**Body Form and Measurements**—The most complete specimen of *Lasalichthys otischalkensis* is the holotype NMMNH P-44698 (Figs. 4A, 5), which preserves most of the skull and a large portion of the flank in lateral view (Fig. 4A). This specimen indicates that *L. otischalkensis* is a medium- to large-sized redfieldiid fish with a fusiform body shape. The complete body is unknown, so it is difficult to estimate the total length of *L. otischalkensis*.

The skull of *L. otischalkensis* is heavily ornamented with rugose ridges (Figs. 4A, 5–8) and dense tuberculation on the snout and jaws (Figs. 4A, 5–7).

**Snout and Skull Roof**—*Lasalichthys otischalkensis* possesses a large (Fig. 6A–C), heavily tuberculated rostral bone that separates the paired premaxillo-antorbital bones (Figs. 5, 6). The rostral bone forms the anteroventral margin of the narial opening. Posteriorly, it articulates with the anterior margins of both paired nasals Figs. 4, 5).

The front of the skull roof contains a pair of nasals that are roughly quadrangular in shape (Figs. 5, 6). They meet at the midline, where the postrostral is absent (Fig. 6G–I). The nasals are tuberculated (Figs. 5, 6). Anteriorly, they meet the median rostral bone, and ventrally they articulate with the supraorbital (adnasal). Posteriorly, they meet the parietals (frontals). The nasal comprises the dorsal margin of the single narial opening of *L. otischalkensis* (Figs. 5, 6F).

Redfieldiiform fishes possess a single external narial opening that likely represents the posterior narial opening due to the position of the narial opening relative to the nasal bone and supraorbital canal (Schaeffer, 1984). There is no evidence of a second, separate anterior narial opening on *L. otischalkensis*, nor is there any evidence of a narial notch along the orbital margin in the premaxillo-antorbital. The posterior margin of the premaxillo-antorbital bone along the orbital rim in *L. otischalkensis* is visible in NMMNH P-78661 (Fig. 6A–F) and clearly shows a smooth margin along the orbital cavity that lacks any notch for a second external narial opening. It is possible that *L. otischalkensis*, like other redfieldiiform fishes, may have had a condition similar to what is observed in *Polypterus*, where a single narial opening possesses two separate, soft tissue tubes that separate incurrent and excurrent flow of water (Pehrson, 1947).

A single supraorbital (adnasal) is present on each side of the skull. The supraorbital is anamestic, triangular to trapezoidal in shape, and occupies the posterodorsal margin of the narial opening (Figs. 5, 6). The ventral margin articulates with the premaxillo-antorbital bone (Fig. 5). Posteriorly, it articulates with the anterior margin of the dermosphenotic (Figs. 5, 6). The supraorbital does not appear to be a part of the orbital rim, as is best observed in the holotype NMMNH P-44698 (Fig. 5). The medial margin of the supraorbital articulates with the nasal and the parietal.

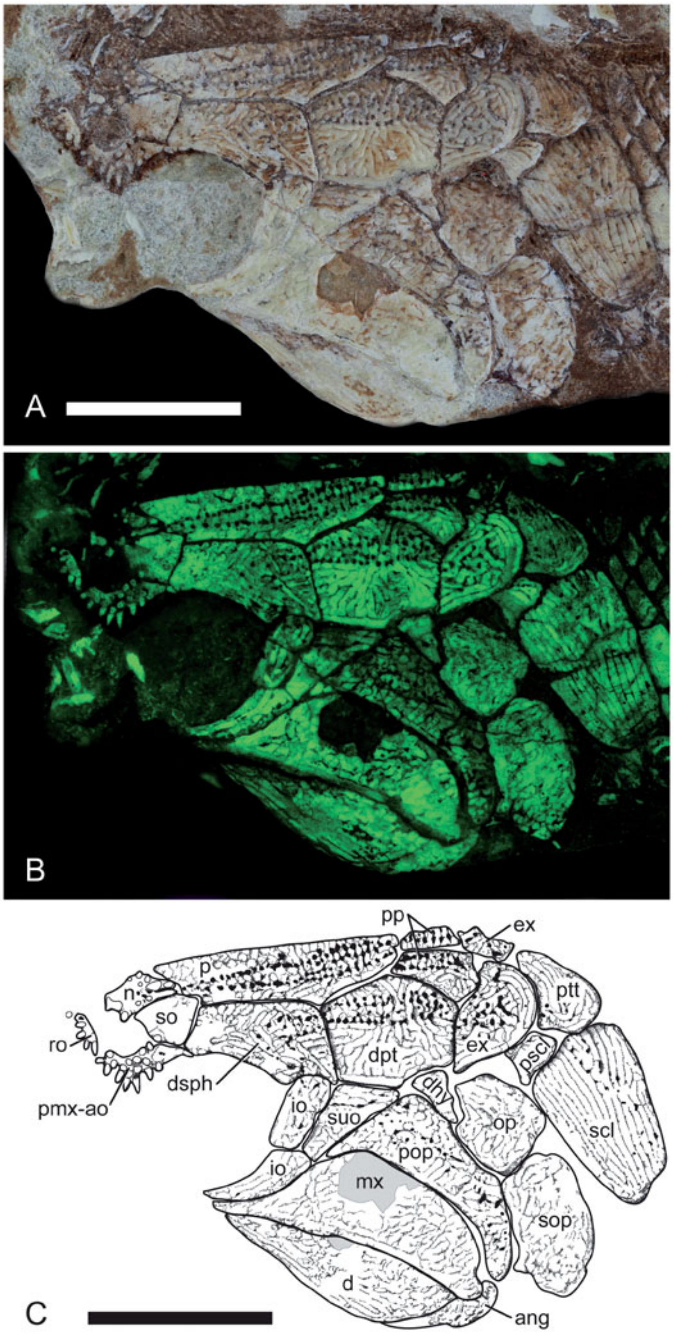

FIGURE 5. *Lasalichthys otischalkensis*, sp. nov., NMMNH P-44698, holotype, skull. **A**, normal lighting. **B**, fluorescence. **C**, line drawing interpretation with bones labeled. Both scale bars equal 5 mm.

A pair of parietals occupy the bulk of the skull roof, and each parietal is long, nearly four times longer than wide (Figs. 5, 6). The midline between the parietals is linear and meets along the whole length of the bones. Each parietal tapers mediad anteriorly and posteriorly, articulating with the nasal anteriorly at a slightly oblique angle. Each parietal turns slightly posteriad as it articulates laterally with the medial margin of the supraorbital. The angle of the lateral margin of the parietal then becomes more posteriad as it articulates with the dermosphenotic. The parietal flares out slightly at its widest point and then is slightly directed medially as it articulates with the medial margin of the dermopterotic. As the

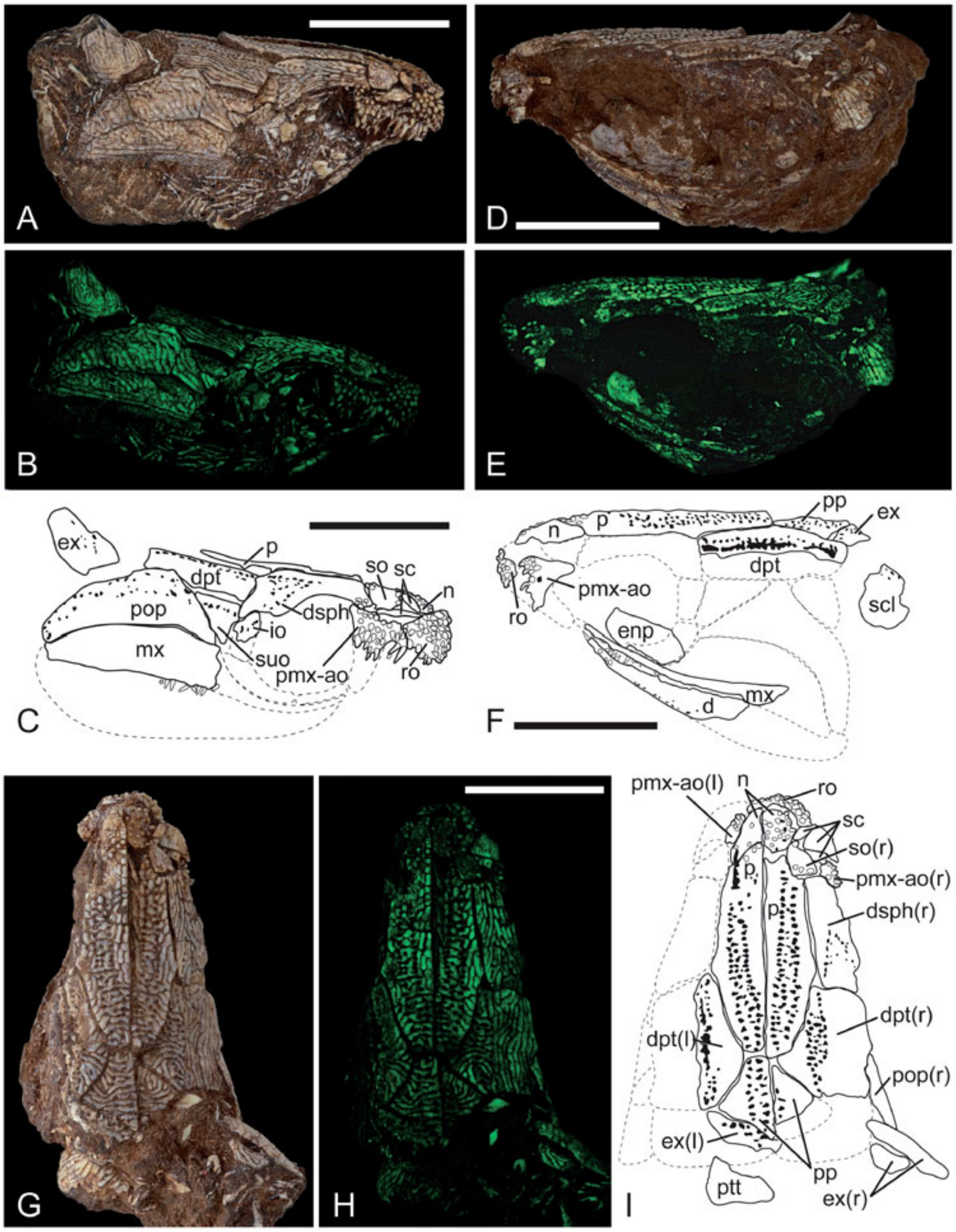

FIGURE 6. *Lasalichthys otischalkensis*, sp. nov., NMMNH P-78661, a three-dimensionally preserved skull shown in **A**–**C**, right lateral, **D**–**F**, left lateral, and **G**–**I**, dorsal views. Each aspect shown in normal lighting (**A**, **D**, **G**), fluorescence (**B**, **E**, **H**), and line drawing interpretations with bones labeled (**C**, **F**, **I**). Scale bars equal 5 mm.

articulation with the dermopterotic ends, the posterior margin of the parietal turns abruptly toward the midline, and the posterior margin articulates with the anterior margin of the postparietals (Figs. 5, 6; Schaeffer, 1967:pl. 19).

*Lasalichthys otischalkensis* possesses a single pair of triangular postparietals. Their longest margin is along the midline, where they meet with a linear articulation, tapering anteriad and posteriad (Figs. 5, 6; Schaeffer, 1967:pl. 19). At their widest points, they are 1.56 times longer than wide and are less than half of the length of the parietals (Figs. 5, 6). Their anteriormost margin articulates with the posterior margin of the parietals, and the anterolateral margin of the postparietal articulates with the posteromedial margin of the dermopterotic (Figs. 5, 6). Posteriorly, they articulate at an oblique suture with the anterior margin of the extrascapular.

The dermopterotics are large bones and pentagonal in shape. Anteriorly, they have a broad abutment with the posterior margin of the dermosphenotics (Figs. 5, 6). The medial margin of the dermopterotic comes to a wide point at the center; anteromedially, the dermopterotic articulates with the parietal, and posteromedially it articulates with the postparietal. Posteriorly, it articulates with the extrascapular (Fig. 5). The ventral margin is not completely straight; it articulates with the suborbital and nears the dorsal expansion of the preopercular bone and has a slight concavity, where it meets the dermohyal (Figs. 5, 6).

*Lasalichthys otischalkensis* possesses a single pair of large extrascapular bones. They meet medially along the dorsal margin and widen laterad (Fig. 5). Anteriorly, they articulate with the postparietals with an oblique suture that extends from the midline slightly anteriorly (Figs. 5, 6). The anterior margin of

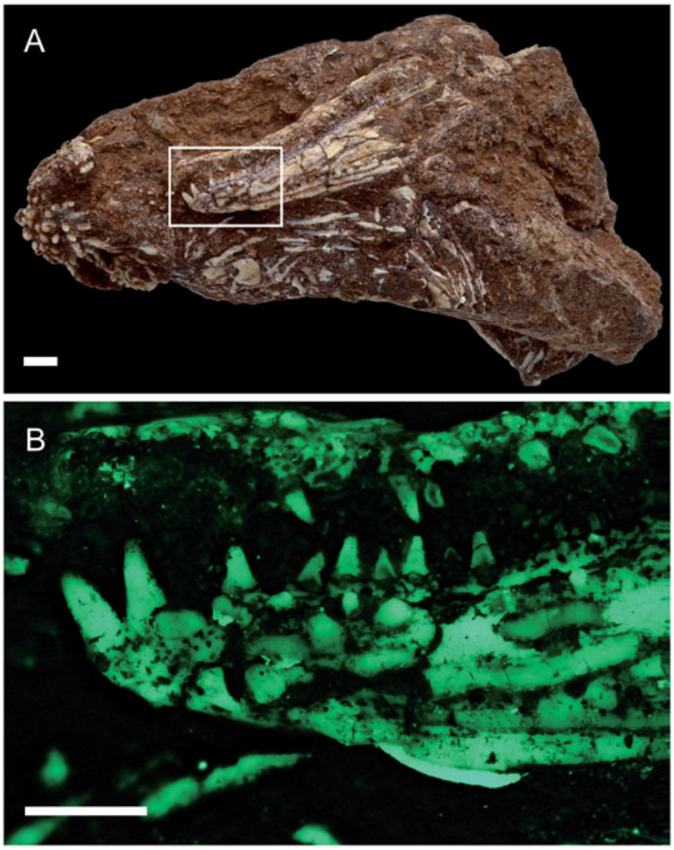

FIGURE 7. *Lasalichthys otischalkensis*, sp. nov., NMMNH P-78661. **A**, ventrolateral view of skull in normal lighting showing underside of rostral bone toward the left and jaws. **B**, close-up of inset area in **A** under fluorescence to show enlarged teeth at the terminal margin of the dentary. Both scale bars equal 1 mm.

the extrascapular bone then orients perpendicular to the length of the body as it articulates with the posterior margin of the large dermopterotic bone (Fig. 5). The posterior margin is heavily rounded, as seen on NMMNH P-44698 (Fig. 5). It articulates with the posttemporal and presupracleithrum. Along the ventral margin, the extrascapular abuts the dorsal margin of the operculum (Fig. 5). The anteroventral tip of the extrascapular bone extends slightly toward the dermohyal but does not necessarily meet the dermohyal, because this cannot be ascertained from the available specimens (Fig. 5).

**Orbital Region**—The premaxillo-antorbital forms the anterior margin of the orbital rim. In the available specimens of *Lasalichthys otischalkensis*, only the dorsal half of the premaxillo-antorbital is preserved (Figs. 5, 6); a portion of the ventral process that forms the front of the orbital rim is preserved in specimen NMMNH -78661 (Fig. 6D–F), indicating that it curves posteroventrally. The premaxillo-antorbital is heavily tuberculated (Fig. 6A–C). Anteriorly, it forms the posterior margin of the narial opening, where it curves anteriad to meet the medial rostral bone (Fig. 5). Posterodorsally, it tapers to a small process that articulates with the front of the dermosphenotic, eliminating the supraorbital from the orbital rim (Figs. 5, 6A–C).

The large and broad dermosphenotic occupies the entirety of the dorsal margin of the orbital rim. Its rectangular anterior margin meets the supraorbital and the premaxillo-antorbitals (Fig. 5). Its ventral margin is a concave embayment and forms the dorsal margin of the orbital rim. It meets along the posteroventral margin with the dorsal margin of the single posterior infraorbital (Fig. 5). Posteriorly, it abuts the dermopterotic, and dorsally it articulates with the parietal (Figs. 5, 6).

The posterior infraorbital is well preserved in the holotype NMMNH P-44698 (Fig. 5) and partially preserved in NMMNH P-78661 (Fig. 6). It is rectangular, deeper than long, and forms the posterior margin of the orbit. Posteriorly, it contacts the suborbital (Figs. 5, 6). Ventrally, it articulates with the long, falcate infraorbital that forms the posteroventral corner of the orbital rim (Fig. 5). This posteroventral infraorbital (jugal) is curved and tapering anteriorly, forming a concave embayment along the orbit (Fig. 5). Its dorsal margin contacts the ventral margin of the posterior infraorbital as well as the ventral margin of the suborbital (Fig. 5). Its posteroventral margin is curved convexly to articulate with the contour of the anterodorsal margin of the posterior expansion of the maxilla (Fig. 5).

The remainder of the infraorbital series is not preserved in any specimen. It is unknown whether there are more infraorbitals forming the ventral margin of the orbit, contacting the premaxillo-antorbital, or whether the anterior portion of the maxilla is directly involved in the orbital rim.

A single suborbital is present in *L. otischalkensis* (Figs. 5, 6). It is triangular in shape. Its dorsal edge meets the anteroventral margin of the dermopterotic. Anteriorly, it articulates with the single posterior infraorbital (Figs. 5, 6A–C). Ventrally, the suborbital contacts the posteroventral infraorbital (Fig. 5). The posterior margin of the suborbital articulates with the preoperculum. It appears to be separated from contact with the dermohyal by the dorsal expansion of the preoperculum (Figs. 5, 6A–C). The suborbital, normally anamestic in stem actinopterygians, displays pores on its surface that connect the preopercular canal to the infraorbital canal (Figs. 5, 6, described below).

**Opercular Region**—The preoperculum is large and hatchet-shaped (Figs. 5, 6). It is slightly anteriorly inclined, gently contouring concavely with the posterior expansion of the maxilla. A small, tapered process on the anterior part of the preoperculum inserts between the posterior margin of the suborbital and the dorsal margin of the maxilla (Figs. 5, 6A–C). The preoperculum reaches dorsally, extending between and separating the suborbital and dermohyal bones (Fig. 5). The posterior border of the preoperculum is convexly curved and articulates with the anterior margins of the dermohyal, operculum, and suboperculum (Fig. 5). The posteroventral process of the preoperculum is robust, tapered, and elongate, extending between the maxilla and the suboperculum to articulate with the angular on the lower jaw (Fig. 5).

The operculum is small and quadrangular (Fig. 5). It articulates with the extrascapular dorsally, dermohyal and preoperculum anteriorly, suboperculum ventrally, and supracleithrum and presupracleithrum posteriorly. It appears to have an embayment to accommodate the dermohyal (Fig. 5).

The suboperculum is large and quadrangular to oval in shape, deeper than long and approximately 1.5 times larger than the operculum (Fig. 5). Dorsally, it articulates with the operculum; anteriorly, it articulates with the ventral process of the preoperculum (Fig. 5). Posteriorly, it articulates with the large supracleithrum, although this is slightly disarticulated in NMMNH P-44698 (Fig. 5). It may also articulate with the cleithrum posteroventrally, but the cleithrum is not preserved in any articulated specimen (i.e., NMMNH P-44698, Fig. 5; NMMNH P-78661, Fig. 6). The area ventral to the suboperculum is also not preserved on either articulated specimen available in this study.

FIGURE 8. *Lasalichthys otischalkensis*, sp. nov., isolated elements from the Otis Chalk fish locality. **A**, NMMNH P-78671, left dermopterotic, in dorsal view. **B**, NMMNH P-78667, left supracleithrum, in lateral view. **C**, NMMNH P-78668, left supracleithrum, in lateral view. **D**, NMMNH P-78669, right supracleithrum, in lateral view. **E**, NMMNH P-78670, dorsal portion of left supracleithrum, in lateral view. **F**, NMMNH P-78665, dorsal half of right cleithrum, in lateral view. **G**, NMMNH P-78666, partial right cleithrum, in lateral view. **H**, NMMNH P-78664, left cleithrum, in lateral view, unidentified element on top. **I**, NMMNH P-78663, left cleithrum, in lateral view, anterior laminate margin visible. **J**, NMMNH P-78662, anal fin and portion of body, in right lateral view, rounded anal scute visible at origin of fin. Scale bars equal 5 mm.

One small bone visible on the holotype NMMNH P-44698 (Fig. 5) is situated posterodorsal to the operculum. Its location on the skull identifies it as the presupracleithrum. It is roughly quadrangular in shape, with a wider anterior margin, tapering slightly posterodorsad (Fig. 5). It lies dorsal to the supracleithrum and posteroventral to the extrascapular bone.

**Jaws**—Because the premaxilla is absent as an independent element in *Lasalichthys otischalkensis* and is interpreted as a fused element with the lacrimal constituting a large component of the snout region, it is described above.

The maxilla is firmly attached to the preopercular bone. It has a narrow anterior process ventral to the orbit and a broad posterior expansion that constitutes part of the cheek region (Figs. 5, 6). The maxilla broadens dorsally posterior to the orbit (Fig. 5). The dorsal margin then curves posteroventrad and tapers to a small posterior process that, on the holotype NMMNH P-44698, extends posteriad (Fig. 5). This posterior process possesses a small embayment that cups the rounded end of the ventral arm of the preoperculum (Fig. 5; slightly disarticulated on NMMNH P-44698). Teeth on the maxilla are present along the occlusal margin of the maxilla. The teeth are small, cylindrical, and lacking serrations (Figs. 5–7).

The lower jaw is partially preserved on both articulated skulls of *L. otischalkensis* (Figs. 5–7). The posterior portion of the dentary is visible on the holotype NMMNH P-44698 (Fig. 5). Although they are fused, there is a clear distinction between the dentary and the angular, with the suture still visible and a change in the pattern of ornamentation between the two bones (Fig. 5B). The angular is narrow and curves anteroventrally from the jaw symphysis. It constitutes the posterior portion of the lower jaw (Fig. 5). The articular is not visible on this specimen and is not preserved on any other specimens.

The dentary is long and tapers anteriad (Fig. 6, 7). The anterior portion of the dentary is preserved on NMMNH P-78661 (Fig. 7). The dentary does not reach the terminal end of the snout; as with other redfieldiids, the dentary terminates just anterior to the orbit, contributing to the prominent snout and subterminal mouth of *L. otischalkensis*. Small teeth line the dentary at the occlusal margin. At the anterior end of the dentary, two prominent, larger teeth are present (Fig. 7); this condition is seen only in one other redfieldiiform fish, *Brookvalia*.

**Hyoid Arch**—The only visible element of the hyoid arch in the available specimens is the dermohyal, situated between the posterodorsal margin of the preoperculum and the anterior margin of the operculum (Fig. 5). The dermohyal is small and triangular.

**Palate and Neurocranium**—A portion of bone that lines the orbital cavity is visible on NMMNH P-78661, dorsal to the thin anterior process of the maxilla (Fig. 6D–F). Although not fully exposed, this bone most likely represents the entopterygoid lining (Fig. 6D–F).

Due to the three-dimensionality and preservation of NMMNH P-78661 and TMM 31098-44, some information is available regarding the neurocranium of *Lasalichthys otischalkensis*. Schaeffer (1967:315, pl. 19) briefly described the morphology of the neurocranium of TMM 31098-44, indicating that

> “[T]he occipital surface has the typical bipartite opening for the foramen magnum and the notochord. There is a prominent craniospinal protuberance that extends anteroventrally as a ridge below the lateral occipital fissure. The wall in the area of the vestibular fontanelle is thin, and it is probable that a fontanelle was present. The hyomandibular facet, preserved on the left side, is somewhat more vertical than that of *Perleidus*. There is apparently an unpaired posterior myodome above the remnant of the ventral orbitotemporal bar. Canals and foramina are not clearly in evidence.”

Further study of the neurocranium is warranted given the quality of the material from Otis Chalk. At the time of writing, the author is analyzing computed tomography (CT) scans of TMM 31098-44 and NMMNH P-78661. The results of these analyses will be presented in a future publication.

**Sensory Canals of the Skull**—The main lateral line enters the skull through the supracleithrum. On the supracleithrum, it is visible as a series of scattered pores, roughly arranged in two parallel rows (Figs. 5, 8B–E) that begin approximately two-thirds down the length of the posterior border of the bone and traverses it at an oblique angle anterodorsally, exiting the supracleithrum on the dorsal margin of the bone. The lateral line is visible as a series of pores that traverses the anteroventral portion of the posttemporal and the dorsal portion of the presupracleithrum, where it continues into the extrascapular bone at its posteroventral margin (Figs. 4, 5, 8B–E). On the extrascapular bone, the lateral line connects to the occipital (supratemporal) commissure that traverses mediad across the midline to the extrascapular bone on the opposite side (partly visible on NMMNH P-78661; Fig. 6G–I) and the temporal canal, which traverses anteriorly to the dermopterotic.

The temporal (otic) canal visibly begins as two parallel series of pores, passing anteriad along the center portion of the medial half of the dermopterotic and continuing along into the dermosphenotic (Figs. 5, 6, 8). The pattern of ‘branching’ in the sensory canal pores varies among individual specimens, but it clearly branches from two rows of pores to multiple rows. In NMMNH P-44698, two rows clearly branch into four rows of pores at the anterior portion of the dermopterotic and condense into three parallel rows of pores at the posterior margin of the bone (Fig. 5). In NMMNH P-78661, two parallel rows on the right dermopterotic branch into four parallel rows in the anterior half of the bone, then condense into two rows and then a single row of pores in the posterior half of the bone (Fig. 6G–I). The left dermopterotic on NMMNH P-78661 is broken and eroded, and the canal is not fully preserved (Fig. 6D–I). However, the bone surface has been partly eroded, exposing a portion of the sensory canal and demonstrating how the pores are connected to the canal (Fig. 6D–I). The specimen clearly demonstrates that the dual parallel rows originate from a single sensory canal. One isolated specimen of a left dermopterotic (NMMNH P-78671; Fig. 8A) also displays similar patterns regarding the temporal canal: two parallel rows of pores beginning at the anterior margin, branching into three to four parallel rows before returning to two parallel rows of pores at the posterior margin (Fig. 8A). Anteriorly, the temporal canal connects to the infraorbital canal in the dermosphenotic bone (Figs. 5, 6).

The supraorbital canal is visible on both NMMNH P-44698 (Fig. 5) and NMMNH P-78661 (Fig. 6D–I). In the parietal, the supraorbital canal begins at the anterior margin as a single row of pores (Figs. 5, 6G–I), which then branches into two parallel rows of pores. As these rows pass posteriad, they duplicate with varying patterns on each individual. On NMMNH P-44698 (Fig. 5), the canal pores first branch in the lateral row, creating three parallel rows, followed by four parallel rows as the medial row branches. Continuing posteriad, the parallel rows have condensed into three rows, finally condensing into two parallel rows by the time the canal has reached the posterior margin of the parietal (Fig. 5). On NMMNH P-78661 (Fig. 6), a similar pattern is observed on each parietal, with two rows splitting into three, then four, then again three parallel rows before condensing into two at the posterior margin of the parietals (Fig. 6D–I). The supraorbital canal passes from the parietal to the postparietal, where the canal is visible as two parallel rows of pores (Figs. 5, 6), passing posteriad along the median portion of the postparietals. It appears to connect to the supratemporal commissure on the extrascapular (Figs. 5, 6D–I). Anteriorly, the supraorbital canal passes from the parietal through the nasal bone just lateral to the midline of the bone and medial to the single external narial opening; it is visible as a single row of pores in the nasal bone.

The infraorbital canal, beginning in the dermosphenotic bone where the temporal canal turns abruptly posteroventrad, is visible as two parallel rows of pores (Figs. 5, 6). The infraorbital canal passes through the posterior infraorbital and is visible as a scattered series of pores on the surface of the posterior infraorbital bone (Figs. 5B, C, 6C). Due to poor preservation, it is difficult to interpret the infraorbital canal in the posteroventral infraorbital (Fig. 5), although under fluorescence (Fig. 5B) it is possible to see a few scattered pores along the ventral margin of the posteroventral infraorbital bone (Fig. 5B). The remainder of the infraorbital sensory canal is unknown. The infraorbital canal is visible on both NMMNH P-44698 (Fig. 5) and NMMNH P-78661 (Fig. 6B, C) as a series of pores. The anterior part of the infraorbital canal can be seen in the premaxillo-antorbital bone as a few visible pores on NMMNH P-44698 (Fig. 5) and NMMNH P-78661 (Fig. 6).

The ethmoid commissure along the front of the skull is obscured by the denticles on the snout on NMMNH P-78661 (Fig. 6), but on NMMNH P-44698 a single canal pore is visible on the rostral bone (Fig. 5).

The preopercular canal is visible as two parallel rows of pores that follow the path of the canal from the jaw articulation dorsad, then curve anterodorsad, following the curvature of the preopercular bone (Figs. 5, 6). It exits near the center of the anterodorsal margin of the preoperculum and continues as a single row of pores through the suborbital bone anteriad (Figs. 5B, C, 6A–C). This connection could be considered the jugal canal, which is defined as the connection between the preopercular and infraorbital canals (Schultze, 2008) and is similar to what is observed in sarcopterygian fishes and uncommon in actinopterygians. It exits on the anterior margin of the suborbital and appears to join the infraorbital canal (Figs. 5C, 6C).

The mandibular canal is preserved on NMMNH 44698 (Fig. 5), visible as a row of pores on the angular and dentary, and on NMMNH P-78661 (Fig. 7) as a single row of pores that traverses near the ventral margin of the dentary.

**Shoulder Girdle**—The posttemporals are situated posterior to the extrascapular bones along the skull roof (Fig. 5). They are teardrop-shaped, tapering anteromediad toward the midline. Each posttemporal has a rounded posterior margin where it overlaps the supracleithrum posteroventrally. Anterodorsally, each posttemporal is overlapped by the extrascapular bones (Fig. 5). The main lateral line is visible as a series of scattered pores and passes from the extrascapular bone through the center of the posttemporal and toward the ventral margin of the bone, where it continues into the supracleithrum (Fig. 5).

The supracleithrum is a large bone situated ventral to the posttemporal, preserved on the holotype NMMNH P-44698 (Fig. 5) and in four isolated samples (NMMNH P-68667–68670; Fig. 8B–E). The supracleithrum is long and 'narrow,' tapering slightly ventrad. Anteriorly, the supracleithrum articulates with the presupracleithrum, operculum, and suboperculum (Fig. 5).

No postcleithrum was visible in any available specimens.

The cleithrum is not preserved on either articulated skull (NMMNH P-44698, NMMNH P-78661). However, there are several complete and partial cleithra preserved as isolated elements from the material collected at Otis Chalk (NMMNH P-78663–78666; Fig. 8F–I). Although they are not articulated to a specimen, they are identified as belonging to *L. otischalkensis* based on the size of the bones relative to the articulated specimens and the shared type of rugose ornamentation. The cleithrum of *L. otischalkensis* is a highly concave bone with an anterior-facing laminate margin that constitutes the posterior boundary of the branchial cavity (Fig. 8H, I). The dorsal process of the cleithrum is tapered dorsally (Fig. 8F–I). The anteroventral process of the cleithrum is not preserved in the available specimens. The posterior border of the cleithrum is convex, with a notch located at the posteroventral corner of the bone (Fig. 8G–I). This notch is an embayment that allows for the insertion of the pectoral fin into the shoulder girdle.

**Paired Fins**—No paired fins are preserved on the available specimens.

**Median Fins**—The dorsal fin is not preserved on any of the available specimens, but based on the preservation of NMMNH P-44698 (Fig. 4), which retains a large portion of the anterior trunk, it would have been situated far along the back of *L. otischalkensis*, as with other redfieldiiform fishes.

One specimen, NMMNH P-78662 (Fig. 8J), recognized as *L. otischalkensis* because of the similar scale morphology on the flank to NMMNH P-44698 (Fig. 4), possesses an isolated portion of the anal fin and a small portion of the scales near the anal area, including a rounded anal scute/scale just anterior to the origin of the anal fin (Fig. 8J). The anal fin possesses paired fringing fulcra along the first lepidotrichium, and at least six to eight lepidotrichia are exposed (Fig. 8J).

The caudal fin is not preserved on any specimen.

**Squamation**—The surface of the scales of *L. otischalkensis* is relatively devoid of ornamentation or ridges (Figs. 4A–C, 8J). Each scale is smooth, except for very small pits scattered irregularly along the surface of each scale (Fig. 4C). The scales are rhombic in shape and become shallower ventrally. There are 29 rows of scales preserved on NMMNH P-44698, so *L. otischalkensis* possessed at least that many rows of scales, if not more, anterior to the origin of the dorsal and anal fins. The main lateral line passes from the supracleithrum along the midflank scales (Fig. 4C). The lateral line scales are notched along the posterior margin; these notches allow for an opening of the lateral line canal to surface (Fig. 4). Additionally, some scales along the lateral line have distinct pits on the surface, representing the pit organs (Fig. 4C; Schultze, 1966).

## DISCUSSION

When Schaeffer (1967) first discussed fish fossil remains he collected near Otis Chalk (AMNH 5722 and TMM 31098-44), he commented on the exceptional uncrushed preservation of TMM 31098-44, a partial skull roof and neurocranium (Schaeffer, 1967:pl. 19, figs. 1–4). Schaeffer commented that, upon returning to the Otis Chalk sites, he was unable to find any additional specimens and thus was not able to diagnose the specimens beyond '*Synorichthys-Lasalichthys*' (Schaeffer, 1967). The addition of the NMMNH specimens, preserved in a similar three-dimensional state, provides further morphological information regarding this species, and thus finally the ability to diagnose these specimens as a new species of redfieldiiform fish, *Lasalichthys otischalkensis.*

As was discussed above, only the condition of the postrostral initially separated the genera *Lasalichthys* and *Synorichthys*, with little or no other variation occurring to justify the splitting of these two genera. Further examination of specimens of *Lasalichthys hillsi*, *Lasalichthys otischalkensis*, '*Synorichthys*' sp., and '*Synorichthys*' *stewarti* has indicated that these taxa share many morphological characteristics, but that they also display a mosaic of characters that should be distinguishable at the species level rather than the generic level. As such, *Synorichthys stewarti* is now assigned to the genus *Lasalichthys*, under the new combination *Lasalichthys stewarti*. Some characters that are present in *Lasalichthys otischalkensis* would classify it as *Synorichthys* in the traditional definition, such as the absence of the postrostral, but *L. otischalkensis* also shares characters with *L. hillsi*, such as the dual parallel rows of pores in the preoperculum that pass through the suborbital and reach the infraorbital series, that are not seen in *L. stewarti*. *Lasalichthys otischalkensis* also possesses a presupracleithrum, a bone not observed in *L. stewarti* or *L. hillsi*, but is visible in '*Synorichthys*' sp. from the Newark Supergroup.

*Lasalichthys otischalkensis* has been assigned to the genus *Lasalichthys* based on the following shared characters: absent or highly reduced postrostral; quadrangular nasals fully articulating along the midline; large, broad dermosphenotic; large dermopterotic; triangular, paired postparietals; and duplicated, parallel rows of pores. *Lasalichthys otischalkensis* is distinguished from all other redfieldiiforms by the condition of the sensory canal pores. *Lasalichthys otischalkensis* possesses parallel rows of pores, similar to the condition seen in *L. stewarti* and *L. hillsi*, but in those two taxa the pores are visible as two distinct parallel rows. In all available specimens of *L. otischalkensis*, the pores split into two rows but then split again into three or four parallel rows. Although there is some individual variation, this character is consistent with every specimen of *L. otischalkensis* recovered thus far, even isolated bones (Fig. 8). *Lasalichthys otischalkensis* is also unique among all redfieldiiforms in that the preopercular sensory canal is visible as a dual row of pores that extends anteriad through the suborbital bone. In *Lasalichthys stewarti*, the preopercular canal is visible only as a single row of pores that ends blindly in the middle region of the preopercular bone. In *L. hillsi*, the preopercular canal is a dual row of pores that extends the entire length of the preoperculum, dorsad from the mandible, then turning anteriad and reaching the anterior margin of the preoperculum, but not passing through the suborbital as is seen in *L. otischalkensis*.

Within species from eastern North America, '*Synorichthys*' sp. from the Lockatong Formation of the Newark Supergroup near North Bergen, New Jersey, also possesses dual rows of pores (Schaeffer and Mangus, 1970). Another species, *Rushlandia gilli* Bock, 1959, was recovered from the Lockatong Formation of the Newark Supergroup, from two localities in Pennsylvania (Rushland and Fairview Village). *Rushlandia gilli* is based on very minimal and highly disarticulated dermal skull elements that show an affinity to *Lasalichthys*, such as the dermal ornamentation pattern and a dual row of sensory pores on a single isolated element. Because it is so incompletely known, *Rushlandia gilli* likely represents a nomen dubium and possibly belongs in *Lasalichthys*. Further investigation of the specimens of *Rushlandia* is needed.

Other morphological differences distinguish *L. otischalkensis* as a species different from *L. stewarti*, *L. hillsi*, or '*S.*' sp. On *L. otischalkensis*, the suborbital bone articulates with the posteroventral infraorbital (Fig. 5), whereas this articulation does not occur in *L. stewarti* or *hillsi*. The dermosphenotic of *L. stewarti* + *L. hillsi* possesses a row of denticles on the anteroventral margin along the orbit; there is no evidence of these denticles on *L. otischalkensis.* The dermosphenotic of '*S.*' sp. from the Newark Supergroup is much narrower than those of *L. stewarti* and *L. otischalkensis* and is not determinable on '*S.*' sp. The supraorbital bone in *L. hillsi* and *L. stewarti* appears to participate in the orbital margin, whereas in *L. otischalkensis* this bone is isolated from the orbital margin by the articulation of the premaxillo-antorbital and dermosphenotic (Figs. 5, 6). The participation of the supraorbital in the orbital rim of '*S.*' sp. is unclear due to the disarticulation of the premaxillo-antorbital (Schaeffer and Mangus, 1970:fig. 1A, pl. 6.).

*Dictyopyge*, a genus of redfieldiiform fishes from the Newark Supergroup (Schaeffer and McDonald, 1978), possesses similar skull ornamentation and narrow rounded belly scales as are observed in *Lasalichthys* (Schaeffer, 1967). *Dictyopyge* also has a similar articulation between the suborbital and posteroventral infraorbital to what is observed in *L. otischalkensis*. *Dictyopyge* also possesses a single pair of weakly shaped, triangular postparietals, similar to all species of *Lasalichthys*. However, similarities beyond those characters in the two taxa are minimal; *Dictyopyge* possesses singular rows of pores along the sensory canals with different patterns along the respective bones, and it is difficult to interpret the snout characteristics of *Dictyopyge* due to the extreme tuberculation of the snout (Schaeffer and McDonald, 1978).

*Redfieldius gracilis* from the Newark Supergroup (Schaeffer and McDonald, 1978) and *L. otischalkensis* also share very few morphological similarities. *Redfieldius* possesses three postparietals, with one medial postparietal and two somewhat rounded lateral postparietals, whereas all species of *Lasalichthys* possess only one pair of triangular postparietals. The supraorbital sensory canal in *Redfieldius* terminates in the parietal bones, whereas it continues posteriad through the postparietals in *L. otischalkensis* as well as other species of *Lasalichthys*.

*Cionichthys* is a genus of redfieldiiforms that co-occurs with *Lasalichthys* in both the Chinle Formation and the Dockum Group (Schaeffer, 1967). *Cionichthys greeni* from the Dockum Group and *C. dunklei* from the Chinle Formation share more similarities morphologically with *Redfieldius* than they do with *Lasalichthys*. Both species have a large postrostral that separates the nasals medially and articulates with the rostral (the postrostral being absent or highly reduced in *Lasalichthys*). *Cionichthys* has a single pair of postparietals, but they are roughly square in shape, as opposed to the triangular postparietals of *Lasalichthys*. *Cionichthys* possesses two pairs of extrascapular bones, whereas *L. otischalkensis* possesses a single pair of extrascapulars, like other species of *Lasalichthys.* The sensory canals are represented by minimal singular rows of pores in the dermal skull bones, and the supraorbital canal terminates posteriorly in the parietal, as opposed to continuing through the postparietals in *Lasalichthys*. *Cionichthys* also lacks the heavy rugose ornamentation observed in all species of *Lasalichthys*.

*Lasalichthys otischalkensis* possesses a presupracleithrum, which is observed in '*Synorichthys*' sp. but is not present in *L. stewarti* or *L. hillsi*. The presupracleithrum is also present in *Helichthys browni*, a redfieldiiform fish from the Triassic Karoo Supergroup of South Africa (Hutchinson, 1973, 1978). *Helichthys browni* also possesses a large dermosphenotic, similar to *L. otischalkensis*, but similarities beyond that are not present in the two taxa. *Helichthys browni* possesses a large postrostral bone that articulates with the rostral bone and separates the narrow nasal bones medially. *Helichthys browni* possesses two pairs of postparietals, compared with the one pair observed in all species of *Lasalichthys*; however, the posterior pair of postparietals in *H. browni* is similar in shape (triangular with a pointed lateral process) to the single pair of postparietals observed in *Lasalichthys*. *Helichthys browni* also differs in that it possesses an antoperculum, a small bone situated between the posterior margin of the dermohyal and the anterodorsal corner of the operculum. The antoperculum is present in some South African and Australian redfieldiiform fishes (e.g., *Atopocephala*, *Brookvalia*, *Ischnolepis*, *Phlyctaenichthys*, *Schizurichthys*; Hutchinson, 1973) but is absent in all North American redfieldiiform taxa (including *L. otischalkensis*) and other global redfieldiiforms (e.g., *Daedalichthys*, *Denwoodichthys*, *Geitonichthys*, *Molybdichthys*, *Pacorichthys*; Hutchinson, 1973; Sytchevskaya et al., 2009; Lombardo, 2013).

The pattern of the supraorbital canal posteriad along the skull roof also shows variation among different redfieldiiform fishes. In taxa such as *Molybdichthys*, *Lasalichthys*, and possibly *Helichthys*, the supraorbital canal passes into the postparietal; however, for *Molybdichthys*, this canal terminates in the middle region of the postparietal, whereas it traverses the entire length of the postparietal in all species of *Lasalichthys*, possibly connecting to the supratemporal commissure. In the redfieldiiform taxa *Redfieldius*, *Cionichthys*, *Dictyopyge*, and *Pacorichthys*, the supraorbital canal terminates posteriorly in the parietal bones (Schaeffer, 1967; Schaeffer and McDonald, 1978; Lombardo, 2013). In the redfieldiiform taxa *Brookvalia* and *Phlyctaenichthys*, the supraorbital sensory canal passes into the dermopterotic dorsolaterally, rather than passing into the postparietals (Hutchinson, 1973). This pattern is also observed in a few stem actinopterygians, such as *Fukangichthys* (e.g., Xu et al., 2014; Giles et al., 2017) and *Aeduella* (Westoll, 1937).

**Comparisons with Other Actinopterygian Groups**—*Lasalichthys otischalkensis* clearly belongs to the order Redfieldiiformes based on its shared morphology with other redfieldiiforms, as described above. Redfieldiiforms possess many characteristics that are of a ‘generalized stem actinopterygian’ nature and can been seen in other early Mesozoic actinopterygians such as Perleidiformes or Scanilepiformes, for example. These general characteristics include fixed maxillae, more upright suspensoria than those present in Paleozoic actinopterygians, reduced heterocercal tails, and scales possessing ganoin. However, Redfieldiiformes can be easily distinguished by their prominent snouts and snout bone morphology. *Lasalichthys otischalkensis* possesses a heavily tuberculated, bullet-shaped snout like other North American redfieldiiforms, which is strikingly different when compared with other actinopterygians such as Perleidiformes (e.g., López-Arbarello and Zavattieri, 2008; Sun et al., 2008; Marramá et al., 2017) or Scanilepiformes (e.g., Xu et al., 2014). Another difference of note is the anterior margin of the orbit; in *Lasalichthys otischalkensis* and other redfieldiiform fishes, this anterior margin is composed almost entirely of the premaxillo-antorbital, whereas in Perleidiformes, Scanilepiformes, or various stem actinopterygian groups, this anterior margin is composed of the supraorbitals (adnasal) and/or nasal bones. In redfieldiiform fishes, the nasal bone is completely isolated from the orbital margin.

**Comments on the Evolutionary Relationships of *Lasalichthys otischalkensis* and Redfieldiiformes**—Many early studies offered informed opinions regarding the relationships of the Redfieldiiformes to other actinopterygian lineages. Some early studies suggested a close affinity to the Perleidiformes (sensu Stensiö, 1921; Lehman, 1966; Hutchinson, 1973), Dicellopygidae (sensu Brough, 1931, 1934), or generalized ‘palaeoniscoids’ (sensu Schaeffer, 1984). However, the Redfieldiiformes as a whole has been absent in most recent phylogenetic hypotheses regarding evolutionary relationships of stem actinopterygians, with only one or two representatives present in a few studies (e.g., Gardiner and Schaeffer, 1989; Poplin and Dutheil, 2005; Mickle, 2015). Those studies that have included members of the Redfieldiiformes have demonstrated that the position of the order has been unstable or inconsistent. Gardiner and Schaeffer (1989) recovered the ‘*Redfieldius*’ group as sister to the ‘*Haplolepis*’ group. Poplin and Dutheil (2005) recovered the redfieldiiform *Brookvalia* as sister to the clade containing actinopterygians *Commentrya*, *Howqualepis*, *Moythomasia*, *Paramblypterus*, *Pteronisculus*, and *Wendyichthys*. Mickle (2015) used the redfieldiiform representatives *Dictyopyge* and *Redfieldius* and recovered them as sister taxa closely related to the ptycholepid *Boreosomus* and actinopterygian *Mesopoma*.

Schaeffer (1984) examined the relationships within the Redfieldiiformes using a nonquantitative cladistic analysis of morphological characters. In his study, he recovered *Lasalichthys* and *Synorichthys* as sister taxa. However, Schaeffer (1984) was unsuccessful in ascertaining a sister-group relationship to other actinopterygian fishes. To date, the placement of Redfieldiiformes remains unclear, and a broad, comprehensive analysis of evolutionary relationships within Redfieldiiformes and to other actinopterygians is outside of the scope of this study and will be the subject of a future work by the author.

**Biogeographic and Age Remarks**—Redfieldiiformes dates back to the Middle Triassic (Anisian), with representatives in an approximately Gondwanan distribution: Argentina (e.g., *Calaichthys*; Gouric-Cavalli et el., 2017), Australia (e.g., *Daedalichthys*; Brough, 1931; Hutchinson, 1973), Madagascar (e.g., *Sakamenichthys*; Lehman et al., 1959), South Africa (e.g., *Atopocephala*, *Helichthys*; Brough, 1931, 1934; Hutchinson, 1973, 1978), and Zambia (e.g., *Ischnolepis*; Haughton, 1934; Hutchinson, 1973). A later diversification of redfieldiiforms can be found in an approximately Laurasian distribution: Morocco (e.g., *Mauritanichthys*; Martin, 1980, 1982) and North America (e.g., *Cionichthys*, *Dictyopyge*, *Lasalichthys*, *Redfieldius*; Schaeffer, 1967), with few examples still recovered in Gondwana (e.g., *Denwoodichthys* in South Africa; Sytchevskaya et al., 2009). Most of the known examples in North America are Norian to Rhaetian in age, with the representatives from the Chinle Formation being recovered in Rhaetian deposits approximately 208–201 Ma (Martz et al., 2014) The youngest redfieldiiform, *Redfieldius*, extends into the Early Jurassic Newark Supergroup deposits (Schaeffer and McDonald, 1978).

*Lasalichthys otischalkensis* and the redfieldiiform *Cionichthys dunklei* represent the oldest redfieldiiforms in North America to date. They are both recovered from the Dockum Group of Howard County, western Texas, in deposits that are approximately 228–230 million years old (Carnian, Adamanian; Martz, 2008). This might indicate a diversification shift northward across Pangaea over time, with early speciation events occurring in the Middle Triassic across Gondwana and later speciation occurring across Laurasia in the Late Triassic and Early Jurassic, with the oldest representatives in Laurasia occurring in a more southern part of the region relative to other North American taxa. A model for this distribution pattern, however, is unclear, because this predominantly freshwater group of fishes would meet several terrestrial geographic barriers. Future studies of Redfieldiiformes including putative new species, taxonomy, and hypotheses of evolutionary relationships will lend further insight into this seemingly broad Pangaean distribution and the biodiversity of these fishes.

## CONCLUSIONS

Based on morphological evidence and comparison, *Lasalichthys otischalkensis* represents a new species co-occurring with *Cionichthys greeni* in isolated pond deposits in the Dockum Group. The age of these deposits (Carnian) is older than those of the Rhaetian Chinle Formation and Norian–Hettangian Newark Supergroup taxa (e.g., Schaeffer, 1967; Lucas et al., 1993; Heckert, 2004; Martz, 2008), thus making *Lasalichthys otischalkensis* and *Cionichthys greeni* the oldest known redfieldiiform fishes found in North America.

*Synorichthys* is placed into synonymy with *Lasalichthys*, with *S. stewarti* under the new combination *Lasalichthys stewarti*.

This has implications with regard to the recognized biodiversity of redfieldiiform fishes from Triassic and Early Jurassic North American deposits. Further investigation is needed on putative '*Synorichthys*' specimens from the Newark Supergroup.

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## APPENDIX 1

### Materials examined

*Atopocephala watsoni*: AMNH 10487 (peel); NHMUK PV 16079, 16080; FMNH UF 313. *Belichthys minimus*: NHMUK PV 15864–5, 15870, P 16360.

*Boreosomus gillioti*: NHMUK PV 19691, 50125, 50126, 63969; NMNH V 21468.

*Brookvalia gracilis*: AMNH 4707; NHMUK PV 15813, 15827, 24711, 24722.

*Brookvalia latipennis*: NHMUK PV 15883.

*Brookvalia propennis*: NHMUK PV 15825, 15868, 24710.

*Brookvalia spinosa*: NHMUK PV 16211–16212.

*Cheirolepis canadensis*: MCZ VPF-6041, 6079.

*Cheirolepis traillii*: MCZ VPF-6038–6039, 6042–6043, 6045–6046, 11587.

*Cionichthys dunklei*: AMNH 5615–19, 5621–32, 5645, 5650–51, 5670; MCZ VPF-9026–9028; NMNH V 23411, V 23413; UMNH VP 22906, VP 22909, LVF10-29, LVF12-07, LVF12-52, LVF12-69.

*Cionichthys greeni*: AMNH 5600.

*Cionichthys* sp.: AMNH 5593, 5620, 5661; DMNH 1997-161; UMNH VP 22902, VP 22907, LV05-53, LV05-87, LVF12-04.

*Daedalichthys formosa*: NHMUK PV 17532–17533, 17238.

*Dictyopyge catoptera*: NHMUK PV 1033, 3490–3491; NMNH V 21371.

*Dictyopyge macrurus*: AMNH 654G, 1541, 4764, 4766, 4769, 4877, 5241, 6770; NHMUK PV 11129.

*Dictyopyge meekeri*: AMNH 4733, 4740–41, 4743, 4756, 4762, 4876, 4927, 5244.

*Dictyopyge* sp.: MCZ VPF-5068, 13401–13402; 13410–13411.

*Geitonichthys ornatus*: NHMUK PV 15859, 15880, 24698.

*Helichthys browni*: AMNH 8062–63, 8065, 11213–14; FMNH UF 298–299, UF 301–303.

*Helichthys* sp.: NHMUK PV 3568, 6269, 6271, 16086–16087, 16099, 16117, 18110–1, 33239; FMNH UF 311, UF 10379; NMNH V 1831.

*Ischnolepis bancrofti*: NHMUK PV 27577–27578.

*Lasalichthys* (=“*Synorichthys*”) sp. (Chinle Fm.): AMNH 5674.

*Lasalichthys* (=“*Synorichthys*”) sp. (Newark Spgp.): AMNH 3983.

*Lasalichthys* (=“*Synorichthys*”) *stewarti*: AMNH 5646, 5663–69, 5671–73, 5675–5678; MCZ VPF-9031–9032; NMNH V 23415–16; UMNH LVF12-23.

*Lasalichthys hillsi*: AMNH 5636–44, 5647, 5722; MCZ VPF-9029–9030; NMNH V 23414; UMNH LVF15-24.

*Mauritanichthys rugosus*: MNHN ALM 312 (photographs), AMNH 10488 (peel of ALM 312).

*Molybdichthys junior*: NHMUK PV 16822, 16204, 24696–24696.

*Perleidus madagascarensis*: MCZ VPF-8416.

*Phlyctaenichthys pectinatus*: NHMUK PV 16205–16206.

*Pseudobeaconia bracaccinii*: MCZ VPF-12883, 12891, 12898–12899, 12901.

*Ptycholepis marshi*: AMNH 575; MCZ VPF-6254, 6258, 8824.

*Redfieldius gracilis*: AMNH 639, 648G, 4827–28; FMNH P 15152–15155; MCZ VPF-1561, 6176, 8191, 8197–8198, 9939, 9942–9943; NMNH PAL 279569–70, PAL 279575, PAL 279578–81, NMNH V 1942, V 3050–51, V 4651, V 4662, V 6051, V 8105, V 8115, V 21658, V 215153, V 279554, V 279558, V 279559, V 279566.

*Redfieldius redfieldi*: MCZ VPF-8184, 8189, 8190; NMNH PAL 279462, PAL 279469–70, V 1862–63, V 1938.

*Redfieldius* sp.: AMNH 6704–05, 6707, 6709–16, 6718, 6721–22; FMNH PF 15151, UC 2007, UF 450–451; NMNH PAL 215150, PAL 215152, PAL 283117, V 14935, V 18328–30, V 22742

*Sakamenichthys germaini*: MNHN MAT13 a, b (photographs).

*Schizuricthys pulcher*: NHMUK PV 15891–15892.

*Tanaocrossus kalliokoskii*: AMNH 5700; UMNH VP 22905.

*Turseodus dolorensis*: AMNH 5603–15, 5633–34, 5648.

Redfieldiiformes indet: MCZ VPF-9271; UMNH VP 22908, LV05-55, LV05-53, LV05-74, LV05-76, LV05-87, LV05-93, LV05-109, LVF10-01, LVF10-05, LVF10-10, LVF10-12, LVF10-14, LVF10-30, LVF12-37, LVF12-93, LVF15-13.