Cranial anatomy of *Libognathus sheddi* Small, 1997 (Parareptilia, Procolophonidae) from the Upper Triassic Dockum Group of West Texas, USA

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**Abstract**

*Libognathus sheddi*, a leptopleuronine procolophonid from the Upper Triassic Cooper Canyon Formation, Dockum Group, West Texas, was based on an isolated left dentary and partial coronoid. New material referable to *Libognathus sheddi*, from the Cooper Canyon Formation, provides new information on the cranial anatomy. This new cranial material includes the antorbital portion of a skull, a left maxilla and premaxilla, quadratojugals, and dentaries, including intact tooth rows in the upper and lower jaws. *Libognathus* shows autapomorphies including: dentary deep with ventral margin oblique to tooth row immediately from the symphysis at ≥23°; anterior projecting coronoid contacting the lingual surface of the dentary underlying the last two dentary teeth; reduced contact between the lacrimal and the nasal; suborbital foramen formed by the maxilla and ectopterygoid, excluding the palatine; a posterior supralabial foramen shared by the maxilla and jugal; a Y-shaped antorbital pillar formed by the palatine, and massive orbitonasale and facial foramina (shared with unnamed southwest USA leptopleuroniines). Phylogenetic analysis indicates that *Libognathus* is a highly derived leptopleuronine procolophonid, closely related to *Hypsognathus fenneri* and other southwest USA Revuel-tian leptopleuroniines, which fall out as sister taxa to *Hypsognathus*, a relationship supported by a maxillary dentition restricted anterior to the orbital margin, a possibly synapomorphic orbitonasale septum in the form of an “antorbital pillar” created by the palatine, an anteroven tral process of the jugal, and the presence of a small diastema between the first dentary tooth and the more posterior dentition. *Libognathus* exhibits a possible ankylosed protothecodont tooth implantation with frequent replacement, differing from some other proposed procolophonid implantation and replacement models. Chinle Formation and Dockum Group

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leptopleuronines are restricted to the Revueltian teilzone/holochrone-zone, making them possible Revueltian index taxa.

KEYWORDS
Dockum group, late Triassic Revueltian, Procolophonidae, Texas

1 INTRODUCTION

The Procolophonidae are a group of small parareptiles that achieved a global distribution during the Triassic (Cisneros, 2008a; Martinelli et al., 2016; Modesto et al., 2010; Tsuji, 2018). Procolophonids have been known from the Late Triassic of North America since the description of *Hypsognathus fenneri* by Gilmore (1928). The majority of North American procolophonid taxa and specimens have been found in eastern North America, in the Newark Supergroup. *H. fenneri* is the best-known procolophonid from North America, with over a dozen specimens coming from Nova Scotia, Connecticut, New Jersey, and Pennsylvania (Norian–Rhaetian) (Baird, 1986; Colbert, 1946; Gilmore, 1928; Sues et al., 2000). Sues and Olsen (1993) described the procolophonid *Gomphiosauridion baileyae* from a section of right maxilla (USNM 448630) from the Tomahawk Member of the Turkey Branch Formation, Newark Supergroup (Late Carnian).

Sues and Baird (1998) described three procolophonid taxa from the Wolfville Formation, Fundy Group, Newark Supergroup of Nova Scotia (Late Carnian): *Acadiella psalidodon*, *Haligonia bolodon*, and *Scoloparia glyphanodon* (see also Jenkins & Bhullar, 2022). *Leptopleuron* was also reported from the Wolfville Formation by Baird and Olsen (1983); however, Sues and Baird (1998) determined that this record was based on a small specimen of *Scoloparia*. Also of note is the recent description of *Scoloparia* non-leptopleuronine procolophonids from the Economy member of the Newark Supergroup of Nova Scotia, Canada (Sues et al., 2022).

Procolophonids from the Triassic of the southwestern United States are much less common and sometimes have a problematic taxonomic history. Sues and Olsen (1993) erected the procolophonid genus *Chinleogomphius jacobsi* based on material previously referred to the allokotosaurian archosauromorph *Trilophosaurus jacobsi* from the Chinle Formation of Arizona (Murry, 1987). However, Heckert et al., 2006 described the first known skull from *T. jacobsi*, demonstrating the trilophosaurid affinities of the material. New, undescribed specimens from the Museum of Texas Tech and Petrified Forest National Park (BDM, pers. obs.) further support this relationship.

The enigmatic taxon *Colognathus obscurus*, from the Upper Triassic Dockum Group of West Texas, is known from partial jaws and teeth and has been thought to possibly represent a procolophonid based on its large, bulbous teeth (Murry, 1986). However, it is also considered to be of lepidosaurian affinities (Heckert, 2004), an archosauromorph (Heckert et al., 2012), a reptile of unknown affinities, or even a fish (Case, 1928; Sues & Olsen, 1993). There are no apomorphies that place *Colognathus* within Procolophonia to the exclusion of other reptiles; labiolingually broadened teeth are present in several durophagous diapsid groups including sauropterygians, lepidosauromorphs, and archosauromorphs (Kligman et al., 2020; Neenan et al., 2013; Rauhut et al., 2012).

The first definitive procolophonid described from the Upper Triassic of the southwestern USA was the leptopleurinone *Libognathus sheddi* Small, 1997, from the Cooper Canyon Formation (Revueltian), Dockum Group of Texas. It is known from a left dentary and partial coronoid, making it difficult to use in procolophonid phylogenetic analyses. Sues et al. (2000) mentioned but did not describe two leptopleurinone skulls (MCZ 9312 and 9313) and postcrania from the Owl Rock Member (Norian: Revueltian) of the Chinle Formation of Arizona, referred to here as the “Glen’s Ferry form.” These skulls will be used in comparisons and phylogenetic analysis, though the information on the skulls is preliminary, and the skulls are currently under study by some of the authors (Xavier Jenkins and Bryan J. Small). Fraser et al. (2005) described a definitive small, unnamed leptopleuronine procolophonid skull from the Owl Rock Member (Revueltian) in Utah that is referred to here as the “Abajo form.”

More recently, a mandible (DMNH 56657) tentatively identified as *Libognathus* was reported from the “red siltstone” member of the Chinle Formation of Colorado (Revueltian) (Martz & Small, 2019). The dentary is similar to that of leptopleuronines and resembles the holotype dentary of *Libognathus*; however, the specimen is in need of further preparation and study to reveal more details, so it will not figure into the present description of *Libognathus* (Bryan J. Small, pers. obs.).

The discovery of additional cranial material, first reported by Mueller and Chatterjee (2003), from the Cooper Canyon Formation, Upper Triassic Dockum Group (Revueltian), western Texas, from locality (MOTT VPL 3874) 4.5 km from the type locality of *Libognathus sheddi* provides new and supplemental information on the cranial
and mandibular anatomy of *Libognathus sheddi*. In the summer of 2000, Troy Simpson, the son of a local rancher, brought a small partial skull (TTU-P10068) to the Museum of Texas Tech where it was tentatively identified to be a partial skull (from the orbits forward) of *Libognathus* on the basis of the dental structure. An examination of the locality led to the recovery of additional specimens. TTU-P10069 is a right dentary with partial coronoid that compares well with the holotype of *Libognathus*. TTU-P10081 is comprised of a left premaxilla and maxilla. On a subsequent visit to the locality, a quadratojugal (TTU-P10523) of *Libognathus* was found. A variety of other cranial material was also collected from the locality (see below). Fragmentary postcranial material was also collected in close proximity to the cranial material, including the distal end of a femur (TTU-P10524), the distal end of a humerus (TTU-P11151), and a vertebra (TTU-P10525). All new specimens were found within a few meters of each other. The only non-procolophonid materials collected from MOTT VPL 3874 are fragmentary phytosaur bones and teeth.

This new material has allowed for the description of cranial bones of *Libognathus sheddi* that were previously unknown. The new mandible material allows for a direct comparison with the holotype (Small, 1997). This is the most detailed description of a procolophonid from the Late Triassic of the western USA where they are rare faunal components. With the description of this new material, *Libognathus* can now be placed into a phylogenetic analysis of the Procolophonidae.
The new *Libognathus sheddi* material came from the Simpson Ranch locality (MOTT 3874), 4.5 kilometers from the holotype locality, UU Sand Ranch (MOTT 3882) (Figure 1). Both *Libognathus* localities occur in the Cooper Canyon Formation of the Dockum Group, in Garza County, Texas. The Cooper Canyon Formation was first named by Chatterjee (1986) as the Cooper Formation and emended by Lehman et al. (1992) to the Cooper Canyon Formation for the predominate mudstone unit in Garza County, Texas. The Cooper Canyon Formation has since, in some publications, subsumed the underlying Trujillo Sandstone and Tecovas Formation and subdivided the Cooper Canyon Formation into three units, the lower, middle, and upper (Martz, 2008; Martz et al., 2013), though in Martz et al. (2013) both lower, middle, and upper units of the Cooper Canyon, and “correlative with the Tecovas Formation,” “correlative with the Trujillo Formation,” and “correlative with the Bull Canyon Formation” were used.

However, in an alternative nomenclature of the Dockum Group in Garza County, the Cooper Canyon Formation has been abandoned altogether, instead using the older nomenclature, in ascending order, the Tecovas Formation, Trujillo Formation and Bull Canyon Formation (Cather et al., 2013; Mueller, 2016; Mueller et al., 2016; Sarigül et al., 2018 (in part); Mueller et al., 2023). For this study, we will provisionally follow the Cooper Canyon terminology of Martz (2008).

The Simpson Ranch locality (MOTT 3874), lies in the upper unit of the Cooper Canyon Formation. The locality is a purplish-red lag deposit at the base of a mudstone unit (B.D.M, J. Martz field notes). The Simpson Ranch locality is stratigraphically between the UU Ranch Sandstone and the Kirkpatrick Ranch Sandstone, roughly equivalent stratigraphically to the Macy Ranch Locality (MOTT 3927) (Martz, 2008). This places the new *Libognathus* material in the upper half of the Revuelitan teilzone/holochozone (Lessner et al., 2018; Martz & Parker, 2017).

The holotype of *Libognathus sheddi* (DMNH 20491) (Figure 2), along with the new aetosaur, *Garzapelta muelleri* (Reyes et al., in press), and a vertebra of “Procoelosaurus” (Atanassov, 2002; Martz et al., 2013), come from the UU Sand Creek Locality (MOTT 3882), approximately 4.5 km from the Simpson Ranch locality, but stratigraphically lower. The UU Sand Creek consists of a 10 cm thick medium-coarse-grained sandstone that sits near the top of the Miller Ranch Sandstone in the middle unit of the Cooper Canyon Formation (Martz, 2008). This places the fauna of the UU Sand Creek locality in the lower half of the Revuelitian (Martz et al., 2013; Martz & Parker, 2017). This placement in the lower half of the

![Figure 2](image-url)
Revueltian is based on the stratigraphic position of UU Sand Creek locality (MOTT 3882) approximately 15 m above the lowest known occurrence of the phytosaur *Machaeroprosopus* (MOTT 3892) (Hungerbühler et al., 2013; Lessner et al., 2018; Martz, 2008; Martz et al., 2013) The occurrence of *Machaeroprosopus* defines the base of the Revueltian teilzone / holochronozone, with a temporal range of ~215–207 Ma, mid-Norian–Rhaetian (Martz & Parker, 2017). Hence, based on the occurrences of *Libognathus* in the Cooper Canyon Formation, the range of *Libognathus* spans much of the Revueltian.

3 | PHYLOGENETIC METHODS

To determine the relationships of *Libognathus sheddi* among procolophonids, we conducted a phylogenetic analysis using the latest renditions of the Cisneros (2008a) analysis of procolophonid relationships, that of Hamley et al. (2021), Pinheiro et al. (2021), and Butler et al. (2023). We merged these three matrices, adding the scorings of *Orytoporan insolitus* by Pinheiro et al. (2021), and *Hwiccewyrm* (Butler et al., 2023) into the more unified matrix of Hamley et al. (2021). We replaced the taxon “Owenettidae” with three separate owenettid taxa: *Saurodaktes kitchingorum*, based on personal observation of the holotype BP/1/4195; *Barasaurus besairei*, based on the descriptions of Meckert (1995); and *Candelaria barbouri* based on the descriptions of Cisneros et al. (2004) and Müller (2021). We also added several leptopleuronine specimens from the North American southwest, specifically *Libognathus*, the “Glen’s Ferry form” from the Owl Rock Member of the Chinle Formation of Arizona (unpublished data, Xavier Jenkins and Bryan J. Small), and the “Abajo form” from the Owl Rock Member of the Chinle Formation of Utah (Fraser et al., 2005). Additionally, we expanded upon the current matrix by modifying 5 existing characters and adding 26 characters focused on encoding the morphological diversity of Leptopleuroninae concerning primarily the regions of the antorbital buttress and snout, quadratejugal and tympanum, and mandible (see Data S1–S4). Characters 8, 12, 14, 18, 25, 26, 31, 32, 39, and 81 were treated as additive following (Cisneros, 2008a).

The resulting data matrix of 38 taxa and/or specimens and 90 characters was compiled as a matrix in Morphobank.org and run on TNT 1.6 (Goloboff & Morales, 2023). Two analyses were conducted, the first analysis used the New Technology Search Algorithm, searching for a minimum length 100 times with the default Ratcheting, Drift, and Tree-fusing parameters, and the second analysis used the traditional (heuristic) search algorithm, saving 10 replicates (TBR) and collapsing branches with ambiguous support. Branch supports were calculated with a bootstrap analysis, also in TNT 1.6, using frequency differences (“GC”).

3.1 | Institutional abbreviations


4 | SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768.
LEPTOPLEURONIDAE Seeley, 1888.
LEPTOPLEURONINAE Ivakhnenko, 1979.
LIBOGNATHUS Small, 1997.
LIBOGNATHUS SHEDDI Small, 1997.

4.1 | Holotype

DMNH 20491, left dentary with teeth and a fragment of the coronoid.

4.2 | Newly referred material

All of the referred material described comes from the Simpson Ranch locality (MOTT VPL 3874) in the middle unit of the Cooper Canyon Formation, Dockum Group near Post, Garza County, Texas. TTU-P10068, antorbital portion of a skull; TTU-P10069, right dentary with teeth and a portion of the coronoid; TTU-P10081, associated left maxilla and premaxilla with teeth, with a small fragment of the ectopterygoid attached; TTU-P14493, the fragment of left dentary; TTU-P23576, partial left dentary, splenial, and coronoid; TTU-P10523, partial right quadratejugal; TTU-P12544X, partial right quadratejugal; TTU-P23575, partial quadratejugal; TTU-P10524, distal half of left femur; TTU-P10525, vertebra; TTU-P11151, and distal end of a right humerus.
4.3 Distribution

Cooper Canyon Formation, Revueltan teilzone/holochronozone, of the Dockum Group, Late Triassic (Norian), western Texas. Detailed descriptions of the type locality, UU Sand Creek (BDM-451: MOT VPL 3882) and Simpson Ranch (MOTT VPL 3874) (referred specimens) are on file in the Paleontology Division of the Museum of Texas Tech.

4.4 Emended diagnosis

Dentary deep, ventral margin of bone extends oblique to the dorsal margin (≥23°) immediately from the symphysis; coronoid extends anteriorly, underlying the posteriormost teeth of the dentary on the lingual surface; lacrimal-nasal contact reduced; suborbital foramen formed by maxilla and ectopterygoid, excluding the palatine; posterior supralabial foramen shared by maxilla and ectopterygoid, excluding the pala-tine; posterior supralabial foramen shared by maxilla and jugal. A robust, Y-shaped antorbital pillar formed primarily by the palatine, and massive orbitonasale and facial foramina (shared with unnamed southwest USA leptopleuronines).

5 | OSTEOLOGICAL DESCRIPTION

5.1 General remarks

The referred postcranial material will not be described in this study as it is fragmentary and provides no useful phylogenetic information. Some isolated cranial elements that do not possess any autapomorphies of the holotype (DMNH 20491) have been included in Libognathus. However, all referred materials come from a single locality, at the same stratigraphic level, and have procolophonid apomorphies, and the dentary material from the new locality does possess Libognathus autapomorphies. Due to the overall rarity of procolophonids in the Late Triassic of the southwest USA, and the occurrence of definitive dentary material at the locality, the circumstantial evidence makes it likely that the isolated elements belong to Libognathus. This can be nullified with the discovery of additional material. There is precedence for this methodology being used in the past when dealing with isolated definitive elements associated with other autapomorphic elements in a single locality (e.g., Langer & Ferigolo, 2013; Martz & Small, 2019).

Most of the description of the skull is based on TTU-P10068 (Figures 3 and 4) with supporting information from TTU-P10081, TTU-P10069, TTU-P14493, TTU-P23576, TTU-P12544X and TTU-P10253 (Figures 5–8).

The skull is estimated to have been 70 mm in length and 64 mm in width, excluding the spines on the quadratojugal. The skull and jaw together are estimated to be 44 mm in height. Libognathus sheddi exhibits characters of the Procolophonidae including a very shallow anterolateral depression of the maxilla posterior to the external nares; transversely expanded molariform teeth with transverse ridge bounded by two cusps; and quadratojugal with spines. Using the formula for determining the depth of snout of Cisneros (2008a), the rostrum of Libognathus is deep (0.67), being proportionally deeper than the “Abajo form” (~0.50), shallower than Leptopleuron lacertinum (~0.73, our measurement contra Cisneros, 2008a), and similar to but deeper than Hypsognathus fenneri (~0.63, our measurement contra Cisneros (2008a)) (Figure 6). The jaw is much deeper dorsoventrally than Hypsognathus and Leptopleuron in that the dentary deepens immediately at the symphysis, whereas in Hypsognathus and Leptopleuron the ventral margin is almost parallel to the dorsal alveolar margin for part of the dentary length before diverging (Säilä, 2010; Sues et al., 2000). The external naris is dorsoventrally expanded and proportionally larger than in Hypsognathus, and similar in size and proportion to that of Leptopleuron (Säilä, 2010), the “Abajo form” (Fraser et al., 2005), and the “Glen’s Ferry form” (unpublished data, Xavier Jenkins and Bryan J. Small).

5.2 Premaxilla

The dorsal margin of the premaxilla of Libognathus contacts the nasal both anterodorsally and posterior to the external nares, excluding a maxillary contribution to the external nares in lateral view (Figures 3–5). The supranarial process of the premaxilla extends postero-dorsally to contact the nasal slightly posterior to the anterior margin of the external nares. The posterior margin of the supranarial process forms part of the internarial bar extending between the external nares. The external nares is anteroposteriorly enlarged, similar to Hypsognathus (Sues et al., 2000) but different from Leptopleuron (Säilä, 2010) or Hviccewyrm (Butler et al., 2023) which possess an external naris which is narrower anteroposteriorly. Along the posterior margin of the premaxilla, just dorsal to the second tooth, there is a small projection of the maxilla into the premaxilla. The supranarial process of the premaxilla extends dorsally, forming most of the posterior border of the external nares along with the nasal. Posteriorly, the premaxilla is bordered exclusively by the maxilla. In the right lateral view, there is a foramen located near the posterior margin of the external nares at the premaxilla-nasal contact and a smaller foramen located ventral to the premaxilla-
nasal foramen. These foramina are not visible on the left side.

The palatal portion of the premaxilla extends posteriorly past the anterior margin of the second tooth in the maxilla in both TTU-P10068 and TTUP-10081, as in most procolophonomorphs (Carroll & Lindsey, 1985). In the palatal view (Figure 4a, b), there is a foramen surrounded by a depression on the premaxilla for the reception of the crown of the anterior dentary tooth as observed in the leptopleuro­nines Hypsognathus (Sues et al., 2000), Leptopleuron (Säilä, 2010) Soturnia (Cisneros & Schultz, 2003), and Hvic­cewyrm (Butler et al., 2023) which may be homologous to the prepalatal foramen (Heaton, 1979). A smaller prepalatal foramen that presumably did not receive the anteriormost
dentary tooth is present in some non-leptopleuronine proco-lopophonids (e.g., *Eomurruna yurrgensis*, Hamley et al., 2021).

As in other leptopleuronines, the premaxillae of *Libognathus* possesses two teeth. The anteriormost portion of the premaxillae and the incisiform teeth are damaged in TTU-P10068. Much of the incisiform crowns are damaged with infilled pulp cavities of the teeth exposed. The base of the anterior tooth of each premaxilla is noticeably larger in diameter than the second tooth, similar to *Hypsognathus* (Sues et al., 2000) but unlike other leptopleuronines, such as *Hwiccewyrm* (Butler et al., 2023), in which the premaxillary teeth are subequal. Although only the pulp cores and bases are preserved, the incisors appear to be oriented vertically. The second premaxillary tooth, though incomplete is better preserved on the right premaxilla. It had a circular cross section, and distally, it was worn into a wear facet. It is smaller than the first incisiform tooth and the proceeding first maxillary tooth. The first premaxillary tooth is preserved in TTU-P10081 (Figure 5). It is vertically oriented, labiolingually expanded, and incisiform as in *Hypsognathus* (Sues et al., 2000) and the “Abajo form” (Fraser et al., 2005). The second premaxillary tooth is circular in cross section at the base and the tip is less worn than the second premaxillary tooth of TTU-P10068. The second premaxillary tooth is slightly smaller than the first premaxillary tooth and slightly larger than the first maxillary tooth in both specimens.

### 5.3 Maxilla

Anteriorly, the maxilla of *Libognathus* is dorsoventrally deep above the tooth row, but posteriorly it is dorsoventrally shallow above the tooth row due to the anterior
projection of the jugal (Figures 3–5). The maxilla possesses an almost imperceptible, slight maxillary depression just posterior to the external naris; far reduced compared to the large, maxillary depression seen in most other procolophonids (e.g., *Coletta seca*, Modesto et al., 2003). There are two supralabial foramina in the lateral margin of the maxilla, one above the tooth row between the first and second tooth, and a larger foramen above the third tooth at the contact of the maxilla and anteroventral extension of the jugal. This differs from the typical condition as seen in leptopleuronines, exemplified by *Hypsognathus* (Sues et al., 2000) and *Leptopleuron* (Säilä, 2010) where the two foramina are totally enclosed by the maxilla, however, similarly placed foramina are present in the “Glen’s Ferry form” (unpublished data, Xavier Jenkins and Bryan J. Small) and *Hwiccewyrm* (Butler et al., 2023).

Dorsally, the maxilla of *Libognathus* shares an extensive border with the nasal. Posteriorly, the right maxilla has a contact with the enlarged lacrimal. However, the left maxilla is separated from the lacrimal by the jugal. In *Hypsognathus* (Sues et al., 2000) there is a small lacrimal/maxilla contact, and no maxilla/lacrimal contact in *Leptopleuron* (Säilä, 2010).

The tooth row ends posteriorly just anterior to the anterior margin of the orbit. In the ventral view, the maxilla and ectopterygoid form the border of the suborbital foramen. This differs from other procolophonids in that either the condition is unknown, or the suborbital foramen border is shared by the ectopterygoid, palatine (e.g., Carroll & Lindsey, 1985), and sometimes the maxilla (e.g., MacDougall & Modesto, 2011).

Posteriorly, the maxilla of *Libognathus* overhangs the tooth row, forming a laterally extending shelf from the tooth row as in other leptopleuronines. This maxillary shelf is overlain laterally by the jugal.

In the ventral view (Figure 4a, b), on the anterior portion of the maxilla, there is a small shelf medial to the first and second maxillary teeth that, along with the premaxilla, contributes to the anterior border of the internal naris. In TTU-P10068, there are five teeth on the right maxilla and four teeth on the left maxilla with no
evidence of a fifth tooth. Maxillary tooth counts of five or fewer are diagnostic of late Triassic leptopleuronines (e.g., *Hwiccewyrm*, Butler et al., 2023). Five of the maxillary teeth are labiolingually expanded, with the first maxillary tooth being the smallest. The tooth crowns bear cusps on the labial and lingual margins. There is a thin, connecting ridge between the two cusps along the posterior margin of the teeth. The cusps are equal in height and are formed by anterodorsally directed occlusal basin.

In TTU-P10081 (Figure 5), the first maxillary tooth is also the smallest maxillary tooth and is unworn, labiolingually expanded, bicuspid, and may be a newly erupted tooth. There are 5 maxillary teeth in TTU-P10081. There is evidence of early development of resorption pits on the lingual maxilla surface under maxillary teeth three and five. The resorption pit on the maxilla under tooth 4 is well developed, with a small replacement tooth forming.

### 5.4 Nasal

The nasal of *Libognathus* forms the dorsal margin and a small portion of the anterior and posterior margins of the external naris (Figure 3). The nasal contacts the premaxilla and maxilla ventrally, the lacrimal posteriorly, and the frontal and prefrontal posteriorly. On the left side of the skull, the nasal makes a posterodorsal contact with the jugal. On the right side, the skull surface is damaged in this region, making determinations of sutures difficult. The best interpretation is that the lacrimal and maxilla make contact, blocking the nasal-jugal contact. The nasal-jugal contact is present. The sutured contact between the nasal and the frontal is interdigitated and perpendicular to the sagittal plane of the skull. Several foramina pierce the nasal at the posterodorsal narial margin, similar to *Hwiccewyrm* (Butler et al., 2023) although damage to the external surface of the nasal in this region precludes an exact count.

### 5.5 Frontal

The frontals of *Libognathus* are incompletely known (Figures 3 and 4c,d). In specimen TTU-P10068, the frontals are incomplete posteriorly. The dorsal surface of the frontal is flat and smooth and forms the interorbital platform. The anterolateral margin of the frontal is bordered by the prefrontal. The suture between the frontal and the prefrontal is smooth and roughly parallel to the sagittal plane of the skull. The frontal of *Libognathus* lacks a raised orbitotemporal crest, similar to *Hypsognathus* (Sues et al., 2000), but unlike the European leptopleuronines *Leptopleuron* (Säilä, 2010) or *Hwiccewyrm* (Butler et al., 2023).

### 5.6 Prefrontal

The prefrontals are present but reduced in comparison to *Leptopleuron* (Säilä, 2010) and differs from *Hypsognathus* (Sues et al., 2000) in which the prefrontals are not present on the skull roof, although the sutures are often not observable in *Hypsognathus* (Figures 3 and 4c,d). The prefrontal is bounded medially by a smooth suture with the frontal. Laterally, there is an interdigitating suture between the prefrontal and lacrimal. Anteriorly there is a small contact with the nasal. The prefrontal does not extend ventrally, but, along with the lacrimal forms the dorsal rim of the enlarged orbitonasale foramen (see palatine description below) (Figure 4). The enlarged orbitonasal foramen of *Libognathus* is much larger than the typical orbitonasal foramen of other procolophonids (e.g., Carroll & Lindsey, 1985; Hamley et al., 2021), including *Hwiccewyrm* (Butler et al., 2023:Figure 2f). The prefrontal has a slight contact with the dorsomedial branch of the large, robust, pillar-like orbitonasal septum (see palatine description below). Instead, the frontal makes most of the dorsal palatine contact with the dorsomedial branch of the pillar-like orbitonasal septum.

### 5.7 Lacrimal

The lacrimal of *Libognathus* is a wedge-shaped element that forms the anterior portion of the orbit between the prefrontal and the jugal, and along the posterior margin of the lacrimal is the opening for the lacrimal duct (Figures 3 and 4c,d). There is a discrepancy between the right and left lacrimals in relation to the maxilla. Though the sutures are difficult to discern, the right lacrimal is bordered ventrally by the jugal and the maxilla, dorsally by the prefrontal, and anterodorsally by the nasal. The left lacrimal is bordered dorsally by the prefrontal, dorsally, and anteriorly in part by the nasal. The jugal borders the lacrimal ventrally and in part anteriorly, excluding a maxillary contact with the lacrimal and to the orbit. The lacrimal forms the part of the dorsal border of the very large orbitonasal foramen, which is on the dorsal edge of the orbitonasale septum. The exact sutures for the lacrimal-orbitonasale septum are unclear.

### 5.8 Jugal

The jugal of *Libognathus* is incomplete, but probably dorsoventrally deep, projecting far ventral to the maxillary dentition, as in *Hypsognathus* but unlike *Leptopleuron* (Säilä, 2010) or *Mandaphon nadra* (Tsuji, 2018) (Figures 3–5). The ventral and anterior margin of the
The jugal is bordered by the maxilla. The jugal contacts the nasal anterodorsally on the left side. There is no contact with the nasal on the right side, due to the contact of the lacrimal and the maxilla. At the anteroventral limit of the jugal is the large supralabial foramen shared with the maxilla dorsal to the third maxillary tooth. In leptopleuronine fashion, the jugal and the maxilla form a shelf extending laterally from above the tooth row (Cisneros, 2008a). The preserved margin of the jugal medioventrally contacts the ectopterygoid, with much of the posterior portions of both jugals missing. The dorsal margin of the preserved jugal is formed by the lacrimal.

5.9 | Quadratojugal

Two quadratojugals are known from Libognathus (Figure 6). The right quadratojugal fragment (TTU-P12544X) has three spines preserved, similar to other derived leptopleuronines, which usually possess two or more spines (Cisneros, 2008a). Of the two ventral spines, the anterior spine is relatively complete. The anterior spine is in the form of a short, broad, conical process though somewhat dorsoventrally compressed. The posteriorly positioned spine consists of a base only but is much larger and spine-like than the boss in this region in Hwiccewyrm (Butler et al., 2023:Figure 5h). The dorsal spine of the quadratojugal is well-developed and conical. There is a shallow groove surrounding the base of the spines. There is the anteroventral process as described for Hypsognathus (Sues et al., 2000), but the process is incomplete in TTU-P12544X.

TTU-P10523, also a right partial quadratojugal, is more fragmentary. The anterior-most spines are identical in shape and orientation to TTU-P12544X. However, the area of the third more posterior spine is missing. The “Abajo form” (Fraser et al., 2005) possesses three quadratojugal spines, as does the “Glen’s Ferry form.” Leptopleuron (e.g., Säilä, 2010) and more basal leptopleuronines (e.g., Scoloparia (Sues & Baird, 1998), Sclerosaurus (Sues & Reisz, 2008), or Hwiccewyrm (Butler et al., 2023) possess two spines or fewer. The reported spine count in Hypsognathus varies from four (Colbert, 1946) to two (Sues et al., 2000). This discrepancy is not explained, though it is postulated here that the anteroventral projecting spine of Colbert (1946) is, in fact, the anteroventrally curved process described by Sues et al. (2000), which would give the specimens described by Colbert (1946) three spines.

The strong ventral development of the quadratojugal in Libognathus, which would have extended to cover much of the posterior mandible in lateral view, is more similar to Hypsognathus (Sues et al., 2000) and the “Abajo form” (Fraser et al., 2005) and the “Glen’s Ferry form” (unpublished data, X. J. and B. J. S) than any are to Leptopleuron (Säilä, 2010) and other procolophonids, in which the quadratojugal has a weaker ventral extent.

5.10 | Vomer

There is a small, anterior remnant of the vomer preserved (Figure 4a,b). It forms a narrow, posteriorly projecting process. Posteriorly, a fragment of the vomer is sutured to the palatines and possibly the pterygoids. No denticles are present on the preserved portions of the vomer.

5.11 | Ectopterygoid

The ectopterygoid of Libognathus forms a small triangular process with a ridge projecting anteriorly along the medial portion of the maxilla, terminating medial to the last maxillary tooth (Figures 3 and 4). Medially, the ectopterygoid makes extensive contact with the palatine and the pterygoid. The ectopterygoid contacts the jugal laterally. In the ventral view, the ectopterygoid contacts the posterior border of the maxilla. The suborbital fenestra is located on the suture between the posterior edge of the maxilla and anterior edge of the ectopterygoid. As in other procolophonomorphs, the ectopterygoid is edentulous (Ford & Benson, 2020).

5.12 | Palatine

The palatine of Libognathus forms an arch in the ventral view, with the vomer forming a ridge between the palatines (Figures 3 and 4). In the posterior view, due to the missing posterior portion of the skull, the orbitonasale septa in the
form of robust pillars in lieu of the antorbital buttress is visible and projects dorsally and underplates the skull roof. This pillar is made up almost entirely of the palatine. The pillars are situated more medial than the antorbital buttress wall seen in some procolophonids such as *Tichvinskia* (Ivakhnenko, 1973), *Procolophon* (Carroll & Lindsey, 1985), and *Kapes* (Zaher et al., 2018), that are usually made up of a combination of prefrontal, lacrimal and palatine. Medially the orbitonasal septum pillars frame the large cavity for the olfactory tract. Laterally the pillars are bounded by extremely large openings for the facial foramina, a morphology otherwise only known in the Glen’s Ferry leptolepurosines. The dorsal end of the pillar is pierced by the very large foramen orbitonasale. Ventrally the palatine orbitonasal septa suture with each other, the pterygoid, and the ectopterygoid.

This pillar differs from the structure of the typical orbitonasal septum, in the form of an antorbital buttress seen in other parareptiles (e.g., Reisz et al., 2007) and procolophonids (Carroll & Lindsey, 1985; Ivakhnenko, 1973) in which the septum is more of a sheet of bone made of varying combinations of the lacrimal, prefrontal, and the palatine. The procolophonid *Kapes bentoni* (Zaher et al., 2018, supp. mat.) though figured and not described, shows an intermediate condition between a broad orbitonasal septum and the pillar of *Libognathus*. The orbitonasal septum in *K. bentoni* (BRSUG 29950–13) is broader than the pillar of *Libognathus*, but stouter and narrower than the antorbital buttress of other procolophonids (e.g., Carroll & Lindsey, 1985; Ivakhnenko, 1973). The lateral edge of the semi-broad orbitonasal septum of *Kapes* borders a large facial foramen, though this foramen is smaller than that of

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**FIGURE 7**  *Libognathus sheddi* (TTU-P10069) right dentary and coronoid in lingual (a, b), labial (c, d), and occlusal (e, f) views. Scale bar = 5 mm.
the Libognathus foramen. It is unclear which bones make up the orbitonasale septum in *K. bentoni* due to a lack of scan contrast in this region. Interestingly, in Colbert’s (1946) description of *Hypsognathus fenneri*, he interpreted an ascending bone of AMNH 1678, a skull that consists of a snout in interior view, as the palatine. Additionally, the “Glen’s Ferry form” mentioned by Sues et al. (2000) possesses a nearly identical pillar-like orbitonasale septum, strongly resembling the condition in *Libognathus*, though the sutures are unclear (Bryan J. Small, Xavier Jenkins, pers. obs). This feature has been largely ignored in discussions of the antorbital regions of procolophonids, and it is possible that this feature is a synapomorphy of Leptopleuroninae or another group of procolophonids.

### 5.13 Pterygoid

The partial pterygoids of *Libognathus* are visible in the ventral view, but the sutures with the palatines are difficult to discern (Figures 3 and 4). In the posterior view, the partial pterygoids are capped by the palatines (orbitonasale septa) dorsally and ectopterygoids laterally.

### 5.14 Dentary

The holotype left dentary and coronoid of *Libognathus* was described by Small (1997) (Figures 2, 7, and 8). A new right dentary and coronoid (TTU-P10069) supports the original description and confirms the identification of the new material as *Libognathus*. There is also a fragmentary dentary (TTU-P14493). TTU-P23576 is a partial dentary with splenial and coronoid.

TTU-P10069 (Figure 7) can be attributed to *Libognathus* on the basis of a deep dentary where the deepening starts immediately at the symphysis at an oblique angle of at least 30°, and the large lateral foramen under the fourth tooth. There is a circular base to a large, possibly incisiform tooth, followed by a diastema, followed by five molariform teeth. The first tooth is almost twice the diameter of the rest of the dentary teeth, similar to *Hypsognathus* (Sues et al., 2000), differing from *Leptopleuron* (Säilä, 2010), *Soturnia* (Cisneros & Schultz, 2003), and *Hwiccewyrm* (Butler et al., 2023) in which the diameter of the first tooth is close in size to the rest of the dentary teeth.

It was unclear whether there was a small second tooth behind tooth one in the holotype (Small, 1997). It was stated that there was a possibility of a faint resorption pit between the erupting tooth one and the next tooth and that there was a gap in this area. TTU-P10069 clearly shows a diastema at this spot, not a tooth, so the correct dentary tooth count for *Libognathus sheddi* is six. A slight diastema is present between the first and second teeth on the dentaries of *Hypsognathus* (Colbert, 1946: plate 27:4; Sues et al., 2000:Figure 3e) and *Hwiccewyrm* (Butler et al., 2023:Figure 8), and absent in *Leptopleuron* (Säilä, 2010:Figure 3a) and *Soturnia* (Cisneros & Schultz, 2003:Figure 2g, h).

*Libognathus* specimen TTU-P10069 possesses resorption pits on the lingual surface in various stages of
development under teeth 3–5, with the most developed resorption pit under tooth three (Figure 7a, b). None of the dentaries show distinct tooth roots or alveoli, though tooth number 6 in TTU-P10069 shows the tooth penetrating the dentary where a small amount of dentary is missing in the lateral view. Evidence of teeth penetrating the dentary is also visible in the holotype (DMNH 20491), especially in tooth position six in lateral view (Small, 1997: Figure 1a, b). The teeth in all dentaries are anklylosed with a spongy bone of attachment as described by Small (1997; Figure 1c, d).

TTU-P14493 (Figure 8) preserves two teeth, possibly teeth three and four, with a damaged alveolar area for tooth two. Below tooth four is a large foramen on the labial surface as in the Libognathus holotype. The teeth are unworn, indicating recent emplacement. Tooth four has damage at the base in labial view, but this is probably due to post-mortem damage. In lingual view, there are no signs of resorption pits, corroborating the recent growth of these teeth. In distal view, a broken surface, the last tooth shows penetration into the dentary. In labial view both preserved tooth four is penetrating the dentary where bone and been broken away.

TTU-P23576 (Figure 8) is fragmentary. The ventral edge diverges from the dorsal edge at approximately 30°. In labial view, the dentary possesses two small foramina under the first two preserved teeth and a large foramen under the last tooth. In DMNH 20491 and TTU-P10069, the large foramen is under tooth four, with a total tooth count of six. TTU-P23576 is proportionally smaller than the other Libognathus dentaries, the last tooth could be tooth four and this could be attributable to ontogeny. In Hypsognathus, the specimens described by Sues et al. (2000), show a difference in tooth count corresponding to specimen size. The large specimen of Hypsognathus, YPM 55831, has a tooth count of six. The smaller specimen, NSM 998GF45.1 has a tooth count of four.

In lingual view, the dentary of Libognathus possesses a large, well-developed resorption pit in the dentary immediately below the last tooth. The resorption pit extends into the base of the tooth above. There is a replacement tooth forming in the resorption pit. The posterior edge of the resorption pit invades the anterior edge of the anteriorly extended coronoid.

5.15 | Splenial

The splenial preserved in TTU-P23576 is the only splenial known for Libognathus (Figure 8). It covers the Meckelian groove. Dorsally and ventrally, in lingual view, the splenial contacts the dentary in straight, loosely fitted sutures.

5.16 | Coronoid

In TTU-P10069 and TTU-P23576, the single coronoid projects under the last one to two teeth in lingual view as in the holotype DMNH 20491 (Figures 7a, b, e, f and 8c, d). The possible extension of the coronoid under the teeth on the labial side cannot be discerned, which, in the holotype specimen (Figure 2), was reported to extend anteriorly under the last two dentary teeth (Small, 1997). However, since the coronoid does not extend laterally on the labial side in other specimens, and a re-examination of the holotype, the labial coronoid extension might be an artifact of preservation.

6 | PHYLOGENETIC ANALYSIS

The phylogenetic analyses recovered 95 and 80 MPTs, respectively, with a length of 214 steps each. The strict consensus trees recovered by both analyses were identical (Figure 9), and were rather well-resolved for “horned procolophonids” (which includes the subclades Procolophoninae and Leptopleuroninae) and in particular leptopleuronine procolophonids. The large polytomies for “horned procolophonids” found by previous studies (e.g., Hamley et al., 2021) are extremely reduced; the remaining, minor polytomies mostly concerned the relationships of early-branching taxa (e.g., Sauropareion, Modesto and Damiani (2007), and Kitchingnathus untabeni, Cisneros (2008b)) and the relationships of North American leptopleuronines. As in previous studies, support for most branches is low except for Procolophonidae and Leptopleuroninae as a whole, and the in-group relationships of Leptopleuroninae. Anomoiodon (Säilä, 2008), Thelephon contritus (Gow, 1977b), and both Kapes species (K. bentoni and K. mejmesculae) are found within the horned procolophonid clade (Procolophoninae + Leptopleuroninae) as basal leptopleuronines in a polytomy with Neoproclophon asiaticus (Young, 1957) and Pentaedrusaurus ordosianus (Li, 1989).

The strict consensus for both analyses (Figure 9) recovered Libognathus in a small polytomy with other leptopleuronines from the Revueltilian of the southwestern USA, specifically the “Glen’s Ferry form” and the “Abajo Form,” the latter of which is incompletely known and notably is lacking a mandible (forming Clade “B” of Figure 9). Clade B is sister to Hypsognathus, forming a North American node that is diagnosable by a strong anteroventral process of the jugal (character 73) and the presence of a diastema between the dentary incisiform tooth and the rest of the dentary dentition (Character 90). This “North American leptopleuronine clade” is found as...
the successive sister to *Hwiccewyrm* (Butler et al., 2023) and then *Soturnia* (Cisneros & Schultz, 2003), forming a clade that is diagnosed by: a posteriorly placed external naris relative to the first premaxillary tooth (Character 2), the occurrence of a deep occlusal depression in the maxillary teeth (Character 34), the lack of vomerine dentition (Character 35), the absence of presacral intercentra (Character 44), and the restriction of the maxillary dentition to being level with or anterior to the anterior orbital margin (Character 69). *Leptopleuron* (Säilä, 2010) is found as the sister to this group, forming a clade (Clade “A,” Figure 9) of possibly all Norian leptopleuronines (Figure 9).

7 | BIOSTRATIGRAPHY OF NORTH AMERICAN LEPTOPLEURONINES

Our support for a *Libognathus—Hypsognathus* clade brings into question the validity of using leptopleuronine procolophonids in vertebrate biostratigraphy. *Hypsognathus* is the index taxon for the Cliftonian LVF of eastern North America, which is roughly Revuelitian and/or Apachean equivalent (Lucas, 1998), although other tetrapod remains of biostratigraphic importance from the Newark Supergroup is lacking (Sues et al., 2000). As argued above, *Libognathus* falls within the Revuelitian
teilzone/holochronozone within the Cooper Canyon Formation (Marsh et al., 2019; Martz et al., 2013). The “Glen’s Ferry Form” and the “Abajo Form” are both known from the Owl Rock Member of the Chinle Formation and are also Revueltian in age (see Kent et al., 2019; Rasmussen et al., 2020 for a discussion on the age of the Owl Rock Member). Procolophonid morphotypes possibly similar to the Libognathus—Hypsognathus clade are also known from the Saints and Sinners Quarry of the Nugget Sandstone, which is probably the latest Triassic in age (Late Norian-Rhaetian, Britt et al., 2018), as well as from the “red siltstone” member of the Chinle Formation, Eagle Basin of Colorado (Revueltian, see Martz & Small, 2019, 2023), although these specimens are in need of an anatomical description. Scoloparia glyphanodon, a leptopleuronine described from the Evangeline Member of the Wolfville Formation of Canada (Carnian, Sues & Olsen, 2015; Fitch et al., 2023), is readily distinguished from the Libognathus-Hypsognathus clade by the presence of only two spines on the quadratojugal, the lack of a diastema between the dentary incisor and the rest of the dentary tooth row, and the presence of more than five teeth on the maxilla (Sues & Baird, 1998). Although preliminary, the presence of a leptopleuronine within the Libognathus-Hypsognathus clade is likely indicative of a Late Triassic (Revueltian or later) age and are thus the latest surviving procolophonids (Cisneros & Ruta, 2010), and are possibly a key taxonomic group for regional bi stratigraphic correlations, at least in North American deposits.

8 | TOOTH REPLACEMENT AND IMPLANTATION

Historically, there have been differing views of tooth replacement and implantation in procolophonids. Many authors considered procolophonids to have a subthecodont (=protothecodont) (sensu Bertin et al., 2018) implantation, where the teeth are set in shallow sockets, and show little if any signs of replacement activity (Broili & Schröder, 1936; Gow, 1977a; Säilä, 2009). Yet, others (Broom, 1905; Colbert, 1946) considered procolophonid implantation to be acrodont, a condition where the tooth is fused to the summit of the jawbone without sockets, or penetration into the jaw bone (e.g., Peyer, 1968).

Small (1997) described the dentary of Libognathus sheddi (Figure 2) and considered the mode of implantation to be subthecodont. Tooth replacement was also described as occurring at different stages throughout the dentary, including a well-developed replacement tooth about to erupt in alveolus number one. Due to the various stages of resorption pit development in Libognathus, it could be inferred that replacement was frequent. With evidence of an alveolus with a replacement tooth in the holotype of Libognathus, resorption pits, a replacement tooth forming in a resorption pit, and evidence of teeth penetrating the dentary, Small (1997) concluded a subthecodont implantation with the teeth subsequently “firmly anchored by spongy bone of attachment” (ankylosis). This form of implantation and replacement was also reported in Hypsognathus (Sues et al., 2000).

Cabreira and Cisneros (2009) did a histological analysis of the leptopleuronine procolophonid Soturnia caliodon and concluded that the method of implantation was acrodont with tooth replacement through resorption or recycling, and not through the old teeth falling or being pushed out. Interestingly, the teeth have what appear to be rooted, or as they termed, “pedicles,” which would be unusual for acrodonty, which, as defined by Bertin et al. (2018), “the apex of the tooth is set at the top of the tooth-bearing element, without any mediolateral tooth-bone contact. The tooth is neither set in a groove nor in alveoli because no bony wall is present on side of tooth.” Tooth replacement was slow. They implied that this method of implantation and replacement might be the norm for leptopleuronines, not the subthecodont implantation and replacement suggested by others (Säilä, 2009; Small, 1997; Sues et al., 2000). Cabreira and Cisneros (2009) saw no evidence of periodontal tissues attaching tooth to bone, suggesting that in a subthecodont condition, any fusion of tooth root to sockets without periodontal tissues was not likely in any tetrapod. However, fusion (ankylosis) of roots to sockets with replacement has been amply demonstrated in recent years (e.g., LeBlanc & Reisz, 2013, 2015).

Yet another combination of implantation types in one procolophonid specimen was demonstrated in Scoloparia glyphanodon in which the mandibular teeth demonstrated both subthecodonty and acrodonty, with no apparent replacement, and with new teeth added posteriorly (Jenkins & Bhullar, 2022).

MacDougall and Modesto (2011) described the skull of the procolophonid Sauropareion anoplus. On the lingual surface of the Sauropareion mandible described, a clear replacement tooth erupting at the base of a functional tooth, within a resorption pit was visible. They came to the conclusion that the method of implantation and replacement was subthecodont in which ankylosis occurred after the eruption of the new tooth and that the implantation of Soturnia caliodon (Cabreira & Cisneros, 2009) was a modified form of subthecodonty, and that there are no modern analogs that demonstrate tooth replacement coupled with acrodonty (see below).
The recent discovery of new tooth-bearing elements of *Libognathus sheddi* (this study) validates the earlier description of implantation and replacement in *L. sheddi* (Small, 1997). The right dentary TTU-P10069 has resorption pits of various stages of development under teeth three, four, and five (Figure 7a,b). The left maxilla TTU-P 10081 (Figure 5c, d) shows resorption pits of various stages of development in the dentary under teeth three, four, and five, with a replacement tooth forming in the resorption pit in the maxilla under tooth four, again implying frequent tooth replacement. TTU-P23576 (Figure 8c, d) shows a large, well-developed resorption pit under the last tooth with the dentary, a small part of the coronoid, and the base of the tooth involved in the pit. A replacement tooth is present in the resorption pit. TTU-P14493 (Figure 8) shows teeth penetrating the dentary where the bone is missing due to damage, especially in the posterior view (Figure 8g, h). The new *L. sheddi* material shows ankylosis of tooth to dentary, but it is unclear how the teeth ankylosed to the alveolar bone, compared to the plesiomorphic condition in Amniota (LeBlanc & Reisz, 2013).

Haridy et al. (2018) described a Permian captorhinid *Opisthodontosaurus carrolli*, exhibiting acrodont implantation and tooth replacement. Replacement teeth form lingual to functional teeth in soft tissue. The replacement tooth migrates to the tooth to be replaced, where a resorption pit forms in the base of the functional tooth, not in the dentary bone. Replacement appears to be infrequent. Once the replacement tooth moves into position, ankylosis is rapid. However, in regards to Cabreira and Cisneros (2009), there is no pedicle or root penetrating the dentary.

It does not appear that the acrodont teeth of extant rhynchocephalians, agamid lizards, or chameleons show any “pedicle” penetrating the dentary, nor does tooth replacement occur (Dosedélová et al., 2016; Jenkins et al., 2017; Smirina & Ananjeva, 2007). Haridy (2018) described a different form of “acrodonty” in some agamids in which the squamates start with a pleurodont form of implantation and achieve a form of acrodonty during ontogeny, but again no pedicles or replacement in the acrodont teeth. The extinct and extant examples of acrodonty differ from the condition described by Cabreira and Cisneros (2009).

It appears that it is possible that the procolophonids *Sauropareion*, *Scloparia*, *Libognathus*, and *Soturnia* (if acrodonty is the case) demonstrate four different modes of tooth replacement and implantation. *Sauropareion* shows a possible subtheodont implantation with infrequent replacement, where the replacement tooth forms lingual to the functional tooth and moves into a resorption pit that forms on the base of the functional tooth instead of the dentary bone. *L. sheddi* shows a possible subtheodont implantation where the tooth is ankylosed to the dentary/maxilla with frequent replacement, and the replacement tooth forming in a resorption pit on the lingual side of the dentary below the functional tooth to be replaced. *Soturnia* shows possible acrodont or subtheodont implantation with no or infrequent replacement. If there is a replacement, the replacement tooth forms after the resorption of the old functional tooth. *Scloparia* demonstrates two modes of implantation, subtheodonty and acrodonty with no replacement and new teeth added from the rear. It could be that in procolophonids in general, experimentation with different modes of implantation and replacement was common. However, as stated by Cabreira and Cisneros (2009), many of the observations of procolophonid dentitions were not supported by detailed histological analyses. Part of this problem is the small number of specimens in most taxa, which discourages destructive analysis, or simply no one has undertaken such analyses yet. Still, more study is needed to definitively resolve tooth implantation and replacement in procolophonids.

9 | CONCLUSIONS

New cranial material of *Libognathus sheddi* confirms its placement as a leptopleurine procolophonid, including an anterolateral depression of the maxilla posterior to the external naris; transversely expanded molariform teeth with a transverse ridge bounded by two cusps; and quadratojugal with numerous spines (Figure 10). The phylogenetic hypothesis generated, groups *Libognathus* in a clade with the “Glen’s Ferry form” and the “Abajo form,” as a
sister group to Hypsognathus. Libognathus and Hypsognathus share several synapomorphies including the prefrontals being restricted to the rim of the orbit and the reduced number of teeth. Libognathus is distinguished from Hypsognathus in having the autapomorphies of the premaxilla contacting the nasal posterior to the external naris and the suborbital foramen being surrounded by the ectopterygoid and maxilla. The skull of Libognathus is slightly deeper dorsoventrally than the skull of Hypsognathus. The “Abajo form” shares some characters with Libognathus such as the maxillary tooth row being inset laterally, two premaxillary teeth, and three quadratojugal spines. Libognathus differs from the “Abajo form” in that the snout is deeper in Libognathus (0.67) than in the “Abajo form” (~0.50). The unusual pillar-like orbitonasal septum in Libognathus is also shared by the “Glen’s Ferry form” and possibly Hypsognathus (Colbert, 1946).

The analysis of the additional material confirms that Libognathus is a derived procolophonid more closely related to the three Owl Rock leptopleuronines and then Hypsognathus than to any other procolophonid. Libognathus shows a possible protothecodont implantation, wherein the teeth are ankylosed to the jawbone, and replacement was frequent. In the Late Triassic of western North America, leptopleuronine procolophonids seem to be restricted to the Late Norian (Revueltian), with some undescribed procolophonids from the Nugget Sandstone extending into the Rhaetian.

AUTHOR CONTRIBUTIONS
Bryan J. Small: Investigation; writing – review and editing; formal analysis. Bill D. Mueller: Conceptualization; investigation; writing – original draft; data curation. Xavier Jenkins: Writing – review and editing; formal analysis; methodology. Adam K. Huttenlocker: Writing – review and editing; formal analysis; methodology. Sankar Chatterjee: Conceptualization; investigation; writing – original draft; data curation.

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