




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

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Funding information

The Museum of Texas Tech University

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 $\geq 23^\circ$; 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 leptopleuronines). Phylogenetic analysis indicates that *Libognathus* is a highly derived leptopleuronine procolophonid, closely related to *Hypsognathus fenneri* and other southwest USA Revuelian leptopleuronines, 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 anteroventral 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/holochronozone, 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 Middle Triassic 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 *Cognathus 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 *Cognathus* within Procolophonina 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 southwest USA was the leptopleuronine *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 leptopleuronine 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, per. 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

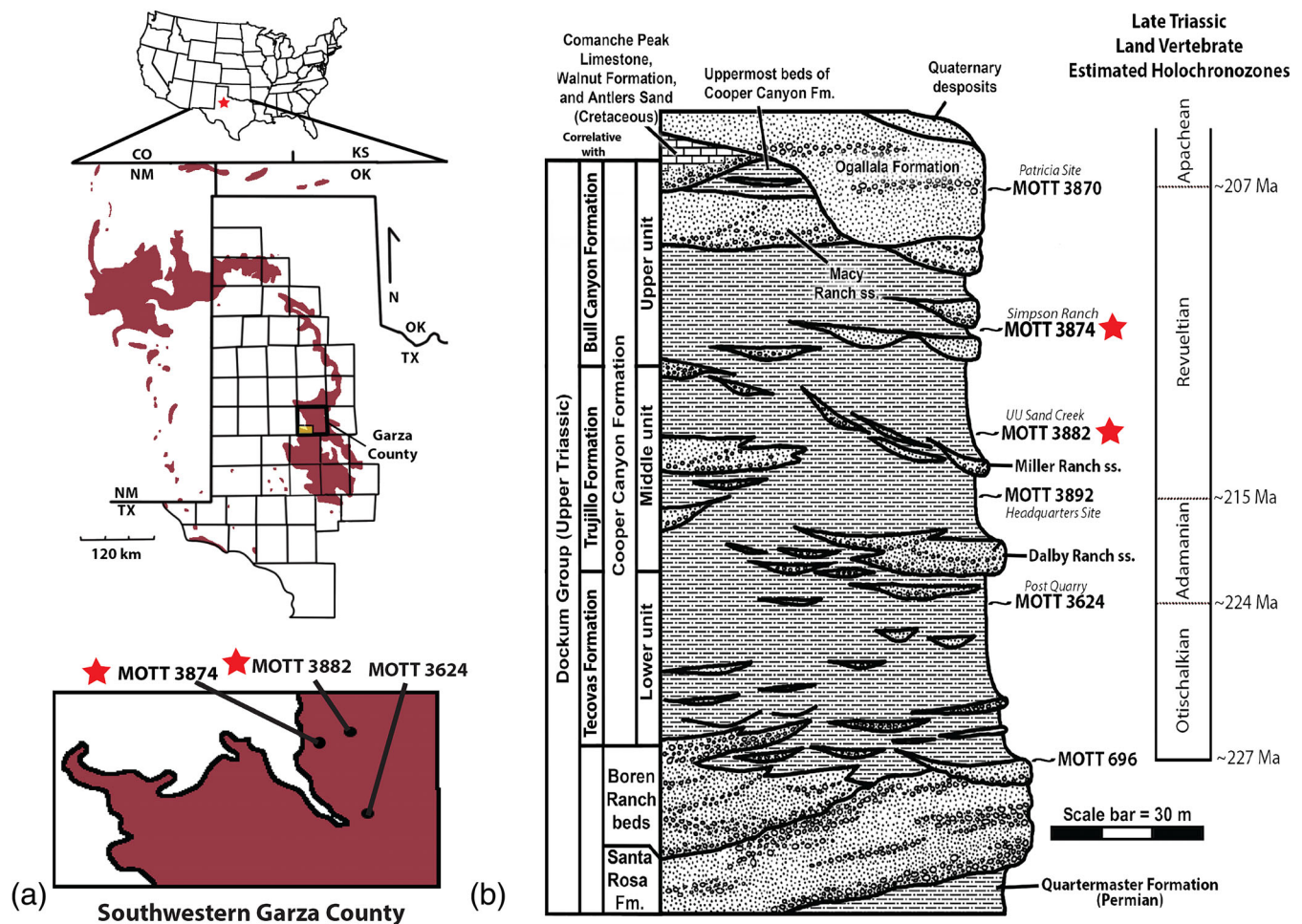


FIGURE 1 (a) Geographic and (b) stratigraphic occurrences of *Libognathus sheddi*, type locality UU Sand Creek (MOTT 3882) and referred locality Simpson Ranch (MOTT 3874) and that of other relevant localities within the Cooper Canyon Formation in Garza County, Texas, USA. The red stars denote the *Libognathus* localities. The figure is modified from Lessner et al. (2018) and Martz and Parker (2017). (a) Geographic exposures of the Dockum Group are shaded in red. Locality data is based on Martz (2008) and Bill D. Mueller (field data). The temporal range of Late Triassic Land Vertebrate Estimate Holochronozones is based on Martz and Parker (2017), with absolute ages derived from Dunlavey et al. (2009), Atchley et al. (2013), Ramezani et al. (2011, 2014), and Rasmussen et al. (2020). CO, Colorado; Ka, Kansas; Ma, Million years; MOTT, Museum of Texas Tech; NM, New Mexico; OK, Oklahoma; TX, Texas. Figure 1 modified from Reyes et al., *in press*, this issue.

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.

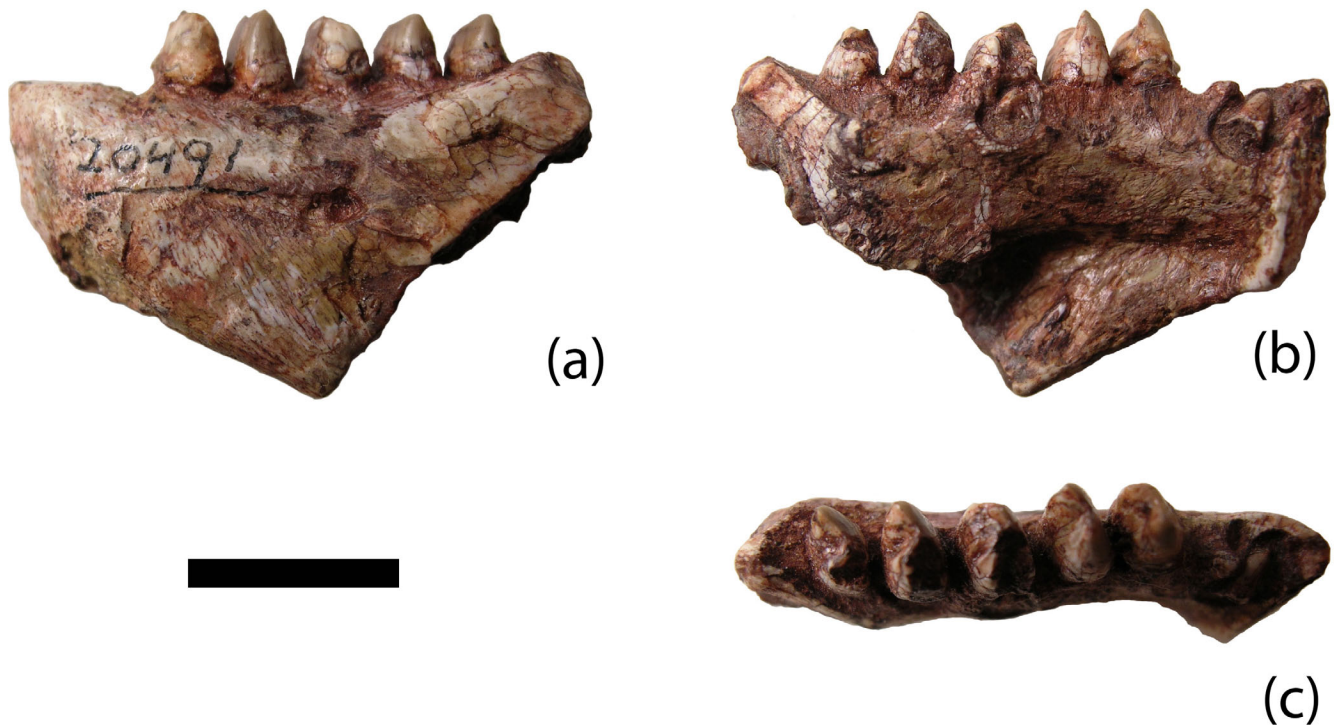


FIGURE 2 *Libognathus sheddi*, holotype (DMNH 20491). Dentary in labial (a), dentary and coronoid in lingual (b) and occlusal (c) views. Scale bar = 1 cm.

2 | GEOLOGY

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 Revueltian teilzone/holochronozone (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 “*Procoelosaurius*” (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 Revueltian (Martz et al., 2013; Martz & Parker, 2017). This placement in the lower half of the

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 *Machaeroprotopus* (MOTT 3892) (Hungerbühler et al., 2013; Lessner et al., 2018; Martz, 2008; Martz et al., 2013). The occurrence of *Machaeroprotopus* 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 *Oryporan insolitus* by Pinheiro et al. (2021), and *Hwiccewyrms* (Butler et al., 2023) into the more unified matrix of Hamley et al. (2021). We replaced the taxon “Owenettidae” with three separate owenettid taxa: *Saurodekteles 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, quadratojugal 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](https://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

AMNH, American Museum of Natural History, New York; BRSUG, University of Bristol, Geological Collection, Bristol; DMNH, Denver Museum of Nature and Science, Denver; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNA, Museum of Northern Arizona, Flagstaff; MOTT VPL, Museum of Texas Tech Vertebrate Paleontology locality; NSM, Nova Scotia Museum, Halifax, Nova Scotia; TTU, Texas Tech University, Lubbock; USNM, National Museum of Natural History, Washington, D.C.; YPM, Yale Peabody Museum, New Haven.

4 | SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768.

PARAREPTILIA Olson, 1947 sensu Laurin & Reisz, 1995.

PROCOLOPHONIDAE 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 quadratojugal; TTU-P12544X, partial right quadratojugal; TTU-P23575, partial quadratojugal; 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, Revueltian teilzone/holo-chronozone, of the Dockum Group, Late Triassic (Norian), western Texas. Detailed descriptions of the type locality, UU Sand Creek (BDM-451: MOTT 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 ($\geq 23^\circ$) immediately from the symphysis; coronoid extends anteriorly, underlying the posterior-most 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 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 naris; 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 naris, excluding a maxillary contribution to the external nares in lateral view (Figures 3–5). The supranarial process of the premaxilla extends posterodorsally to contact the nasal slightly posterior to the anterior margin of the external naris. The posterior margin of the supranarial process forms part of the internarial bar extending between the external nares. The external naris is anteroposteriorly enlarged, similar to *Hypsognathus* (Sues et al., 2000) but different from *Leptopleuron* (Säilä, 2010) or *Hwiccewyrms* (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 subnarial process of the premaxilla extends dorsally, forming most of the posterior border of the external naris 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-

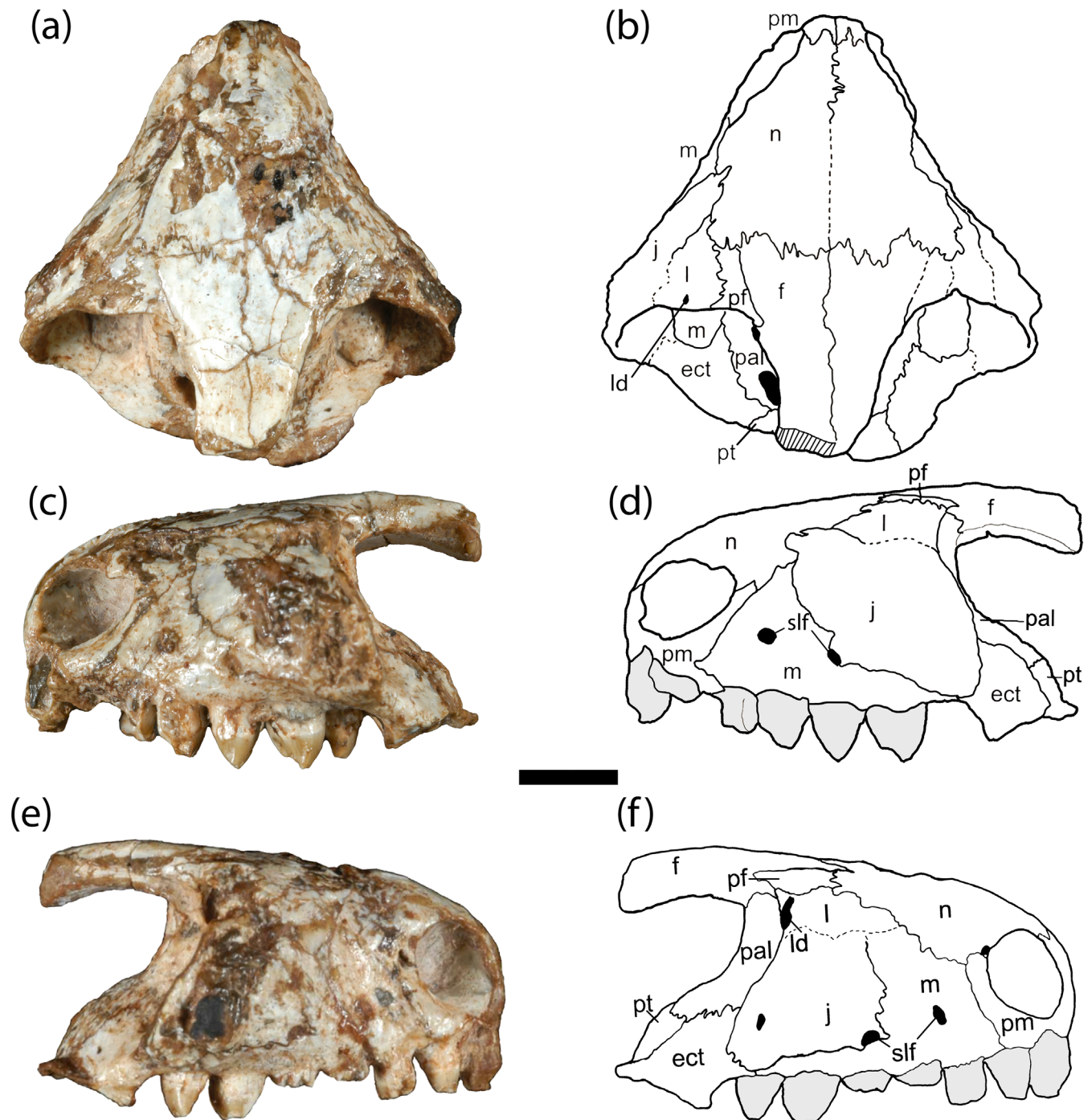


FIGURE 3 *Libognathus sheddi* (TTU-P10068). Partial skull in dorsal (a, b), left lateral (c, d), and right lateral (e, f) views. ect, ectopterygoid; f, frontal; j, jugal; l, lacrimal; ld, lacrimal duct; m, maxilla; n, nasal; pal, palatine; pf, prefrontal; pm, premaxilla; pt, pterygoid; slf, supralabial foramen. Scale bar = 5 mm.

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 *Hwiccewyrn* (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

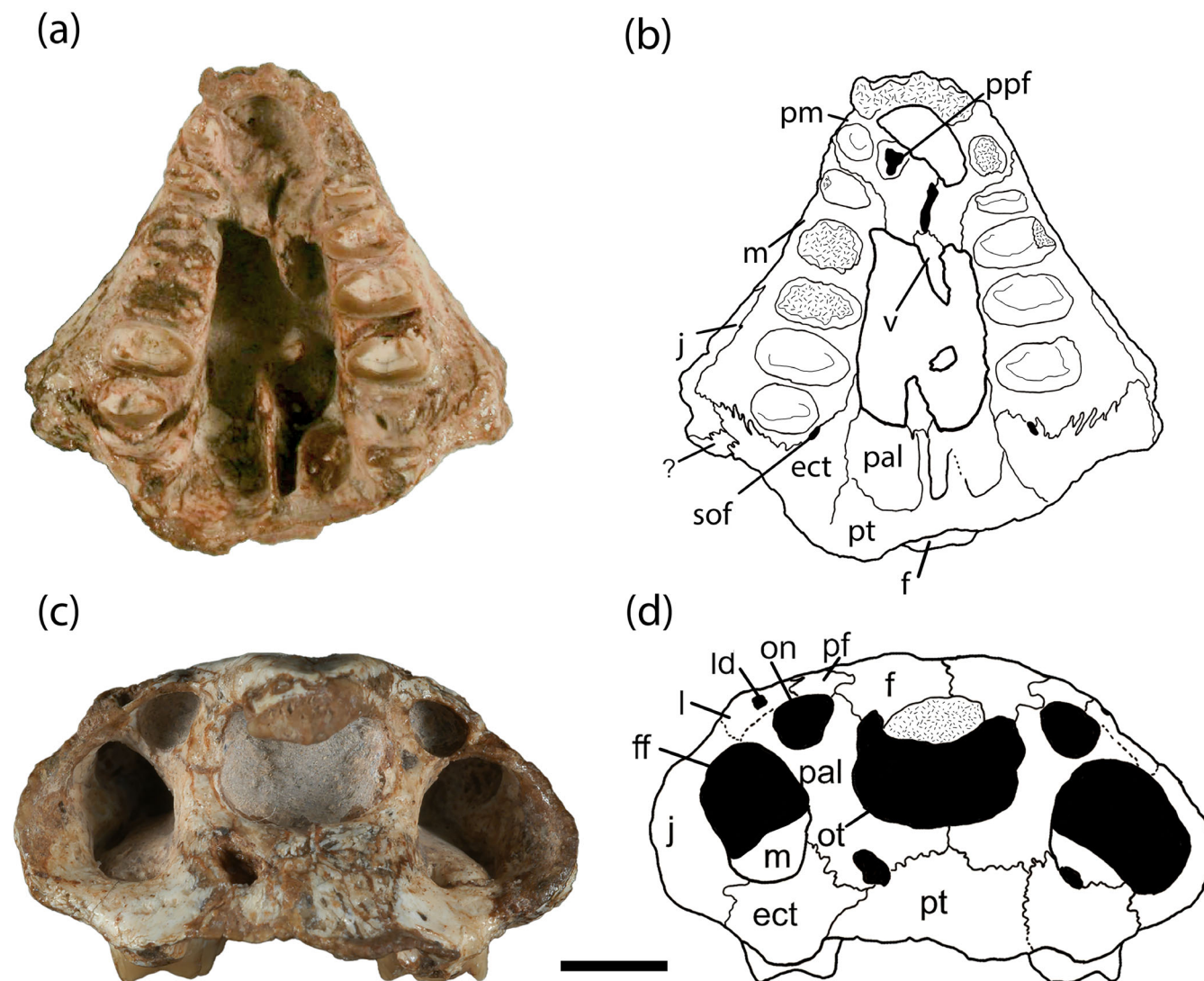


FIGURE 4 *Libognathus sheddi* (TTU-P10068). Partial skull in ventral (a, b), posterior (c, d) views. ect, ectopterygoid; f, frontal; ff, facial foramen; j, jugal; l, lacrimal; ld, lacrimal duct; m, maxilla; on, foramen orbitonasale; ot, olfactory tract; pal, palatine; pf, prefrontal; pm, premaxilla; ppt, prepalatal foramen; pt, pterygoid; sof, suborbital foramen; v, vomer. Scale bar = 5 mm.

dentary tooth is present in some non-leptopleuronine procoelophonids (e.g., *Eomurruna yurgensis*, 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 *Hwiccewyrn* (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

preceding 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

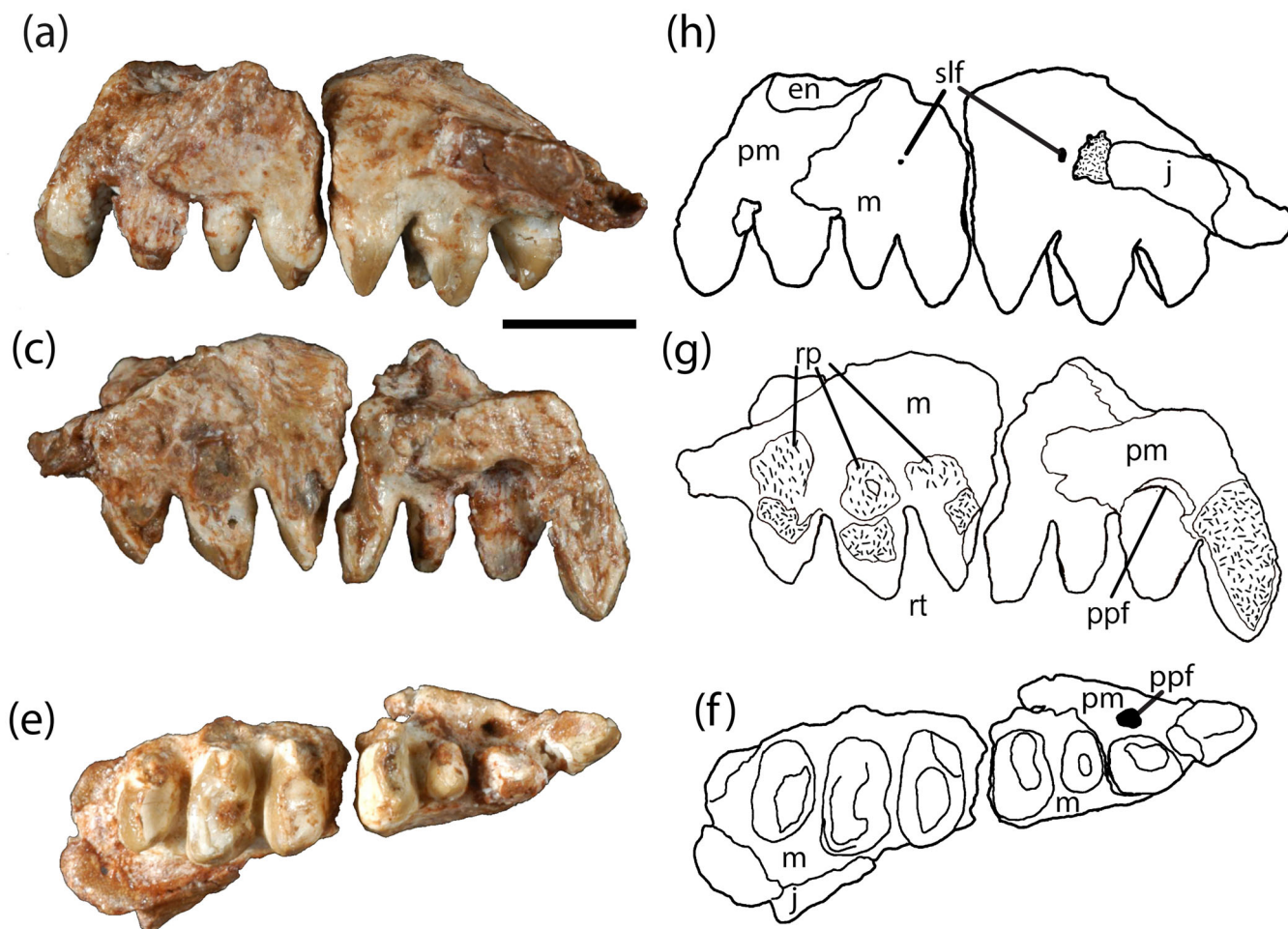


FIGURE 5 *Libognathus sheddi* (TTU P-10081). Partial skull in lateral (a, b), medial (c, d), and occlusal (e, f) views. en, external naris; m, maxilla; j, jugal; pm, premaxilla; ppt, prepalatal foramen; rp, resorption pit; rt, replacement tooth; slf, supralabial foramen. Scale bar = 5 mm.

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 *Hwiccewyrn* (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., *Hwiccewyrms*, 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 posteroventral 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 *Hwiccewyrms* (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 *Hwiccewyrms* (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 orbitonasale foramen of *Libognathus* is much larger than the typical orbitonasale foramen of other procolophonids (e.g., Carroll & Lindsey, 1985; Hamley et al., 2021), including *Hwiccewyrms* (Butler et al., 2023:Figure 2f). The prefrontal has a slight contact with the dorsomedial branch of the large, robust, pillar-like orbitonasale septum (see palatine description below). Instead, the frontal makes most of the dorsal palatine contact with the dorsomedial branch of the pillar-like orbitonasale 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 orbitonasale 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

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 *Hwiccewyrms* (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”

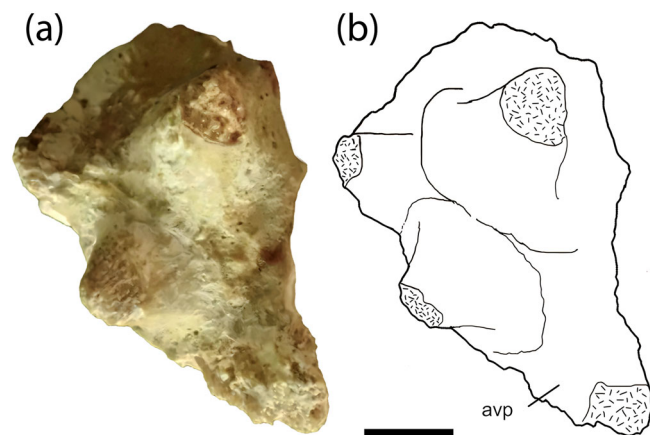


FIGURE 6 *Libognathus sheddi* (TTU P-12544X). Right quadratojugal in (a, b) lateral view. avp, anteroventral process. Scale bar = 5 mm.

(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 *Hwiccewyrms* (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 orbitonasale 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 leptopleuromorphs. The dorsal end of the pillar is pierced by the very large foramen orbitonasale. Ventrally the palatine orbitonasale septa suture with each other, the pterygoid, and the ectopterygoid.

This pillar differs from the structure of the typical orbitonasale 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 orbitonasale septum and the pillar of *Libognathus*. The orbitonasale 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 orbitonasale septum of *Kapes* borders a large facial foramen, though this foramen is smaller than that of

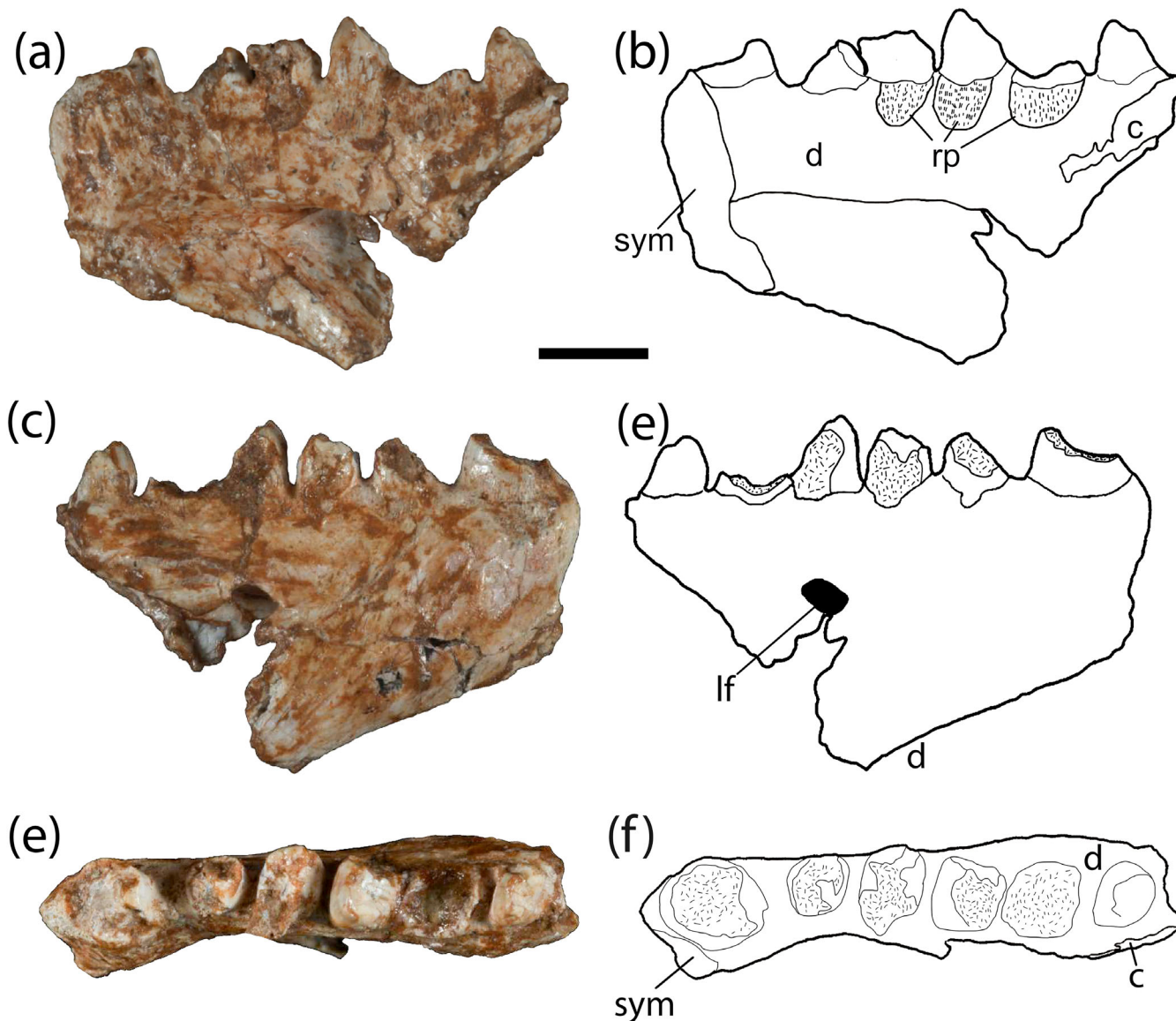


FIGURE 7 *Libognathus sheddi* (TTU-P10069) right dentary and coronoid in lingual (a, b), labial (c, d), and occlusal (e, f) views. Scale bar = 5 mm.

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 Leptopleuroniinae 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 *Hwiccewyrn* (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

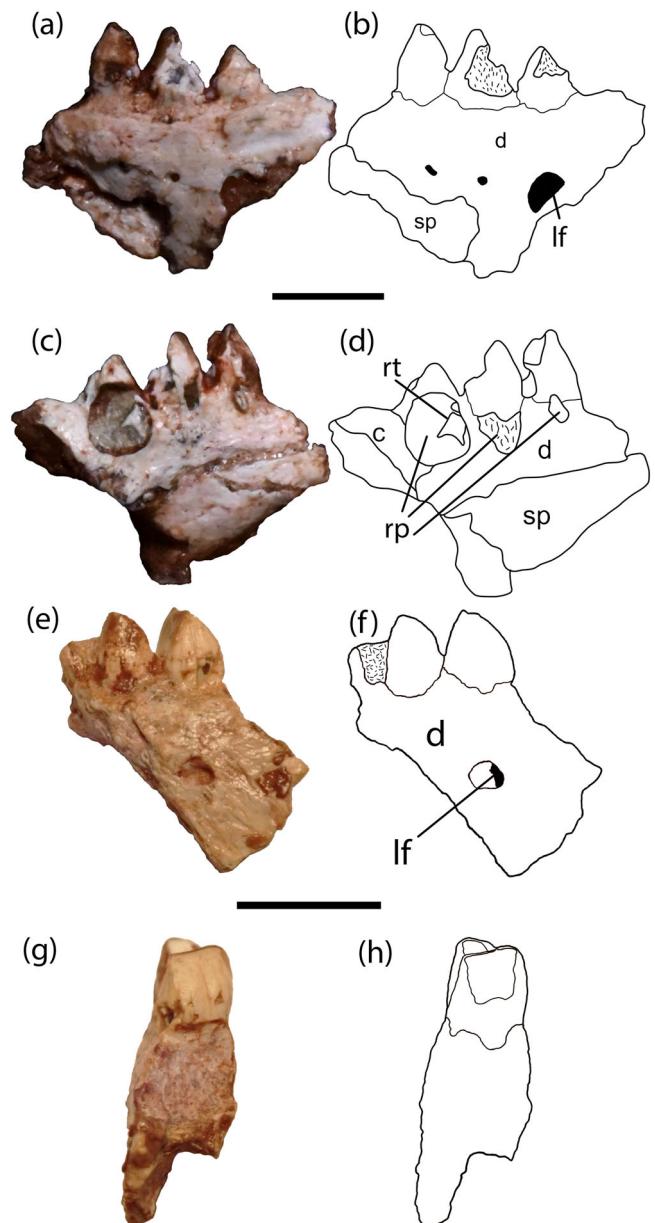


FIGURE 8 *Libognathus sheddi* (TTU P-23576). Left mandible in lateral (a, b), medial (c, d) views and (TTU P-14493), left dentary in labial (e, f), and posterior (g, h) views. c, coronoid; d, dentary; lf, lateral foramen.; rp, resorption pit; rt, replacement tooth; sp, splenial Scale bar = 5 mm.

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 *Hwiccewyrn* (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 ankylosed 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

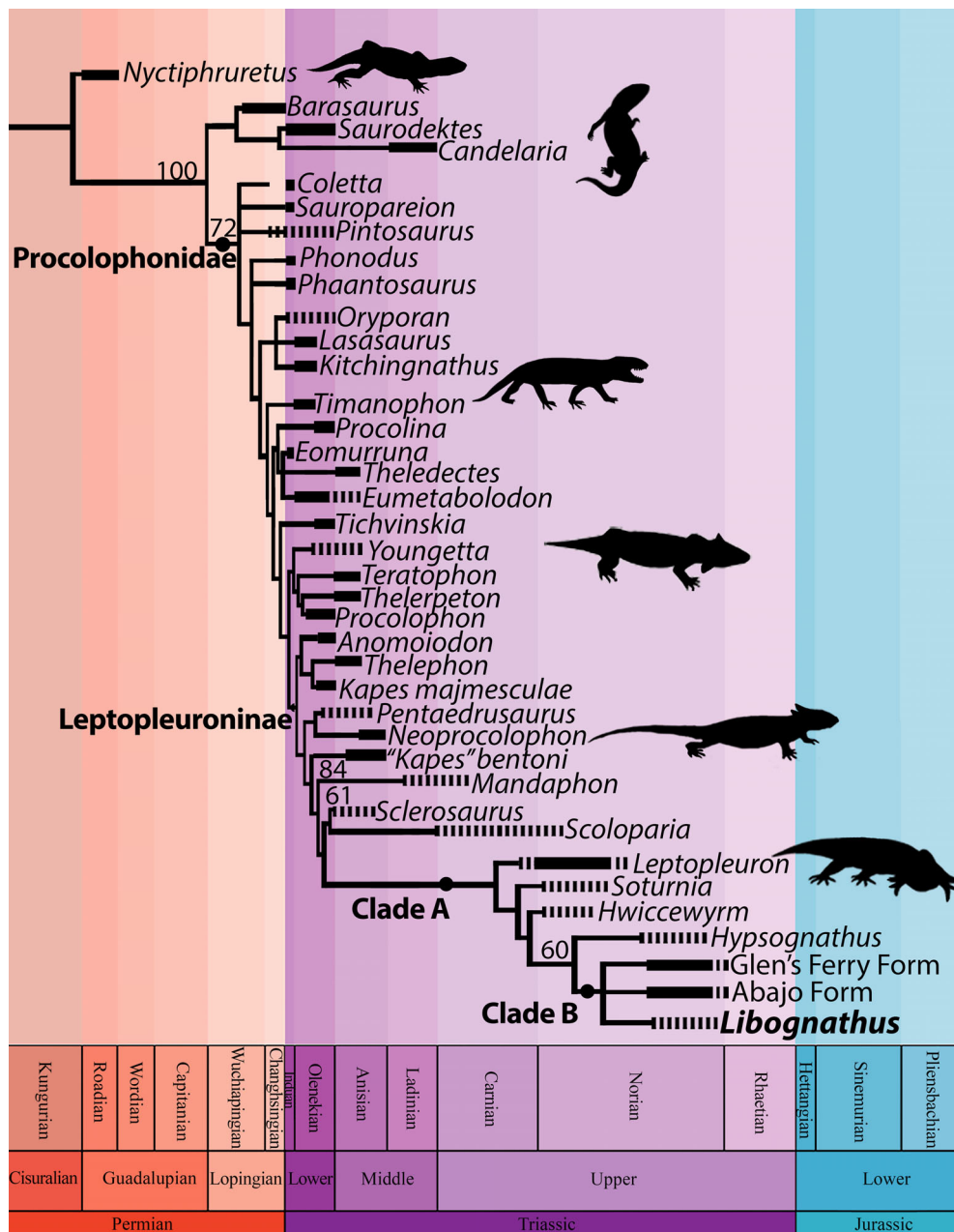
In TTU-P10069 and TTU-P23576, the single coronoid projects under the last one to two teeth in lingual view as in the holotype DMNH 20491 (Figures 7a, b, e, f and 8c, d). The possible extension of the coronoid under the teeth on the labial side cannot be discerned, which, in the holotype specimen (Figure 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 *Neoprocolophon 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 Revueltian 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

FIGURE 9 Temporally calibrated strict consensus tree demonstrating the phylogenetic relationships of Procolophonoidea, emphasizing the relationships of *Libognathus* with other leptopleuronines. Strict consensus from the 100 most-parsimonious trees. Numbers at the base of the nodes are symmetric resampling values (10,000 replicates, change probability = 33) higher than 50%. Silhouettes of *Nyctiphruretus*, *Leptopleuron*, and *Hypsognathus*©Nobu Tamura, silhouette of *Eomurruna* © Gaige Wright, and silhouette of *Owenetta* ©Smokebjb.



the successive sister to *Hwiccewurm* (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 Revueltian 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 Revueltian

tealzone/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 biostratigraphic 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-P10081 (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 (Dosedělová 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*, *Scoloparia*, *Libognathus*, and *Soturnia* (if acrodonty is the case) demonstrate four different modes of tooth replacement and implantation. *Sauropareion* shows a possible subthecodont 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 subthecodont 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 subthecodont implantation with no or infrequent replacement. If there is a replacement, the replacement tooth forms after the resorption of the old functional tooth. *Scoloparia* demonstrates two modes of implantation, subthecodonty 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 leptopleuronine 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

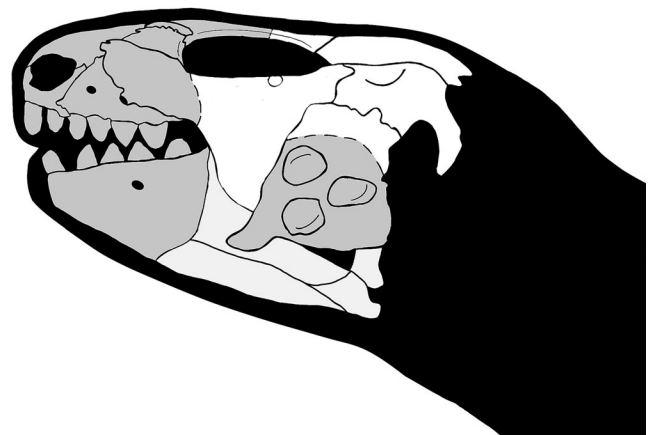


FIGURE 10 Skull reconstruction of *Libognathus sheddi* in lateral view. Gray shading represents preserved elements. Missing elements in white are based on *Hypsognathus fenneri* specimen YPM 55831 (Sues et al., 2000).

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 orbitonasale 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 (Revuelitian), 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.

ACKNOWLEDGMENTS




We would like to thank the landowners, R. L. and Jimella Simpson, and their son Troy for donating the specimens to the Museum of Texas Tech University and allowing us permission to collect from the locality. We thank Marianna Ivanova and Bryce McElvogue for preparing the specimens, the field crew for their collecting efforts, and Axel Hungerbühler for comments and review of an earlier version of the manuscript. Hans-Dieter Sues and Juan Carlos Cisneros for helpful discussions. Kendra Dean for assistance with the TTU specimens in her care and for some photography. Sean Modesto and Juan Cisneros for helpful comments that greatly improved the manuscript. The research was supported by Texas Tech

University and the Museum of Texas Tech University, and, in part, from the estates of Sun Youli and Kristen Waller.

FUNDING INFORMATION

This work was supported by the Museum of Texas Tech University; the estates of Kristen Waller and Sun Youli.

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REFERENCES

- Atanassov, M. N. (2002). Two new archosaur reptiles from the late Triassic of Texas [PhD dissertation] (352 p.). Lubbock: Texas Tech University.
- Atchley, S. C., Nordt, L. C., Dworkin, S. I., Ramezani, J., Parker, W. G., Ash, S. R., & Bowring, S. A. (2013). A linkage among pangean tectonism, cyclic alluviation, climate change, and biological turnover in the late Triassic: The record from the Chinle formation, southwestern United States. *Journal of Sedimentary Research*, 83, 1147–1161.
- Baird, D. (1986). Some upper Triassic reptiles, footprints, and an amphibian from New Jersey. *Mosasauro*, 3, 123–135.
- Baird, D., & Olsen, P. E. (1983). Late Triassic herpetofauna from the Wolfville formation of the Minas Basin (Fundy Basin), Nova Scotia, Canada. *Geological Society of America (Abstracts with Programs)*, 15, 122.
- Bertin, T. J. C., Thivichon-Prince, B., LeBlanc, A. R. H., Caldwell, M. W., & Viriot, L. (2018). Current perspectives on tooth implantation, attachment, and replacement in Amniota. *Frontiers in Physiology*, 9, 1630. <https://doi.org/10.3389/fphys.2018.01630>
- Britt, B. B., Dalla Vecchia, F. M., Chure, D. J., Engelmann, G. F., Whiting, M. F., & Scheetz, R. D. (2018). *Caelestiventus hanseni* gen. Et sp. nov. extends the desert-dwelling pterosaur record back 65 million years. *Nature Ecology and Evolution*, 2(9), 1386–1392.
- Broili, F., & Schröder, J. (1936). Beobachtungen an Wirbeltieren der Karrooformation. XII. Über *Procolophon* Owen. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche, Abteilung*, 1936, 239–256. [German].
- Broom, R. (1905). On the affinities of the primitive reptile *Procolophon*. *Proceedings of the Zoological Society of London*, 1905, 212–217.
- Butler, R. J., Meade, L. E., Cleary, T. J., McWhirter, K. T., Brown, E. E., Kemp, T. S., Benito, J., & Fraser, N. C. (2023). *Hwiccewyrms trispiculum* gen. et sp. nov., a new leptopleuronine procolophonid from the late Triassic of Southwest England. *The Anatomical Record*, 1–31. <https://doi.org/10.1002/ar.25316>
- Cabreira, S. F., & Cisneros, J. C. (2009). Tooth histology of the parareptile *Soturnia caliodon* from the upper Triassic of Rio Grande do Sul, Brazil. *Acta Palaeontologica Polonica*, 54(4), 743–748.

- Carroll, R. R., & Lindsey, W. (1985). Cranial anatomy of the primitive reptile *Procolophon*. *Canadian Journal of Earth Sciences*, 22(11), 1571–1587.
- Case, E. C. (1928). A cotylosaur from the upper Triassic of western Texas. *Journal of the Washington Academy of Science*, 18, 177–178.
- Cather, S. M., Zeigler, K. E., Mack, G. H., & Kelley, S. A. (2013). Toward standardization of Phanerozoic stratigraphic nomenclature in New Mexico. *Rocky Mountain Geology*, 48, 101–124.
- Chatterjee, S. (1986). The late Triassic Dockum vertebrates: Their stratigraphic and paleobiogeographic significance. In K. Padian (Ed.), *The beginning of the age of dinosaurs: Faunal change across the Triassic-Jurassic boundary* (pp. 139–150). Cambridge University Press.
- Cisneros, J. C. (2008a). Phylogenetic relationships of procolophonid parareptiles with remarks on their geological record. *Journal of Systematic Palaeontology*, 6, 345–366.
- Cisneros, J. C. (2008b). New basal procolophonid reptile from the Katberg formation (lower Triassic) of the south African Karoo. *Palaeoworld*, 17, 126–134.
- Cisneros, J. C., Damiani, R., Schultz, C., da Rosa, A., Schwanke, C., Neto, L. W., & Aurélio, P. L. P. (2004). A procolophonid reptile with temporal fenestration from the middle Triassic of Brazil. *Proceedings of the Royal Society of London B*, 271, 1541–1546.
- Cisneros, J. C., & Ruta, M. (2010). Morphological diversity and biogeography of procolophonids (Amniota: Parareptilia). *Journal of Systematic Palaeontology*, 8(4), 607–625.
- Cisneros, J. C., & Schultz, C. L. (2003). *Soturnia caliodon* n. g. n. sp., a procolophonid reptile from the upper Triassic of Brazil. *Neues Jahrbuch für Geologie Und Paläontologie, Abhandlungen*, 227(3), 365–380.
- Colbert, E. H. (1946). *Hypsognathus*, a Triassic reptile from New Jersey. *Bulletin of the American Museum of Natural History*, 86, 225–274.
- Dosedělová, H., Štěpánková, K., Zikmund, T., Lesot, H., Kaiser, J., Novotný, K., Štembírek, J., Knotek, Z., Zahradníček, O., & Buchtová, M. (2016). Age-related changes in the tooth-bone interface area of acrodont dentition in the chameleon. *Journal of Anatomy*, 229, 356–368.
- Dunlavey, M. G., Whiteside, J. H., & Irmis, R. B. (2009). Ecosystem instability during the rise of the dinosaurs: Evidence from the late Triassic in New Mexico and Arizona. *Geological Society of America Abstracts with Programs*, 41, 477.
- Fitch, A. J., Haas, M., CHair, W., Ridgley, E., Ridgley, B., Oldman, D., Reynolds, C., & Lovelace, D. M. (2023). A new rhynchosaur taxon from the Popo Agie formation, WY: Implications for a northern Pangean Early-Late Triassic (Carnian) Fauna. *Diversity*, 15(4), 544p.
- Ford, D. P., & Benson, R. B. (2020). The phylogeny of early amniotes and the affinities of Parareptilia and Varanopidae. *Nature Ecology & Evolution*, 4(1), 57–65.
- Fraser, N. C., Irmis, R. B., & Elliott, D. K. (2005). A procolophonid (Parareptilia) from the owl rock member, Chinle formation of Utah, USA. *Palaeontologia Electronica*, 8(1), 1–7. http://palaeo-electronica.org/paleo/2005_1/fraser13/issue1_05.htm
- Gilmore, C. W. (1928). A new fossil reptile from the Triassic of New Jersey. *Proceedings of the U.S. National Museum*, 73(7), 1–8.
- Goloboff, P. A., & Morales, M. E. (2023). TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics*, 39(2), 144–153.
- Gow, C. E. (1977a). Tooth function and succession in the Triassic reptile *Procolophon trigoniceps*. *Palaeontology*, 20, 695–704.
- Gow, C. E. (1977b). New procolophonids from the Triassic Cynognathus zone of South Africa. *Annals of the South African Museum*, 72(6), 109–124.
- Hamley, T., Cisneros, J. C., & Damiani, R. (2021). A procolophonid reptile from the lower Triassic of Australia. *Zoological Journal of the Linnean Society*, 192, 554–609. <https://doi.org/10.1093/zoolinnean/zlaa056>
- Haridy, Y. (2018). Histological analysis of post-eruption tooth wear adaptations, and ontogenetic changes in tooth implantation in the acrodontan squamate *Pogona vitticeps*. *PeerJ*, 6, e5923. <https://doi.org/10.7717/peerj.5923>
- Haridy, Y., LeBlanc, A. R. H., & Reisz, R. R. (2018). The Permian reptile *Opisthodontosaurus carrolli*: A model for acrodont tooth replacement and dental ontogeny. *Journal of Anatomy*, 232, 371–382.
- Heaton, M. J. (1979). Cranial anatomy of primitive captorhinid reptiles from the late Pennsylvanian and early Permian Oklahoma and Texas. *Oklahoma Geological Survey Bulletin*, 127, 1–84.
- Heckert, A. B. (2004). Late Triassic microvertebrates from the lower Chinle Group (Otischalkian-Adamian: Carnian) southwestern USA. *New Mexico Museum of Natural History & Science Bulletin*, 27, 1–170.
- Heckert, A. B., Lucas, S. G., Rinehart, L. F., Spielmann, J. A., Hunt, A. P., & Kahle, R. (2006). Revision of the archosauromorph reptile *Trilophosaurus*, with a description of the first skull of *Trilophosaurus jacobsi*, from the upper Triassic Chinle group, West Texas, USA. *Palaeontology*, 49(3), 621–640.
- Heckert, A. B., Mitchell, J. S., Schneider, V. P., & Olsen, P. E. (2012). Diverse new microvertebrate assemblage from the upper Triassic Cummock formation, Sanford subbasin, North Carolina, USA. *Journal of Paleontology*, 86(2), 368–390.
- Hungerbühler, A., Mueller, B., Chatterjee, S., & Cunningham, D. P. (2013). Cranial anatomy of the late Triassic phytosaur *Machaeroprotopus*, with the description of a new species from West Texas. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103, 269–312.
- Ivakhnenko, M. F. (1973). Skull structure in the early Triassic procolophonian *Tichvinskia vjatkensis*. *Paleontological Journal*, 4, 74–83.
- Ivakhnenko, M. F. (1979). Permian and Triassic procolophonoids of the Russian platform. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, 164, 1–80. [Russian].
- Jenkins, K. M., & Bhullar, B.-A. (2022). Tooth implantation and attachment in *Scoloparia glyphanodon* (Parareptilia: Procolophonidae). *Bulletin of the Peabody Museum of Natural History*, 63(1), 27–30.
- Jenkins, K. M., Jones, M. E. H., Zikmund, T., Boyde, A., & Daza, J. D. (2017). A review of tooth implantation among rhynchocephalians (Lepidosauria). *Journal of Herpetology*, 51(3), 206–300.
- Kent, D. V., Olsen, P. E., Lepre, C., Rasmussen, C., Mundil, R., Gehrels, G. E., Giesler, D., Irmis, R. B., Geissman, J. W., & Parker, W. G. (2019). Magnetostratigraphy of the entire Chinle formation (Norian age) in a scientific drill core from petrified Forest National Park (Arizona, USA) and implications for regional and global correlations in the late Triassic. *Geochemistry, Geophysics, Geosystems*, 20, 4654–4664. <https://doi.org/10.1029/2019GC008474>
- Kligman, B. T., Marsh, A. D., Nesbitt, S. J., Parker, W. G., & Stocker, M. R. (2020). New trilophosaurid species demonstrates a decline in allokotosaur diversity across the Adamian-

- Reuvelian boundary in the late Triassic of western North America. *Palaeodiversity*, 13(1), 25–37.
- Langer, M. C., & Ferigolo, J. (2013). The late Triassic dinosauriform *Sacisaurus agudoensis* (Caturrita formation; Rio Grande do Sul, Brazil): Anatomy and affinities. In S. J. Nesbitt, J. B. Desojo, & R. B. Irmis (Eds.), *The Geological Society of London Anatomy, Phylogeny, and Paleobiology of Early Archosaurs and their Kin* (Vol. 379). Geological Society. <https://doi.org/10.1144/SP379.16>
- Laurenti, J. N. (1768). Specimen medicum, exhibens synopsis Reptilium emendatum, cum experimentis circa venena et antidota Reptilium Austriacorum. Joan Thomae, Nob. de Trattner, Vienna, p. 214 [Latin].
- Laurin, M., & Reisz, R. R. (1995). A re-evaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, 113, 165–223.
- LeBlanc, A. R. H., & Reisz, R. R. (2013). Periodontal ligament, cementum, and alveolar bone in the oldest herbivorous tetrapods, and their evolutionary significance. *PLoS ONE*, 8(9), e74697. <https://doi.org/10.1371/journal.pone.0074697>
- LeBlanc, A. R. H., & Reisz, R. R. (2015). Patterns of tooth development and replacement in captorhinid reptiles: A comparative approach for understanding the origin of multiple tooth rows. *Journal of Vertebrate Paleontology*, 35(3), e919928. <https://doi.org/10.1080/02724634.2014.919928>
- Lehman, T. M., Chatterjee, S., & Schnable, J. P. (1992). The Cooper canyon formation (late Triassic) of western Texas. *Texas Journal of Science*, 44, 349–355.
- Lessner, E. J., Parker, W. G., Marsh, A. D., Nesbitt, S. J., Irmis, R. B., & Mueller, B. D. (2018). New insights into late Triassic dinosauriform-bearing assemblages from Texas using apomorphy-based identifications. *PaleoBios*, 35, 1–41.
- Li, J. L. (1989). A new genus of Procolophonidae from the lower Triassic of Shaanxi, China. *Vertebrata Palasiatica*, 10, 248–267.
- Lucas, S. G. (1998). Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 143(1998), 347–384.
- MacDougall, M. J., & Modesto, S. P. (2011). New information on the skull of the early Triassic parareptile *Sauropareion anoplus*, with a discussion of tooth attachment and replacement in procolophonids. *Journal of Vertebrate Paleontology*, 31, 270–278.
- Marsh, A. D., Parker, W. G., Stockli, D. F., & Martz, J. W. (2019). Regional correlation of the Sonsela member (upper Triassic Chinle formation) and detrital U-Pb zircon data from the Sonsela sandstone bed near the Sonsela buttes, northeastern Arizona, USA, support the presence of a distributive fluvial system. *Geosphere*, 15(4), 1128–1139.
- Martinelli, A. G., Soares, M. B., & Schoch, R. R. (2016). Owenettids and procolophonids from the lower Keuper shed new light on the diversity of parareptiles in the German middle Triassic. *Journal of Paleontology*, 90, 92–101.
- Martz, J. W. (2008). Lithostratigraphy, chemostratigraphy, and vertebrate biostratigraphy of the Dockum group (upper Triassic), of southern Garza County, West Texas [PhD dissertation] (504). Lubbock: Texas Tech University.
- Martz, J. W., Mueller, B., Nesbitt, S. J., Stocker, M. R., Parker, W. J., Atanassov, M., Fraser, N., Weinbaum, J., & Lehane, J. R. (2013). A taxonomic and biostratigraphic re-evaluation of the post quarry vertebrate assemblage from the Cooper canyon formation (Dockum group, upper Triassic) of southern Garza County, western Texas. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103, 339–364. <https://doi.org/10.1017/S1755691013000376>
- Martz, J. W., & Parker, W. G. (2017). Revised formulations of the late Triassic land vertebrate “Faunachrons” of western North America: Recommendations for codifying nascent systems of vertebrate biochronology. In K. E. Zeigler & W. G. Parker (Eds.), *Terrestrial depositional systems: Deciphering complexities through Multiple stratigraphic Methods* (pp. 39–125). Elsevier. <https://doi.org/10.1016/B978-0-12-803243-5.00002-9>
- Martz, J. W., & Small, B. J. (2019). Non-dinosaurian dinosauriforms from the Chinle formation (upper Triassic) of the Eagle Basin, northern Colorado: *Dromomeron romeri* (Lagerpetidae) and a new taxon, *Kwanasaurus williamparkeri* (Silesauridae). *PeerJ*, 7, e7551.
- Martz, J. W., & Small, B. J. (2023). The oldest dinosaurs from Colorado: Theropods from the red siltstone member of the Chinle formation of Colorado and a summary of late Triassic ornithomimid biochronology in western North America. 14th Symposium on Mesozoic Terrestrial Ecosystems and Biota, 193–194.
- Meckert, D. (1995). The procolophonid *Barasaurus* and the phylogeny of early amniotes [PhD dissertation] (195). Montréal: McGill University, Montréal.
- Modesto, S. P., & Damiani, R. (2007). The procolophonoid reptile *Sauropareion anoplus* from the lowermost Triassic of South Africa. *Journal of Vertebrate Paleontology*, 27(2), 337–349.
- Modesto, S. P., Damiani, R. M., & Sues, H.-D. (2003). A reappraisal of *Coletta seca*, a basal procolophonoid reptile from the lower Triassic of South Africa. *Palaeontology*, 45(5), 883–895.
- Modesto, S. P., Scott, D. M., Botha-Brink, J., & Reisz, R. R. (2010). A new and unusual procolophonoid parareptile from the lower Triassic Katberg formation of South Africa. *Journal of Vertebrate Paleontology*, 30, 715–723.
- Mueller, B., & Chatterjee, S. (2003). Skull anatomy of *Libognathus sheddi* (Parareptilia: Procolophonida) from the upper Triassic Cooper canyon formation of West Texas. *Journal of Vertebrate Paleontology*, 23(3), 80A.
- Mueller, B. D. (2016). Triassic tetrapod paleontology and taphonomy of the Boren Quarry, Dockum Group, Garza County, Texas [PhD dissertation] (300). Lubbock: Texas Tech University.
- Mueller, B. D., Huttenlocker, A. K., Small, B. J., Dean, K., & Chatterjee, S. (2023). A new kannemeyeriiform dicynodont (Synapsida) from a late Triassic vertebrate assemblage in West Texas, USA. *Journal of Vertebrate Paleontology*. <https://doi.org/10.1080/0274634.2023.2255236>
- Mueller, B. D., Martz, J. W., Hungerbühler, A., & Nesbitt, S. J. (2016). A diverse late Triassic (Norian) tetrapod fauna and taphonomy of MOTT VPL 3869 from the Tecovas formation (Dockum group) in Garza County, Texas, USA. *Journal of Vertebrate Paleontology, Programs and Abstracts*, 2016, 193.
- Müller, R. T. (2021). An additional specimen of owenettid procolophonoid from the middle Triassic of southern Brazil. *Acta Palaeontologica Polonica*, 66(4), 827–836. <https://doi.org/10.4202/app.00909.2021>
- Murry, P. A. (1986). Vertebrate paleontology of the Dockum group, West Texas and eastern New Mexico. In K. Padian (Ed.), *The beginning of the age of dinosaurs* (pp. 109–137). Cambridge University Press.
- Murry, P. A. (1987). New reptiles of the upper Triassic Chinle formation of Arizona. *Journal of Paleontology*, 61, 773–786.

- Neenan, J. M., Klein, N., & Scheyer, T. M. (2013). European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. *Nature Communications*, 4(1), 1–8.
- Olson, E. C. (1947). The family Diadectidae and its bearing on the classification of reptiles. In *Fieldiana, Geology* (Vol. 11, pp. 1–53). Chicago Natural History Museum.
- Peyer, B. (1968). *Comparative odontology* (p. 349). The University of Chicago Press.
- Pinheiro, F. L., Silva-Neves, E., & Da-Rosa, Á. A. A. (2021). An early-diverging procolophonid from the lowermost Triassic of South America and the origins of herbivory in Procolophonoida. *Papers in Palaeontology*, 2021, 1–12.
- Ramezani, J., Fastovsky, D. E., & Bowring, S. A. (2014). Revised chronostratigraphy of the lower Chinle formation strata in Arizona and New Mexico (USA): High-precision U-Pb geochronological constraints on the late Triassic evolution of dinosaurs. *American Journal of Science*, 314, 981–1008.
- Ramezani, J., Hoke, G. D., Fastovsky, D. E., Bowring, S. A., Therrien, F., Dworkin, S. I., Atchley, S. C., & Nordt, L. E. (2011). High-precision U-Pb zircon geochronology of the late Triassic Chinle formation, petrified Forest National Park (Arizona, USA): Temporal constraints on the early evolution of dinosaurs. *GSA Bulletin*, 23, 2142–2159.
- Rasmussen, C., Mundil, R., Irmis, R. B., Geisler, D., Gehrels, G. E., Olsen, P. E., Kent, D. V., Lepre, C., Kinney, S. T., Geissman, J. W., & Parker, W. G. (2020). U-Pb zircon geochronology and depositional age models for the upper Triassic Chinle formation (petrified Forest National Park, Arizona, USA): Implications for late Triassic paleoecological and paleoenvironmental change. *Geological Society of America Bulletin*, 133(3–4), 539–558.
- Rauhut, O. W., Heyng, A. M., López-Arbarello, A., & Hecker, A. (2012). A new rhynchocephalian from the late Jurassic of Germany with a dentition that is unique amongst tetrapods. *PLoS One*, 7(10), e46839.
- Reisz, R. R., Müller, J., Tsuji, L., & Scott, D. (2007). The cranial osteology of *Belebey vegrandis* (Parareptilia: Bolosauridae), from the middle Permian of Russia, and its bearing on reptilian evolution. *Zoological Journal of the Linnean Society*, 151, 191–214.
- Reyes, W. A., Martz, J. W., Small, B. J., & Mueller, B. D. (in press). *Garzapelta muelleri* gen. et sp. nov., a new aetosaur (Archosauria: Pseudosuchia) from the late Triassic middle Cooper canyon formation (Revueltian: mid-Norian), Dockum Group, Texas, USA, provides insight into the evolution of the Desmatosuchini in the southwestern USA. *The Anatomical Record*.
- Säilä, L. K. (2008). The osteology and affinities of *Anomoiodon liliensterini*, a procolophonid reptile from the lower Triassic Buntsandstein of Germany. *Journal of Vertebrate Paleontology*, 28(4), 1199–1205.
- Säilä, L. K. (2009). Alpha taxonomy of the Russian Permian procolophonoid reptiles. *Acta Palaeontologica Polonica*, 54, 599–608.
- Säilä, L. K. (2010). Osteology of *Leptopleuron lacertinum* Owen, a procolophonoid parareptile from the upper Triassic of Scotland, with remarks on ontogeny, ecology and affinities. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 101, 1–25.
- Sarigiül, V., Agnolín, F., & Chatterjee, S. (2018). Description of a multitaxic bone assemblage from the upper Triassic post quarry of Texas (Dockum group), including a new small basal dinosauriform taxon. *Historia Natural*, 8, 5–24.
- Seeley, H. G. (1888). Researches on the structure, organization and classification of the fossil Reptilia. VI. On the anomodont Reptilia and their allies. *Proceedings of the Royal Society of London*, 44, 381–383.
- Small, B. J. (1997). A new procolophonid from the upper Triassic of Texas, with a description of tooth replacement and implantation. *Journal of Vertebrate Paleontology*, 17, 674–678.
- Smirina, E. M., & Ananjeva, N. B. (2007). Growth layers in bones and acrodont teeth of the agamid lizard *Laudakia stoliczkanazkana* (Blanford, 1875) (Agamidae, Sauria). *Amphibia-Reptilia*, 28, 193–204.
- Sues, H.-D., & Baird, D. (1998). Procolophonidae (Reptilia: Parareptilia) from the upper Triassic Wolfville formation of Nova Scotia, Canada. *Journal of Vertebrate Paleontology*, 18, 525–532.
- Sues, H. D., & Olsen, P. E. (2015). Stratigraphic and temporal context and faunal diversity of Permian-Jurassic continental tetrapod assemblages from the Fundy rift basin, eastern Canada. *Atlantic Geology*, 51, 139–205.
- Sues, H.-D., & Olsen, P. E. (1993). A new procolophonid and a new tetrapod of uncertain, possibly procolophonian affinities from the upper Triassic of Virginia. *Journal of Vertebrate Paleontology*, 13, 282–286.
- Sues, H.-D., Olsen, P. E., Fedak, T. J., & Schoch, R. R. (2022). Diverse assemblage of middle Triassic continental tetrapods from the Newark Supergroup of Nova Scotia (Canada). *Journal of Vertebrate Paleontology*, 41, 4. <https://doi.org/10.1080/02724634.2021.2023168>
- Sues, H.-D., Olsen, P. E., Scott, D. M., & Spencer, P. S. (2000). Cranial osteology of *Hypsognathus fenneri*, a latest Triassic procolophonid reptile from the Newark Supergroup of eastern North America. *Journal of Vertebrate Paleontology*, 20, 275–284.
- Sues, H.-D., & Reisz, R. R. (2008). Anatomy and phylogenetic relationships of *Sclerosaurus armatus* (Amniota: Parareptilia) from the Buntsandstein (Triassic) of Europe. *Journal of Vertebrate Paleontology*, 28(4), 1031–1042.
- Tsuji, L. A. (2018). *Mandaphon nadra*, gen. et sp. nov., a new procolophonid from the Manda Beds of Tanzania. *Journal of Vertebrate Paleontology*, 37(6), 80–87.
- Young, C. C. (1957). *Neoprocolophon asiaticus*, a new cotylosaurian reptile from China. *Vertebrata Palasiatica*, 1, 1–7.
- Zaher, M., Coram, R. A., & Benton, M. J. (2018). The Middle Triassic procolophonid *Kapes bentoni*: Computed tomography of the skull and skeleton. *Papers in Palaeontology*, 5, 111–138. <https://doi.org/10.1002/spp2.1232>

SUPPORTING INFORMATION

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How to cite this article: Mueller, B. D., Small, B. J., Jenkins, X., Huttenlocker, A. K., & Chatterjee, S. (2023). Cranial anatomy of *Libognathus sheddi* Small, 1997 (Parareptilia, Procolophonidae) from the Upper Triassic Dockum Group of West Texas, USA. *The Anatomical Record*, 1–21. <https://doi.org/10.1002/ar.25364>