

# A MARINE VERTEBRATE FAUNA FROM THE EARLY PERMIAN (ARTINSKIAN) LUEDERS FORMATION OF NORTH-CENTRAL TEXAS, USA

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**ABSTRACT**—Fossils of the Permian System in Texas have a long history of study for terrestrial and freshwater vertebrate communities. However, vertebrate communities from fully marine ecosystems are comparatively underreported. This sparse spatial record is especially true for marine communities in the Lower Permian, which makes it difficult to adequately illustrate vertebrate life in Early Permian oceans. Better characterization of these communities provides useful context to biotic responses to environmental perturbations of the Early Permian (e.g., biotic reorganizations and climate changes surrounding the Artinskian Warming Event). Here, we describe a faunal survey that consists of 11 vertebrate taxa from the marine portion of the lower Lueders Formation in Shackelford County, Texas (United States) persisting across multiple bone- and tooth-producing carbonate horizons. Chondrichthyans are represented by hybodontiforms (?*Acrodus*, “*Lissodus*”), ctenacanthids, neoselachians (*Cooleyella*), petalodontids (*Janassa*), holocephalians (*Deltodus*), and spines such as those of *Amelacanthus*. Osteichthyan fish remains consist of mostly Platsomids, along with other paleoniscoids. These new reports paint a clearer picture of marine vertebrate ecosystems in North America’s Permian Basin and update the paleobiogeography of Early Permian taxa reported elsewhere around the globe.

**RESUMEN**—Los fósiles del Sistema Pérmico en Texas tienen una larga historia de estudio para las comunidades de vertebrados terrestres y de agua dulce. Sin embargo, las comunidades de vertebrados de ecosistemas completamente marinos han sido menos estudiados. Esta tendencia es especialmente cierta para las comunidades marinos en el Pérmico Inferior. Este escaso registro de localidades dificulta ilustrar adecuadamente la vida de los vertebrados en los océanos del Pérmico Temprano. Una mejor caracterización de estas comunidades proporciona un contexto útil para las respuestas bióticas a las perturbaciones ambientales del Pérmico Temprano (por ejemplo, las reorganizaciones bióticas y los cambios climáticos que rodean el Evento de Calentamiento Artinskiano). Aquí describimos una fauna que consta de 11 taxones de vertebrados de la porción marina de la Formación Lueders inferior en el condado de Shackelford, Texas (EE. UU.), que persiste a lo largo de múltiples horizontes calcificados productores de huesos y dientes. Los condricios aquí están representados por hibodontiformes (?*Acrodus*, “*Lissodus*”), ctenacántidos, neoselaquios (*Cooleyella*), petalodóntidos (*Janassa*), holocéfalos (*Deltodus*) y *Amelacanthus*. Los restos de peces osteíctico consisten principalmente en Platsomids y otros paleoniscoids. Estos nuevos informes pintan una imagen más clara de los ecosistemas de vertebrados marinos en la cuenca del Pérmico de América del Norte y actualizan la paleobiogeografía de los taxones del Pérmico Temprano reportados en otras partes del mundo.

The Lueders Formation is a series of terrigenous deposits and marine limestones that has been biostratigraphically correlated to the Artinskian Faunal Stage (290.1–283.5 million years ago) of the early Permian Period’s Cisuralian Epoch (Dunbar et al., 1960; Wilson et al., 2011). Surface exposures of this formation can be found in north-central Texas with fossil vertebrate faunas mostly studied in the Lake Kemp region of Baylor County, Texas

(Berman, 1968, 1970). Vertebrate sites in the vicinity of Lake Kemp reveal the Lueders Formation includes freshwater vertebrate genera, such as the chondrichthyans *Barbclabornia* and *Orthacanthus*, and the amphibian *Diplocaulus* (Berman, 1970; Johnson, 1996). The Lueders Formation itself, with its mixture of siliciclastic and carbonate sediments, is generally interpreted as a “delta margin” in this area (Dalquest and Kocurko, 1986).

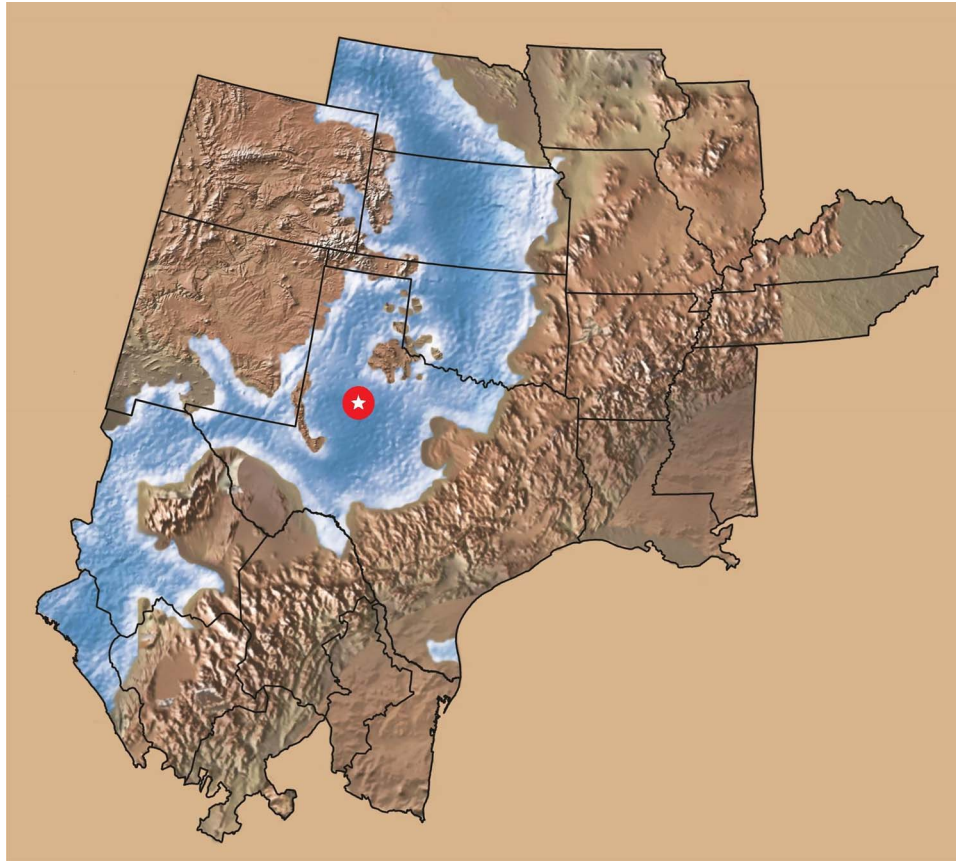


FIG. 1—Conceptual map of the American Midcontinent during the Artinskian Age when North America's Permian Basin was covered by a shallow, epicontinental seaway, shown at its greatest extent in this paleogeographic reconstruction (created based on data from Stoesser et al., 2005). The location of the Lueders Limestone Quarry, which is explored in this study, is marked with a red circle and white star.

The relative paucity of vertebrate remains in the Lueders Formation compared with adjacent units has been noted historically (Romer, 1935). Eberth added to this idea of a formation somewhat desolate in vertebrate remains by creating an inventory of vertebrate diversity throughout the lower Permian of North America and reporting a diversity drop in both the Lueders Formation and the underlying Talpa Formation (Eberth, 1987). Note, however, that the Lueders Formation is not exclusively representative of a freshwater or near shore or estuarine ecosystem. At the Lake Kemp localities, red beds (siliciclastics containing ferric oxides) and shales alternate, indicating alternation of sediment deposition into freshwater facies and marine/estuarine carbonates, respectively (Dalquest and Kocurko, 1986). While further south, the lowermost Lueders Formation (sometimes mapped as the Lueders Quarry Member or Plq) is almost totally composed of marine limestones, and has produced well-known examples of marine invertebrates such as cephalopods and tube worms (Kemp, 1957; Wilson et al., 2011).

Early Permian marine vertebrate localities are rare globally, and sites demonstrating high species richness are quite uncommon (Ivanov, 2005; Kues, 2008). For example, the Copacabana Formation of Bolivia has produced a single marine assemblage (thus far to date),

where platysomids, petalodontid chondrichthyans, and (possibly) psammodontid holocephalians are noted to have grazed upon invertebrate communities and were likely preyed upon by ctenacanthiform chondrichthyans (Merino-Rodo and Janvier, 1986; Janvier, 1996). These were, in turn, likely preyed upon by the giant eugeneodontid *Parahelicoprion* (Merino-Rodo and Janvier, 1986; Janvier, 1996). Ivanov has found similar communities in the Ural Mountains of Russia (Ivanov, 2005). However, the ecosystem in the Urals contained euselachian chondrichthyans and a more diverse ctenacanthiform and neoselachian assemblage, somewhat similar to another early Permian marine fauna from Kansas (Ewell and Everhart, 2005). Although the marine vertebrate assemblages found in these regions do contain commonalities, their differences highlight possible gaps in our understanding of global trends of marine vertebrate ecology during the early Permian.

**GEOLOGIC SETTING**—During the early Artinskian Stage, the Panthalassic Ocean transgressed over the northwestern tropics and subtropics of Pangea (Hou et al., 2023), flooding much of what would become Texas and the American Midcontinent (Fig. 1). Throughout the Permian Period, deserts grew, spread, and fluctuated across

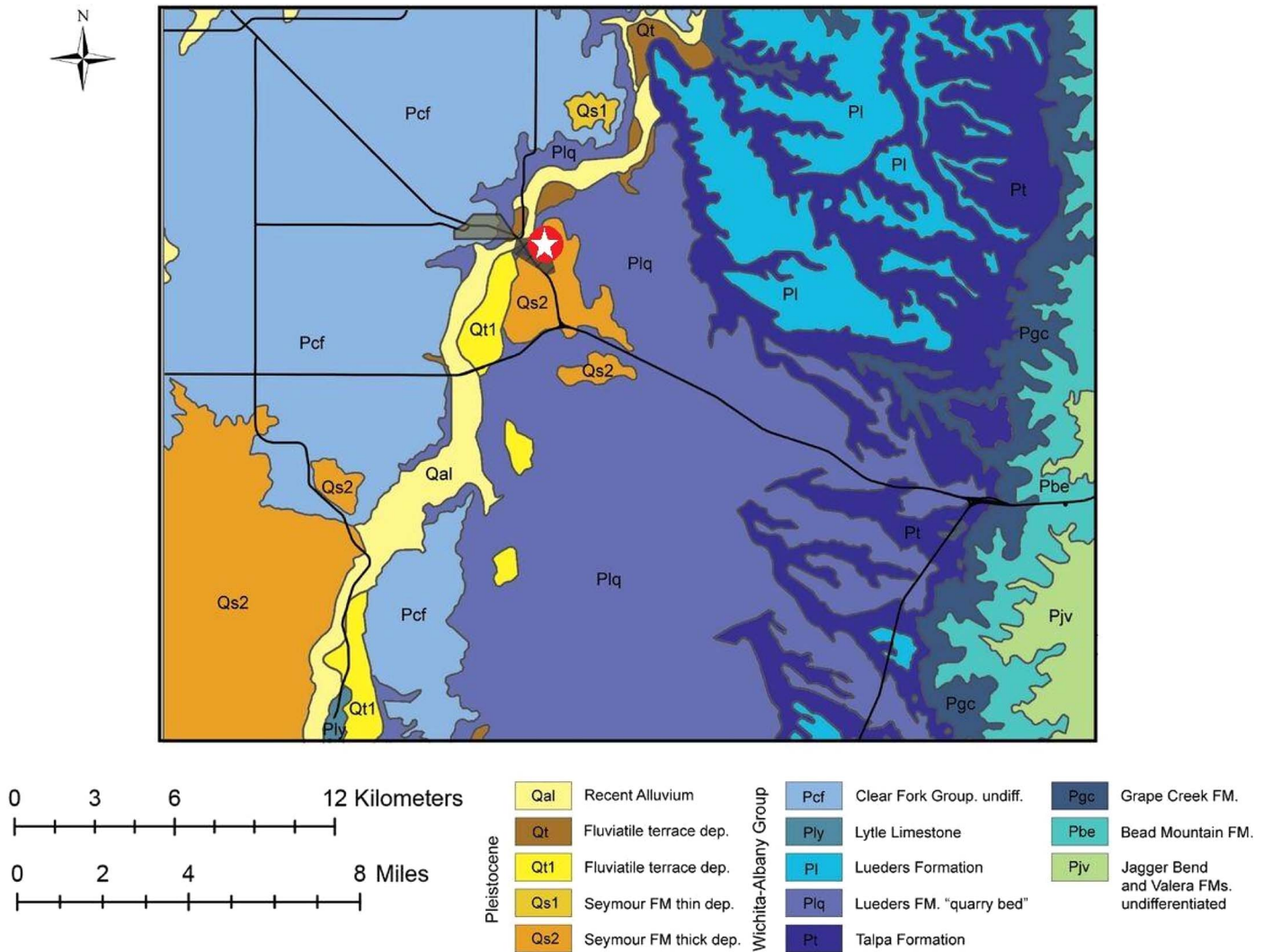


FIG. 2—Geologic map of the Lueders Limestone Quarry and surrounding area in north-central Texas (based on data from Horton et al., 2017). The quarry (marked with a red and white star) is situated along the Cenozoic deposits (map symbols beginning with Q) that are associated with the Brazos River. The quarry pit reaches into Permian carbonates that are mapped as the Lueders Quarry Member (Plq).

much of the craton, and this changing aridity majorly impacted terrestrial faunas and the seabed near many landmasses. Drier settings are supported by sedimentologic analyses (Griffis et al., 2023) and an increase in the abundance of drought-tolerant (xeromorphic) plants (Chaney et al., 2009; Mamay et al., 2009).

The bedrock in the area surrounding the studied locality (Fig. 2) features an approximately north and south trending contact between the Permian Clear Fork Formation and the Lueders Formation. Other Permian units such as the Lytle, Grape Creek, Bead Mountain, Jagger Bend, and Valera Formations are also exposed in the nearby area (Barnes, 1972).

The Lueders Limestone Quarry locality straddles the Shackelford–Jones county line and exposes the lowermost, middle, and upper Lueders Formation (Fig. 2). These strata are expressed as a fossiliferous limestone bed, underlain by

a thick freshwater and terrestrial mudstone sequence, which is followed by alternating sequences of muds and carbonate rocks. The lower facies of the Lueders Formation contains a complex fauna featuring both vertebrates and invertebrates (Holterhoff, 2010; Shell and Ciampaglio, 2016, 2017). Isotopic and floral studies in the region suggest that the early Permian featured a shift from an Upper Carboniferous ice house into a warmer, more arid climate (Tabor et al., 2002; DiMichele et al., 2006). Paleosols elsewhere in the Lueders Formation (see Zhu and Tabor, 2021) imply that the alternating mudstones and limestones preserved here were likely caused by small-scale shifts in aridity on the nearby landmasses, whereby increasing aridity led to increased salinity near the shore and decreased siliclastic deposition. This, in turn, facilitated the shoreward migration of marine sedimentologic units (Holterhoff, 2010). Afterward, a wetter climate led to increased runoff from the



land, decreasing local salinity and depositing fine grained siliciclastics (such as the mudstones observed in many parts of the section) on top of marine carbonates (Holterhoff, 2010).

**MATERIALS AND METHODS**—Several visits to the Lueders Limestone Quarry in Shackelford County, Texas, were made in 2005, 2017, and 2019. We carefully searched the site for macrofossils, and bulk samples of rock from each lithologically distinct layer in sequence were sampled to better understand the local stratigraphy. These layers were also measured in the field.

Vertebrate fossils larger than 1 cm were removed from the surrounding matrix using hand tools or a concrete saw with a 17.8 cm, diamond-coated blade. Once specimens were moved to the lab, the macrofossils were prepared using water, dilute acids, and pneumatic tools to clean away excess rock and expose more detail to aid in the identification of each macrofossil recovered.

Preparation of microvertebrate fossils was carried out by acid dissolution of bulk samples. Large amounts of rock were soaked in a method similar to that of Armstrong and Brasier (2005), where microvertebrate-bearing carbonate rock was submerged in a 10% solution of formic acid mixed with trisodium phosphate. The residual material, following acid dissolution, was then wet sifted in successively smaller mesh sizes down to 250  $\mu\text{m}$  (US number 80 sieve), and washed again to prevent the destructive growth of calcium formate crystals. This dry mix was sorted under a stereomicroscope, and specific microfossil specimens were identified and accessioned into the Wright State University Paleontological Collection.

Imaging was performed using a Canon Rebel XSi digital SLR camera with a standard lens kit and a Nikon D7100 digital SLR with both standard and macro lenses. In addition to macro images taken in the field and laboratory, micrographs of specimens smaller than 1 mm were photographed using a digital image stacking process. In image stacking, an infinity corrected macro lens was attached to a macro extension tube lens, and both were then affixed to the front of the Nikon D7100 digital SLR. This whole apparatus was then attached to a StackShot macro rail. Multiple micrographs were then taken with a fixed focal plane. The macro rail decreased the distance between the lens and the subjects at fixed intervals, which were set to the width of the focal plane. The resulting JPEG files were then stacked digitally using the software Helicon Focus ([www.heliconsoft.com](http://www.heliconsoft.com)), which removed out-of-focus portions and created a photomosaic of the remainder. This process resulted in a composite image of a microfossil in which each visible surface is in uniform true color and high focus, regardless of the topology of the fossil.

#### SYSTEMATIC PALEONTOLOGY

##### Class Chondrichthyes

##### Subclass Elasmobranchii

##### Order Ctenacanthiformes Glikman, 1964

##### Family Ctenacanthidae Dean, 1909

##### Ctenacanthidae indeterminate (indet.)

**Material Studied**—Fragmentary teeth: Wright State University Paleontological Collections, (WSU) 1428A, 1495 (housed at Wright State University's Lake Campus in Celina, Ohio; Figs. 4A–4C).

**Description and Remarks**—Both specimens represent teeth recovered from the lower bone bed at this locality. The WSU 1428A sample is the smaller of the pair, with a length from crown

tip to the farthest lateral edge of the base at 4.5 mm, compared with WSU 1495's 9.3 mm. Both teeth lack a point on the central cusp, though the rounded central cusp of WSU 1428A suggests this wear was from life or taphonomy. Retention of worn teeth (rather than natural loss) is common among ctenacanthid chondrichthyans (Williams, 2001). The WSU 1495 specimen lacks a lateral portion of the base as well as lateral cusps on the remaining portion. Although it is not clear whether the tip of WSU 1495's central cusp was lost during life or postdepositional weathering, the other missing portions were certainly lost during weathering, as the specimen was exposed at the surface before being recovered for study.

Both specimens reveal much of the labial side of the tooth. The robust, triangular central cusp, convex (or flat) in the labial direction, and basolabial depression are indicative of ctenacanthiform genera, such as *Glikmanius*, though it appears to lack the labially oriented intermediate cusps seen in the type species, *Glikmanius occidentalis* (Ginter et al., 2005, 2010). It is also somewhat comparable in size to *Nanoskhalme*, though the central cusp is less compressed, and the basolabial depression is present. The ornamentation on the central cusp, and the slight recurve seen in WSU 1495, are more similar to the genus *Neosaiodus* (Hodnett et al., 2012). Wear and damage obscure most of the detail on the lateral cusps. This wear, the basolabial depression observed in both specimens, and the greater number of cristae compared with the type species, *Neosaiodus flagstaffensis*, cast some doubt on the affinity of these specimens to *N. flagstaffensis* directly.

Elsewhere in the marine Permian, large ctenacanthiform teeth occur in other assemblages and suggest that members of the Ctenacanthiformes were apex predators in many marine ecosystems. The fact that the largest teeth from this locality come from a ctenacanthiform reaffirms this interpretation.

#### Family Heslerodidae Maisey, 2010

##### Genus *Heslerodus* Ginter, 2002

##### *Heslerodus* species

**Material Studied**—Fragmentary tooth, WSU 1496, isolated base, WSU 1487 (Figs. 4E–4G).

**Description**—These specimens, WSU 1487 and 1496, preserve very similar teeth, with different features exposed; WSU 1487 consists of a single base with the crown almost totally removed from weathering. It preserves features such as a deep basolabial depression and paired buttons on the orolingual surface of the base, as well as the underside. These characteristics, along with the apparent number and size of cusps, and small size (widths less than 4 mm), are indicative of *Heslerodus* (Ginter, 2002). Unlike WSU 1487, WSU 1496 represents a more complete tooth (though the central cusp is obscured or missing) preserved in lingual view. Visible on the specimen is another basolabial depression that can also be seen in WSU 1496, as well as the same number of cusps on the crown as in WSU 1487 and other examples of this species (see the following). The lateral-most pair of lateral cusps are similar in size to the main cusp, which is implied in the weathered surface of WSU 1487 and a typical characteristic of *Heslerodus divergens* (see Trautschold, 1879; Ginter, 2002; Ginter et al., 2010).

**Remarks**—In addition to the characteristics listed previously, the specimens used in this study possess other features similar to a number of known examples of *H. divergens*, such as the

holotype PCh/617 (Institute of Zoology at the University of Wrocław, Poland), figured by Ginter (2002).

The overall size and shape of these teeth suggest a predatory, piscivorous lifestyle similar to that of *G. occidentalis*, which often occurs in the same localities as *H. divergens* (Ginter et al., 2010). The thin cusps, however, suggest a more piscivorous diet than *G. occidentalis*, with its wider central crown, which is less suited for catching fish.

Cohort Euselachii Hay, 1902  
Order Hybodontiformes Maisey, 1975  
Hybodontiformes indet.

*Material Studied*—Nearly complete fin spine, WSU 1537 (Fig. 4I).

*Description*—This spine is gently curved toward the posterior, 20.3 cm in total length and 17.9 cm at its thickest point (though the basal-most portion is missing due to postexposure weathering). It is ornamented by 10 parallel costae along the lateral faces, and its anterior edge appears to be ornamented by only a single ridge. The overall shape tapers gently and uniformly to a single point. This distal point of the spine is further ornamented by a single row of at least 11 denticles along its posterior flank.

*Remarks*—This specimen was recovered ex situ from the edge of a block of limestone (approximately 1 m thick) from where the western edge of the quarry meets the Brazos River. That said, its lighter color suggests that it came from the upper portion of the lower Lueders Formation (see Fig. 3). This stratigraphic position is further inferred by the occurrence of hybodontiforms higher in the section compared with the other vertebrates. These features suggest that it came from the uppermost bone bed, or the thicker, but less vertebrate-rich carbonate unit directly underneath.

The relatively smooth surface of this spine, free of orthodontine and denticles, but ornamented by parallel ridges, is more similar to spines of hybodontiforms than ctenacanthiforms. A similar series of parallel to subparallel costae can be seen on the *Amelacanthus* specimen described and figured later; however, this specimen lacks the region where the ventral-most posterior costae intersect those of the rest of the spine due to weathering. Furthermore, the distal-most portion of this spine is ornamented by a single row of denticles on the posterior margin. Although this arrangement cannot be seen in WSU 1498, the *Amelacanthus* specimen described in the following, other reports of this “spine-taxon” report a double row of denticles along the same portion of the spine (Koot et al., 2013). Given the fairly high diversity of hybodontiform teeth from this locality, it is very likely that this spine-taxon represents a body part from another taxon that is also represented by co-occurring teeth. For this reason, it will not be included in Table 1 or Fig. 3 in the following.

Family Acrodontidae Casier, 1959  
Genus *Acrodus* Agassiz, 1838  
? *Acrodus olsoni* Johnson, 1981

*Material Studied*—Tooth crowns, WSU 1419A-D, WSU 1425 (Figs. 5A–5B).

*Description*—Teeth recovered from this locality have an average width of approximately 8 mm, somewhat larger than the 3.8 mm reported by Ginter et al. (2010). The crowns recovered here are generally wide and low, with a number of cristae on both the labial and lingual surface that start at the midline on

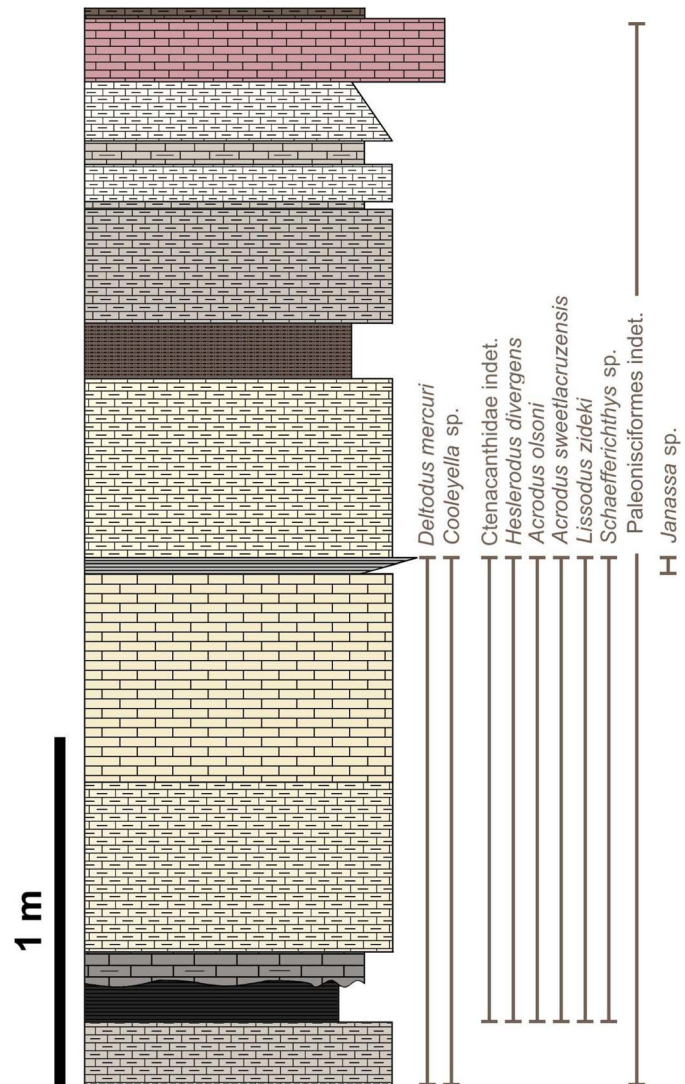


FIG. 3—Stratigraphic occurrences of each distinct taxon from Table 1 across the field-measured section of the Lueders Formation. Note that the coarse limestone unit on top represents the “Texas Rose,” an easily distinguishable unit at the Lueders Limestone Quarry.

the crown surface and extend to the crown–base junction. Many specimens of this species have anterior (?) teeth with sharp, low, triangular crowns, while other forms have lower, bulbous crown apexes or no crown apex at all. The specimens reported previously, WSU 1419 and WSU 1425, are assigned to this species on the basis of overall shape and the crenulations caused by the cristae, which are comparable to other specimens such as the *Acrodus olsoni* paratypes (Shuler Museum of Paleontology at Southern Methodist University, Dallas, Texas, SMP-SMU 64375 and SMP-SMU 64352), as described by Johnson (1981).

*Remarks*—Teeth from this species are only tentatively assigned to this normally Mesozoic genus, as reported by Johnson (1981) when he first described this and another species, ?*Acrodus sweetlacruzensis* (see the following).

? *Acrodus sweetlacruzensis* Johnson, 1981

TABLE 1—This table, listing the vertebrate taxa recovered during this study, contains nine chondrichthyan taxa: six of which are elasmobranchs, while the other three are holocephalans. Among the chondrichthyans, four taxa are reported here for the first time. Three osteichthyan taxa were also recovered, though all represent animals known from other localities within the Lueders Formation.

Name	First report	Reference
" <i>Acrodus</i> " <i>olsoni</i>	No	Johnson, 1981
" <i>Acrodus</i> " <i>sweetlacruzensis</i>	No	Johnson, 1981
" <i>Lissodus</i> " <i>zideki</i>	No	Johnson, 1981
<i>Amelacanthus</i>	Not available	See discussion above
Hybodontiformes indeterminate	Not available	See discussion above
<i>Cooleyella</i>	Yes	Not available
Ctenacanthidae indeterminate	Yes	Not available
<i>Heslerodus</i>	Yes	Not available
<i>Janassa</i>	No	Dalquest and Kocurko, 1986
<i>Deltodus mercurei</i>	Yes	Not available
Paleonisciformes indeterminate	No	Dalquest and Kocurko, 1986
<i>Schaefferichthys</i>	No	Johnson, 1981

*Material Studied*—Teeth, WSU 1421, WSU 1427B, WSU 1489 (Figs. 5C–5E).

*Description*—Teeth belonging to this species are usually 1 to 3 mm in width. Tooth crowns are usually the only portion recovered, though WSU 1489 displays a porous base with several foramen of vascular canals perpendicular to the surface of the root. The shape of the central cusp is generally arcuate (as is the crown–base junction) and takes up the middle third or so of the crown's overall width, while the flanking portions of the crown are reduced in height and point slightly lingually. Although the crown is generally unadorned by cristae, there is a small basolabial projection (see WSU 1489, especially) that may have served to fit each tooth into the overall tooth file.

Similar to that of ?*A. olsoni*, this species is only assigned to the generic level of *Acrodus* on the basis of histologic similarities to its Mesozoic counterpart (Johnson, 1981). *Acrodus sweetlacruzensis* is further distinguished from ?*A. olsoni* by the arcuate contact at the crown–base junction, deep, closed root sulcus, smaller comparative size, and more homodont dentition (Johnson, 1981).

*Remarks*—Ginter et al. (2010) reported that the width of teeth from this species can reach up to 6 mm. However, the holotype for this species, SMP-SMU 64410, is a tooth that is approximately 2 mm in overall width. All teeth recovered during this study were similar in size and comparable to the 2-mm width of the holotype, which is figured by Johnson (1981).

Family Lonchidiidae Herman, 1977

Genus *Lissodus* Brough, 1835

"*Lissodus*" *zideki* Johnson, 1981

*Material Studied*—Tooth, WSU 1488 (Figs. 5F–5H).

*Description*—The specimen figured in this study, WSU 1488, is a symmetric tooth with a worn crown and a transverse crest on the tooth's plane of symmetry. The crown lacks a base but is uniform in the labial–lingual width. The lateral ends of the crown are rounded and bend somewhat aborally, resembling a horse shoe, and are comparable to the specimen SMPSMU 64447 that is figured by Johnson (1981).

Teeth from this species have a euselachian crown histology similar to the genus *Polyacrodus* (Johnson, 1981). The species is

differentiated from other hybodontiform teeth on the basis of the small size, as well as the presence of longitudinal transverse occlusal crests on the crown and noticeable processes on the labial and lingual sides (Johnson, 1981). The dentition of this species is moderately heterodont (with more pointed cusps on anterior teeth) as well, unlike the similarly small-bodied taxa such as ?*A. sweetlacruzensis* (Johnson, 1981).

*Remarks*—The teeth of "*Lissodus*" *zideki* are approximately 2 mm in width. This species was originally placed in the genus *Polyacrodus* when the first material was discovered and described by Johnson (1981). This species has since been moved into *Lissodus*, which is likely a form genus (meaning that similarly shaped teeth are assigned to *Lissodus*, though the relation to one another is suspect; Fischer, 2008). Almost all teeth in the dentition of this species have high central crowns, though this feature becomes flattened in posterior teeth (Ginter et al., 2010). Teeth with superficial similarities to this species have been reported as "*L.*" cf. *zideki* from the Devonian of Belgium, which suggests that Paleozoic members of this genus and species are still poorly understood (Derycke-Khatir, 1994). Although the genus *Lissodus* has been under heavy revision recently, "*L.*" *zideki* is still generally considered a member, and the Paleozoic portion of this genus is under less revision overall than "*Lissodus*" teeth from the Mesozoic (Rees and Underwood, 2002; Fischer, 2008).

Cohort and Order indet.

Genus *Amelacanthus* Maisey, 1983

*Amelacanthus* species

*Material Studied*—Fin spines, WSU 1497; 1498 (Fig. 4H).

*Description*—Complete spines are rare from this locality; however, two examples, WSU 1497 and WSU 1498, were recovered in 2011 and 2019 and are similar in shape and dimension, though WSU 1497 has a worn distal end. It is comparable to other hybodontiform spines in its lack of orthodontine and lack of denticle ornamentation, which is more indicative of the Ctenacanthiformes or Holocephalians (the only other marine chondrichthyans from this time interval with defensive spines). The slightly recurved shape, cross section, and the longitudinal costae and grooves on this specimen are also indicative of the



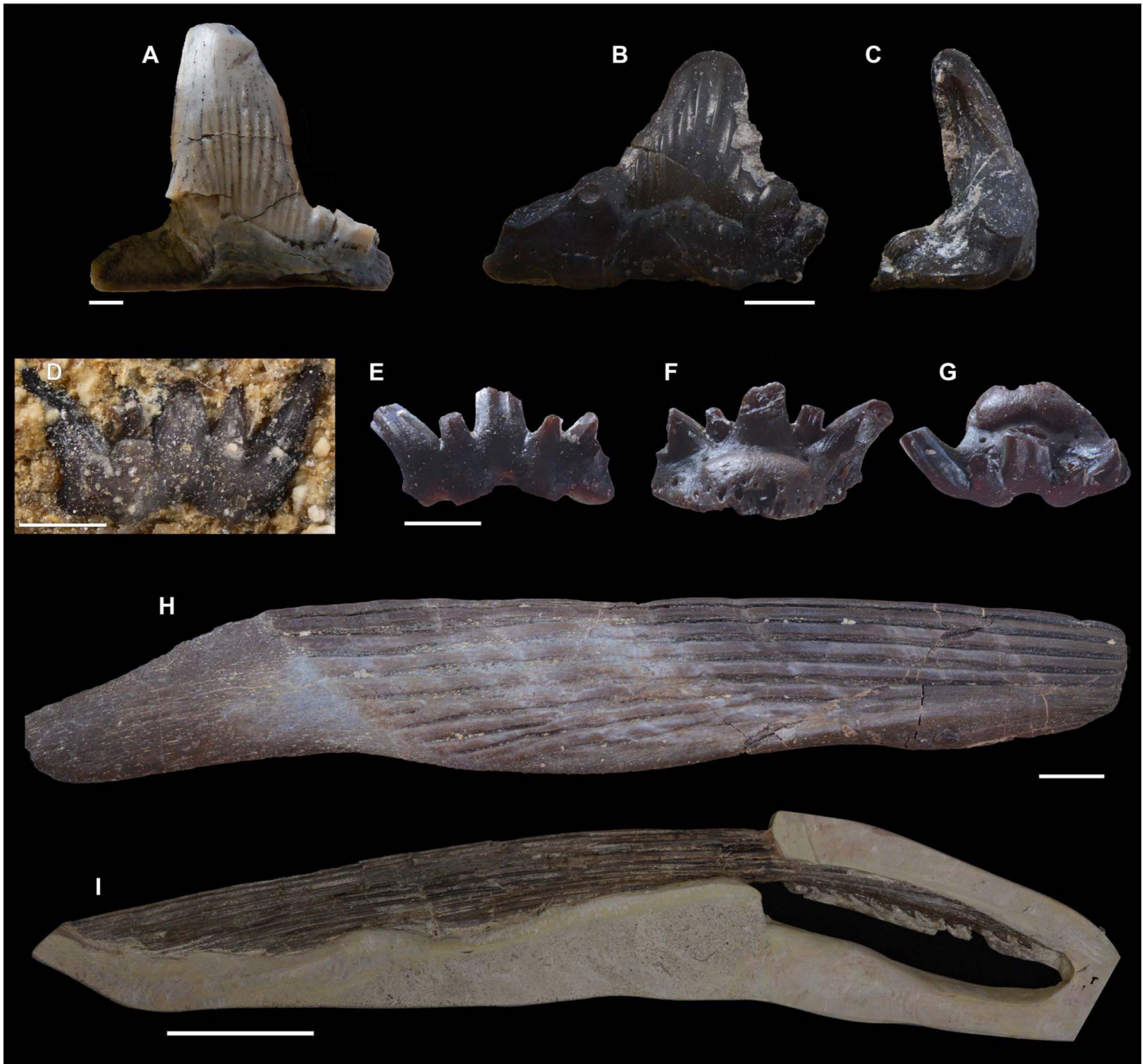


FIG. 4—Ctenacanthiform and other chondrichthyan fossils from the Lueders Limestone Quarry: Ctenacanthidae indeterminate. The WSU 1495 specimen, labial view A); WSU 1428A, labial view B) and lateral view C); *Heslerodus* species, WSU 1496, labial view D); WSU 1487, labial view E), lingual view F), and oral view G); fin spine of *Amelacanthus* species, WSU 1498, lateral view H); and fin spine of a hybodontiform, WSU 1537, lateral view I). Scale bars: A)–G) = 1 mm; H) = 10 mm; I) = 30 mm.

genus *Amelacanthus* (Maisey, 1983; Koot et al., 2013). Specifically, the cross-section outline is subtriangular with an acute, yet rounded, anterior margin. The longitudinal costae are broad and smooth, approximately 10 along each flank, and separated by relatively narrow intercostal grooves. This taxon has also been reported with rounded or pointed hooklike denticles on the posterolateral margin of the spine (Maisey, 1983; Koot et al., 2013). These denticles are not present on WSU 1497 and 1498. However, these spines seem to be worn down during life, though taphonomic processes cannot be definitively ruled out. The ridges, especially the number and truncation of several of

the posterior ridges in this specimen, are especially comparable to forms such as *Amelacanthus sulcatus* (Maisey, 1983).

*Remarks*—Teeth from Hybodontids, which may have come from the same animal as “*Amelacanthus*” spines, are not known from this locality. There are, however, many hybodontiform teeth found in sites containing this morphotaxon (see Dalquest and Kocurko, 1986). This could suggest that the spine-taxon *Amelacanthus* may come from another taxon with teeth described in the genera listed previously or teeth that have yet to be found.



FIG. 5—Euselachian teeth from the Lueders Limestone Quarry; ?*Acroodus olsoni* WSU 1419B, labial view A); WSU 1425, oral view B); ?*Acroodus sweetlacruzensis* WSU 1489 labial view C), lingual view D), and oral view E); “*Lissodus*” *zideki* WSU 1488, labial view F), lingual view G), oral view H); and *Cooleyella* species WSU 1490, labial view I), lateral view J), and oral view K). Scale bars = 1 mm.

Subcohort Neoselachii Compagno, 1977  
 Order *Incertae sedis*  
 Family Anachronistidae Duffin and Ward, 1983  
 Genus *Cooleyella* Gunnell, 1933  
*Cooleyella* species

*Material Studied*—Tooth, WSU 1490 (Figs. 5I–5K).

*Description*—Teeth identifiable as this genus are generally rare from residues at this locality. The figured specimen, WSU 1490, represents a complete tooth (approximately 750  $\mu$ m in width) with a rounded crown and flattened occlusal surface. The labial visor, labial buttress, vascular foramina, and strongly

convex undersurface of the root (which is indicative of *Cooleyella*) are all well preserved in this specimen.

*Remarks*—The shape of the crown is much flatter than many other species of this genus, especially *Cooleyella amazonensis*. However, the overall shape and characters of the base in WSU 1490 are comparable to other specimens assigned to the genus, such as the *Cooleyella fordi* holotype (Natural History Museum, London, United Kingdom, BMNH P.60670), which is a tooth figured by Duffin and Ward (1983).

*Cooleyella* teeth in general are thought to be adapted for gripping and may have a puncturing or cutting and crushing function. It is unclear whether the shape of WSU 1490 differs from



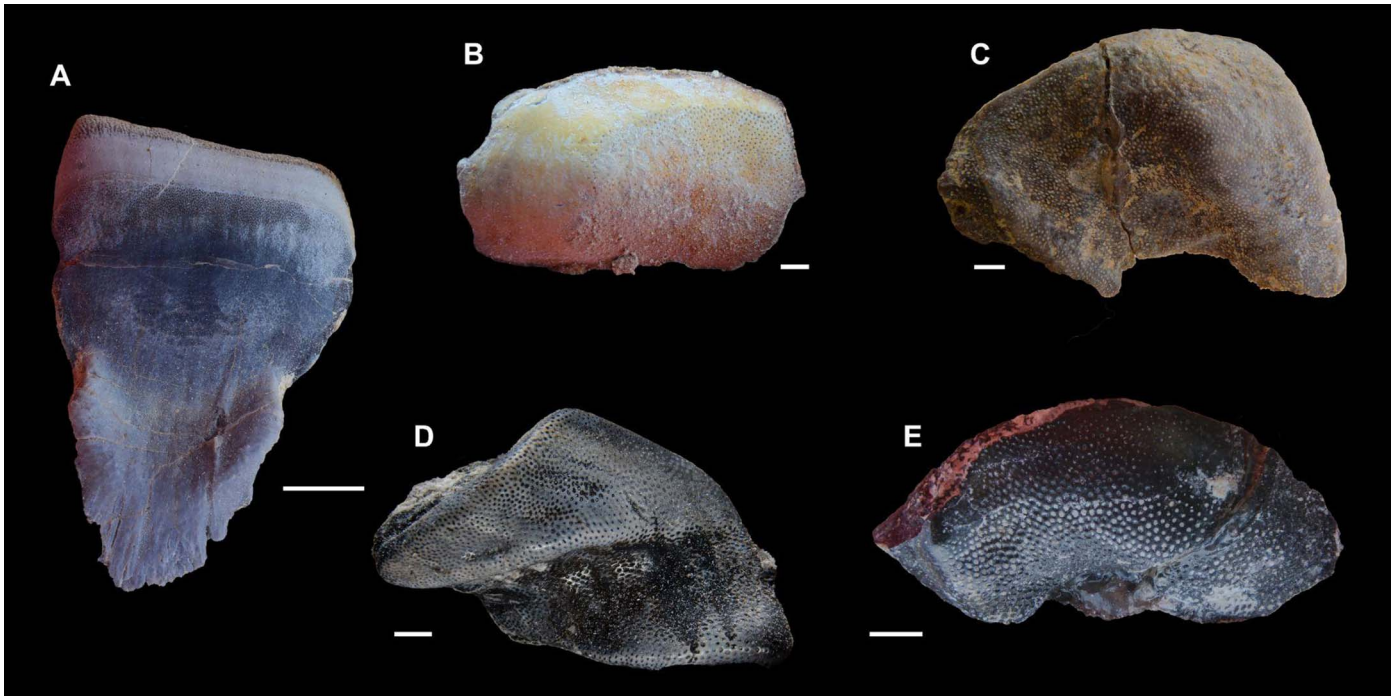


FIG. 6—Holoccephalian teeth and tooth plates from the Lueders Limestone Quarry. *Janassa* species A) WSU 1449 and *Deltodus mercurei* B–F): WSU 1422, 1427A, 1486, and 1499, respectively) Scale bars: A) = 1 cm; B)–F) = 1 mm.

other examples, such a *C. fordi*, due to heterodonty within this taxon, intraspecific variation, or interspecific variation. *Cooleyella* also seems to persist vertically across much of this site. The WSU 1490 specimen was recovered from residues in the uppermost bone bed, and another specimen, WSU 1500, was found much lower in the strata exposed in the quarry (see Fig. 3).

Subclass Euchondrocephali  
Order Petalodontiformes Patterson, 1965  
Family Janassidae Jaekel, 1899  
Genus *Janassa* Münster, 1839  
*Janassa* species

*Material Studied*—Anterior tooth, WSU 1449 (Fig. 6A).

*Description*—The tooth figured in this study, WSU 1449, represents a single, complete tooth, 26 mm in overall length, and preserved in a block of matrix with the labial side exposed. The crown, 15 mm wide and 4 mm high, is weakly concave in the center of the cutting surface, which may be the result of wear from life or a true anatomic feature (see Remarks). The sigmoidal shape in lateral view of this specimen, together with the presumed convex shape of the crown's lingual surface, and pair of low cusps created by the concave occlusal surface, are all indicative of *Janassa* (Ginter et al., 2010).

*Remarks*—The features indicative of *Janassa* on WSU 1449 are complemented by its comparison to the upper symphyseal tooth of the complete *Janassa bituminosa* dentition (Martin-Luther University Halle-Wittenberg in Halle, Germany, MLU.z 461101), figured by Jaekel (1899) and Ginter and colleagues (2010).

Stomach contents from some *Janassa* specimens preserve brachiopods, crinoids, foraminifera, and crustaceans (Ginter et al., 2010). *Janassa* is rare from this locality, which may be explained by the dissimilarity of the invertebrate fauna here to the diet reported

previously: brachiopods and large crustaceans are absent, and crinoid fragments are not especially common (Shell et al., 2020).

Order Cochliodontiformes Obruchev, 1953  
Family Cochliodontidae Owen, 1867  
Genus *Deltodus* Morris and Roberts, 1862  
*Deltodus mercurei* Newberry, 1876  
*Deltodus* cf. *mercurei*

*Material Studied*—Tooth plates, WSU 1422, 1427A, 1486, 1499 (Figs. 6B–6E).

*Description*—At least two of the specimens recovered during this study, WSU 1422 and WSU 1499, represent posterior tooth plates, while the other, WSU 1486, is likely an anterior tooth plate. All plates appear complete with light wear on the tritoral surfaces. Each plate measures between 9 and 12 mm wide in the longest dimension. The tritoral surfaces of the posterior plates are covered in tubular dentine with a central groove that likely articulated with the corresponding plate in the opposite jaw, a typical trait of cochliodontiforms (Janvier, 1996). The overall triangular outline of the posterior plates is indicative of *Deltodus*, and the transverse ripples on the tritoral surface, especially visible on WSU 1499, are indicative of *Deltodus mercurei* (Stahl, 1999).

*Remarks*—Although uncommon, this species is remarkably persistent vertically at this site, being found well below the main bone beds (WSU 1422), in the lowermost (WSU 1499) and in the uppermost bone bed (WSU 1486; Fig. 3). These plates are small compared with Carboniferous examples of the genus and have fairly shallow articulation grooves on the tritoral surface, which are comparable to the *D. mercurei* holotype (U.S. National Museum of Natural History, Washington D.C., NMNH 13091), a tooth reported by Newberry (1876) and figured by Hodnett and Lucas (2015).

Osteichthyes  
Actinopterygii  
Order Palaeonisciformes Hay, 1902  
Palaeonisciformes indet.

*Material Studied*—Teeth, WSU 1417 (A–C), WSU 1501; Maxilla/Palate, WSU 1432A; operculum WSU 1438 (Figs. 7A–7D).

*Description and Remarks*—We assign these remains to the order Palaeonisciformes, the most common actinopterygian order found during this time. These teeth, which occur from a wide stratigraphic range at the site (Fig. 3), are extremely bimodal in overall length with some examples (WSU 1501) as small as 500 µm, while others (WSU 1417A–C) are six times longer (3 and 4 mm). A maxilla or palate, WSU 1432A is approximately 7 mm long, with exposed tooth sockets similar in width to some (WSU 1417A–C) of the longer teeth. This suggests that many of the conical-toothed palaeonisciforms from this locality were small, probably similar to *Lawnia taylorensis*, which has been reported from the Lueders Formation of the Lake Kemp area (Dalquest and Kocurko, 1986). However, it is also clear from these remains that not all palaeonisciform fishes were as small: WSU 1438 represents a large skull element (possibly an operculum and associated bones given its flattened shape) 7 cm in length, with longitudinal ornamentation similar to that of the skull of *Howqualepis*, a much older palaeonisciform fish genus (see Choo, 2009). *Luederia kempi*, a much larger predatory palaeonisciform, is known from the Lake Kemp area; however, the material associated with this taxon only consists of a braincase and possible vertebra (Dalquest and Kocurko, 1986). Neither of these known remains correspond to the recovered specimen (Schaeffer and Dalquest, 1978; Dalquest and Kocurko, 1986). Although it is very likely that palaeonisciform specimens recovered during this study represent multiple taxa, it cannot be definitively stated.

Family Platysomidae Young, 1866  
Genus *Schaefferichthys* Dalquest, 1966  
cf. *Schaefferichthys*

*Material Studied*—Tooth plates, WSU 1534, 1423A–B (Figs. 7E–7I).

*Description*—The tooth plates recovered, while both partial, are clearly phylloodont in overall shape and structure, with a large number of closely spaced, hemispheric (or shallowly conical) teeth 1 mm in width or less. These are stacked together vertically to form the plate (such as those described by Johnson and Zidek, 1981). These fossils were recovered from both the upper and lower bone beds, suggesting persistence of these fishes across multiple events of deposition.

*Remarks*—*Schaefferichthys* is only represented by a single species, *Schaefferichthys luedersensis*, which is known from articulated examples in the Lueders Formation of Lake Kemp (Dalquest, 1966; Dalquest and Kocurko, 1986). The plates recovered during this study are not found in the same paleoenvironment as the type species (components of the local vertebrate assemblage differ, as does the proximity of the site to fresh water; see Dalquest and Kocurko, 1986), and are not associated with any other osteichthyan skeletal material. Following in the tradition of Johnson and Zidek (1981), it is understood that these individual teeth may never be fully identifiable without associated material. The plates are, therefore, assigned to *Schaefferichthys* tentatively because “it is the only Platysomid to possess tooth plates” similar

to those found in this chronostratigraphic position (Johnson and Zidek, 1981).

*Faunal List*—Table 1 lists the vertebrate fauna recovered from the Lueders Formation at this locality. Although 12 taxa are recorded, three have never before been reported from the Lueders Formation. The ecosystem preserved here has much higher alpha diversity and species richness of vertebrate taxa than any other marine Cisuralian vertebrate site reported worldwide thus far (see Merino-Rodo and Janvier, 1986; Ewell and Everhart, 2005; Ivanov, 2005). Although we only report 11 unequivocal taxa, the diversity seen in size and shape in our palaeonisciform specimens indicate that the total species richness here is likely much higher than even reports of high richness faunas from the Neva Formation (see Ewell and Everhart, 2005).

**DISCUSSION**—Fossils of chondrichthyans and osteichthyans recovered from the Lueders Limestone Quarry represent a marine vertebrate community with species richness higher than many similarly aged reported occurrences across the globe (see Merino-Rodo and Janvier, 1986; Ivanov, 2005; Hodnett et al., 2012). Four of the taxa reported by this survey, the unreported ctenacanthid, *Heslerodus*, *Cooleyella*, and *Deltodus* cf. *mercurei*, are recognized from the Lueders Formation for the first time. Although the facies of Lueders Formation are spatially variable, these new occurrences must extend laterally into similar facies deposited by the epicontinental sea that once covered the study locality.

The remains recovered from this locality persist across multiple horizons (Fig. 8), with a few exceptions. First, *Cooleyella* and *Janassa* have been found in the uppermost bone bed only. Second, *Deltodus* remains occur much lower in sequence than other vertebrate remains, though they also occur in the bone beds as well. The unknown palaeonisciform fishes occur in beds both well above and below the most fossiliferous horizons. Because of the stratigraphic overlap in the majority of vertebrate occurrences here, it is likely that these atypical stratigraphic records represent shifts in depositional character rather than the persistence and die off associated with faunal overturn.

Although other marine Cisuralian vertebrate communities have a small number of species adapted for crushing prey (such as that of the Copacabana Formation; see Merino-Rodo and Janvier, 1986), we find the opposite here with three hybodontiform taxa (“A.” *olsoni*, “A.” *sweetlacruzensis*, and “L.” *zideki*), as well as a cochliodontid (*D. mercurei*), a petalodontid (*Janassa*), a palaeoniscoid (*Schaefferichthys*) with teeth that were useful for durophagy: feeding on hard objects such as shells or exoskeletons. *Cooleyella*, an enigmatic taxon of neoselachian, is also known from this community, which further suggests that an emphasis on durophagy, at least in a nonobligate sense, was a common feature in this, and possibly other, Cisuralian marine vertebrate communities, especially where marine invertebrates are common (Shell et al., 2020).

For palaeonisciform fishes, only *Schaefferichthys* had durophagous adaptations. The remaining fish were likely predatory, though it is likely predatory palaeonisciform



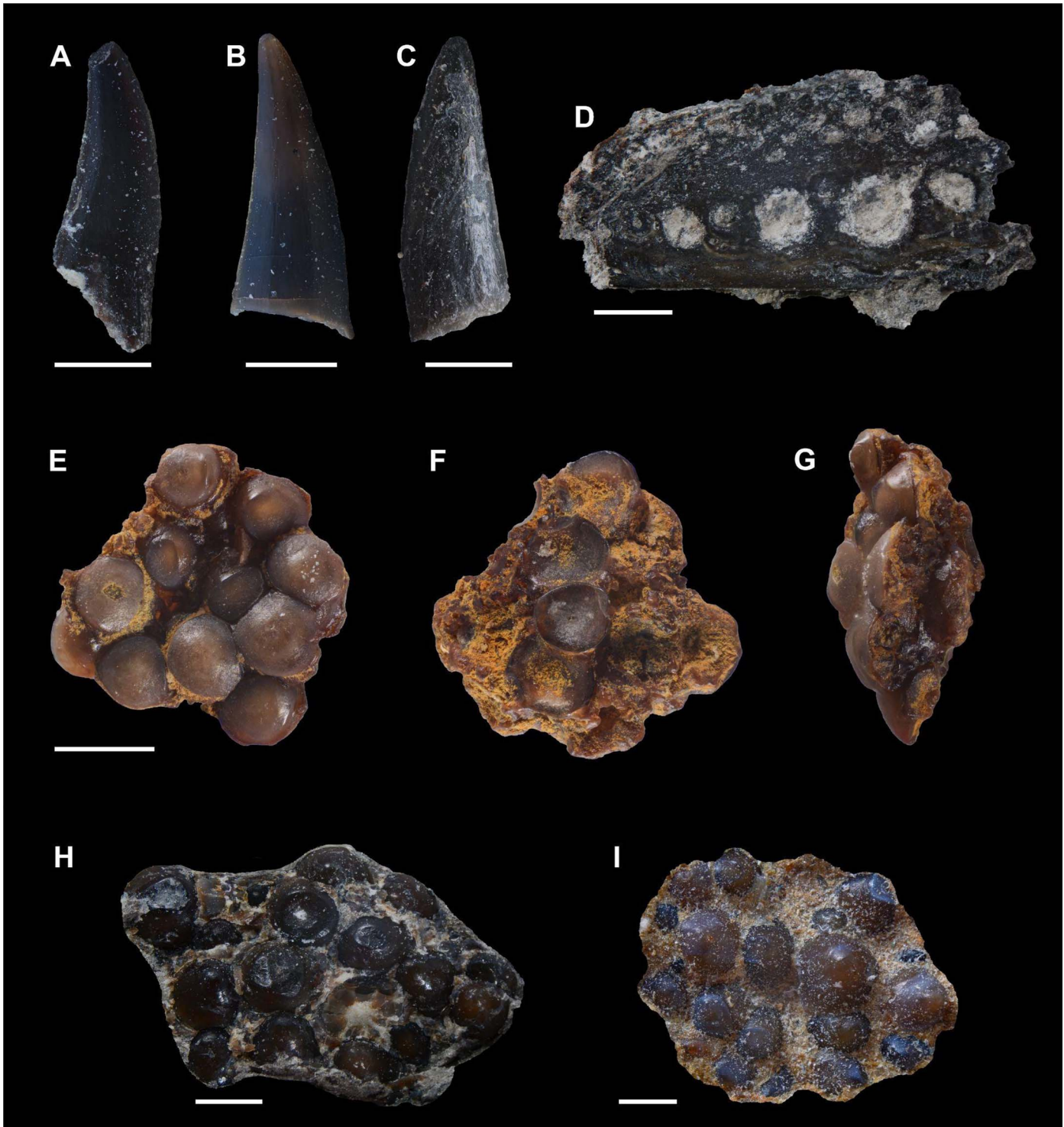


FIG. 7—Osteichthyan fossils from the Lueders Limestone Quarry. Paleonisciformes indeterminate teeth A)–C) WSU 1417A, B, C, respectively, Paleonisciformes indeterminate maxilla D), WSU 1432A. *Schaefferichthys* partial tooth plate (WSU 1534) in occlusal, aboral, and lateral views E), F), and G) and additional *Schaefferichthys* partial tooth plates H) and I), WSU 1423B and 1526, respectively. Scale bars = 1 mm.

fishes from this locality are represented by multiple taxa given the extreme variation in tooth and skull element size recovered here. The largest skull element, WSU 1438, suggests a similar body size to some of the smaller predatory chondrichthyans from this locality, which indicates that the role of midlevel predator in this, and possibly other,

Cisuralian marine communities may not have been uniquely represented by chondrichthyans.

Among the ctenacanthiform chondrichthyans, the shark with teeth described as *Ctenacanthidae* indet. was likely an apex predator in this particular community, given that its teeth represent the largest teeth from the



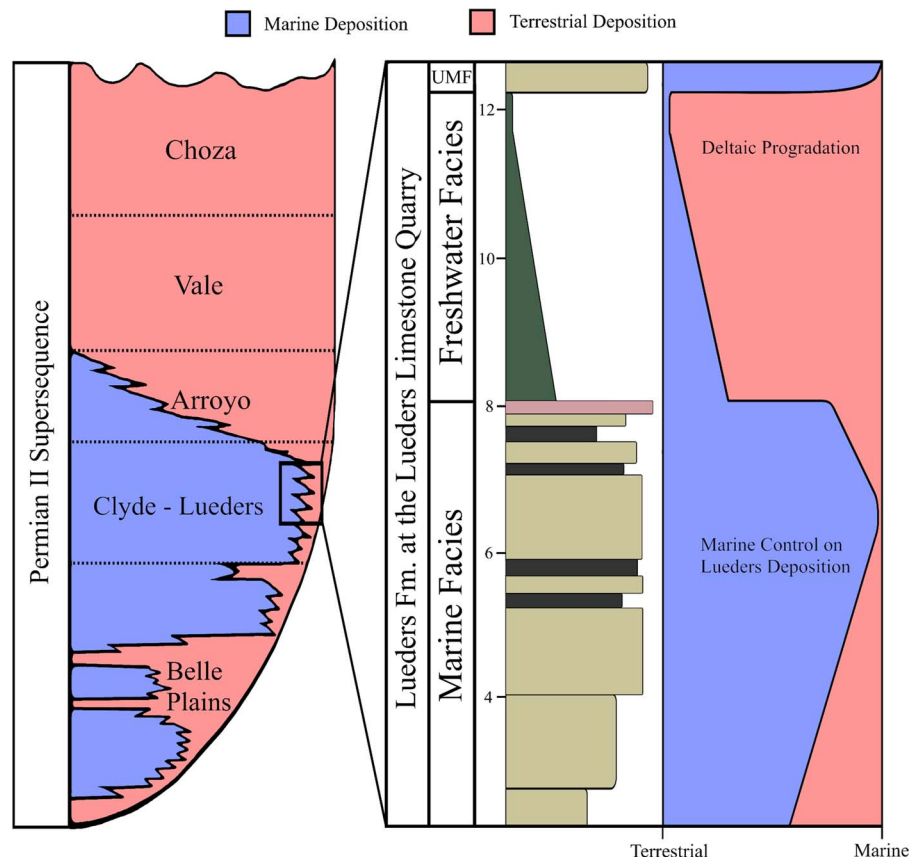


FIG. 8—The Lueders Formation represents the maximum transgression of the Artinskian's Permian II Supersequence (Holterhoff, 2010). During this period, the rocks of the Lueders Quarry were deposited and preserved a record of the shift in depositional character of the site from marine to freshwater control. This shift was, in part, caused by coastal plain progradation into the basin, truncating a period of marine deposition. The y axis measurements are field measurements taken in meters above the quarry floor (~476 m above sea level).

locality that were adapted for a predatory lifestyle. The undetermined ctenacanthid occurs alongside the *Heslerodus* species. This pattern of large and small ctenacanthiform teeth occurring in the same communities is observable in other Upper Paleozoic sites (Ginter et al., 2010). The presence of both species suggests that predation on fishes in this community of Cisuralian marine vertebrates was carried out by ctenacanthiform fishes rather than eugeneodontids, as is the case in other communities (Merino-Rodo and Janvier, 1986).

The reports of vertebrate fossils in this article, along with invertebrate occurrences at the same locality (Shell et al., 2020), better illuminate the depositional history and paleoenvironments preserved in north-central Texas. The fully marine biota reported from certain facies of the Lueders Formation indicate episodes of marine incursions that took place in a region otherwise dominated with terrestrial deposits (Fig. 8). Often, these settings periodically restrict access to the open marine shelf spatially or temporally or both. Eustatic sea level is a sensitive factor in these settings, governing the spatiotemporal distribution of marine environments. During the Artinskian Stage, global transgressions took place (see Marchetti

et al., 2022; Hou et al., 2023) that were responsible for the ecologic reorganization of multiple groups (Leven et al., 1996). Such settings can also drive speciation by reproductively isolating different populations, often resulting in a high degree of endemism. Most of the vertebrate genera reported from the Lueders Limestone Quarry also occur outside of the Permian basin of Texas. Many occurrences are shared along the continental margins of the Paleotethys (now the Ural Mountains) and Tethys Oceans (now Oman), which were on the opposite side of Pangaea (Brandt, 1996; Zidek et al., 2003; Ivanov, 2005; Tverdokhlebov et al., 2005; Wang et al., 2007; Ivanov et al., 2012; Koot et al., 2013; Ivanov, 2016). At the species level, ?*A. olsoni* and ?*A. sweetlacrucensis* are only known from the epicontinental sea that used to cover the study area. The collection of additional fossil material from this area, as well as adjacent deposits, could refine our understanding of the endemic evolution of chondrichthyans and other vertebrates during this Early Permian transgression.

In addition to sea level changes, many marine groups were recovering from a global environmental crisis at the Sakmarian–Artinskian boundary (Leven et al., 1996). Each of these factors suggests that the fully marine

communities of this region during the Early Permian underwent rapid changes in composition and distribution. High disparity among durophagous tooth morphologies for chondrichthyans and osteichthyans suggests adaptation for preying on diverse co-occurring invertebrate groups (Shell et al., 2020). Other tooth morphologies found in the Lueders Limestone Quarry are more consistent with piscivory, indicating a somewhat higher trophic rank. These animals and distributions paint a more complete picture of the complexity of marine communities during the Early Permian. Furthermore, they provide an opportunity to study biotic responses to global changes in sea level and recovery from environmental crises and other ecologic and environmental challenges that marine communities may continue to face.

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