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THE FIRST SMALL-BODIED ORNITHOPOD DINOSAUR FROM THE LEWISVILLE FORMATION (MIDDLE CENOMANIAN) OF TEXAS

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ABSTRACT—Sediments of the Woodbine Group exposed in northeastern Texas were deposited along the southwestern margin of Appalachia as a series of near-shore, shoreline, distal lowland swamp, lake, and fluvial deposits during a regression of the Western Interior Seaway in early and middle Cenomanian time. The Lewisville Formation (upper Woodbine Group) of north Texas preserves the most diverse terrestrial fossil assemblage known from Appalachia, but remains of small ornithischian dinosaurs have been conspicuously absent from it. An almost complete left dentary from the Lewisville Formation represents a new, small-bodied ornithopod taxon, *Ampelognathus coheni* gen. et sp. nov. The dentary is generally similar to those in non-iguanodontian ornithopods such as *Hypsilophodon*, *Changchunsaurus*, *Haya*, and *Convolosaurus*. *Ampelognathus* occupied an expected but previously missing component of the 'mid' Cretaceous terrestrial fauna of southwestern Appalachia. The growing diversity of fossil vertebrates and renewed paleobotanical study in the Lewisville Formation reinforces the importance of the unit's fossil record for understanding eastern North American terrestrial ecosystems during an important transitional period in the earliest Late Cretaceous.

INTRODUCTION

The 'mid' Cretaceous marked a time of great change in North American terrestrial ecosystems. Vertebrate taxa with Asian origins began traversing the newly established connection of Beringia and appear in the North American fossil record, angiosperms were on their rise to dominance in terrestrial floras, and previously diverse North American groups declined or disappeared from the fossil record (Avrahami et al., 2018; Benton et al., 2022; Crepet & Friis, 1987; Russell, 1993; Upchurch & Wolfe, 1987; Wing & Boucher, 1998). The intrusion of the Western Interior Seaway (WIS) during the Cenomanian divided the continent into the landmasses of Appalachia to the east and Laramidia to the west, creating the conditions for independent evolution of the terrestrial biota on each side of the WIS until its large-scale regression in Maastrichtian time (Blakey & Ranney, 2018; Scotese, 2021; Scott et al., 2018; Slattery et al., 2015).

The terrestrial fossil record of Appalachia is poor compared with the relatively rich paleofauna known for Laramidia. Laramidia underwent episodes of widespread orogeny through the Cretaceous that produced large accumulations of terrestrial and near-shore sediments and fossils in foreland basins along the western margin of the WIS (Gates et al., 2010; Lehman, 1987, 2001). In contrast, Appalachia was comprised mainly of a low-relief, stable craton with limited sediment accumulation from westward and southwestward-flowing rivers emptying into the WIS (Scotese, 2021; Slatterly et al., 2015). The differences in depositional conditions and sediment supply partly account for the disparity in sample sizes and subsequent understanding between the terrestrial ecosystems of the two landmasses (Butler et al., 2011b).

The Cenomanian dinosaur record from Appalachia is sparse, and with the exception of the nodosaurid *Silvasaurus condrayi* from the Dakota Formation of Kansas (Eaton, 1960) is comprised mainly of material from the Lewisville Formation of the Woodbine Group (middle Cenomanian) of north Texas

(Head, 1998; Jacobs & Winkler, 1998; Lee, 1997a, 1997b; Noto et al., 2023a). Dinosaur tracks were the first hard evidence for dinosaurs in the Lewisville Formation (Lee, 1997a, 1997b), but soon after came the first descriptions of the hadrosauroid *Protohadros byrdi* from the same area (Head, 1998). Additional hadrosauroid elements are known from other sites in the Lewisville Formation in the Dallas-Fort Worth region (Jacobs et al., 2013; Main, 2013; Main et al., 2014; Noto et al., 2023a). Isolated teeth and postcranial material of nodosaurids are known from exposures along Bear Creek near Dallas-Fort Worth International Airport close to the contact with the overlying Eagle Ford Group (Lee, 1997b), and from near the *Protohadros* type locality. The holotype of the enantiornithine *Flexomornis howei* was collected from along the Grapevine Lake emergency spillway (Tykoski & Fiorillo, 2010), a location that also produced a limited number of isolated dinosaur elements (Noto, 2015; Noto et al., 2023a, 2023b). Non-avian theropods from the Lewisville Formation are represented by teeth and sparse postcranial material of a large carcharodontosauroid, a mid-sized tyrannosauroid, an ornithomimosaur, a troodontid, small and large dromaeosaurids, and indeterminate small coelurosaurs (Noto et al., 2022). Besides the pieces noted above, ornithischian dinosaur remains are rare in the Woodbine Group.

Here we report the first small-bodied ornithischian from the Woodbine Group based on a dentary collected from the Lewisville Formation. The dentary has diagnostic characteristics supporting recognition of a new ornithopod taxon. We also present an assessment of its possible phylogenetic affinities based on the data available, and discuss implications for reconstructing the 'mid' Cretaceous Appalachian ecosystem.

Geology

The specimen (DMNH 2021-05-02) was collected from exposures of the Lewisville Formation along the Grapevine Lake emergency spillway, in northern Tarrant County, Texas (Fig. 1A). The Lewisville Formation is the upper formation of the Woodbine Group following recent revision of Woodbine stratigraphy and nomenclature by Denne et al. (2016) (Fig. 1B), which we follow here. The exact stratigraphic level of the spillway exposures within the Lewisville Formation is difficult to determine because the small, isolated rock exposures and increasing urban cover in the region complicate reconstruction of local Lewisville Formation stratigraphy.

The specimen, along with most other vertebrate fossils from the spillway area, came from a sand-rich zone near the top of the exposure (Noto et al., 2023b). Most of the upper sandy zone is comprised of thin laminated bedding, but at least one large (100 meter) asymmetrical, channel-like feature cuts through the otherwise horizontally laminated bedding. The channel-like feature is overlain by more thin, laminated bedding. The specimen came from almost the same stratigraphic level and within 100 meters of the holotype of the enantiornithine bird *Flexomornis howei* (Tykoski & Fiorillo, 2010). Most vertebrate fossils from the sandy zone are from marine or at least aquatic taxa, including teeth of sharks, rays, sawfish rostral dentition, osteichthyan teeth and bones including articulated skeletons (Noto et al., 2023a). Scrappy remains of indeterminate turtles and at least two taxa of mesoeucrocodylians are rare in the zone, as are isolated dinosaur bones including the aforementioned *Flexomornis* material. Pieces of fossil wood and other plant material are also present in the sandy zone and are part of an ongoing study of the Woodbine paleoflora (Noto et al., 2023b).

Below the sandy zone are several meters of gray marine mudstone. The mix of marine muds, intervals of sandier lenses and layers, and occasional fossil wood, suggests the spillway site is in either the Arlington Member or Tarrant Member of the Lewisville Formation (Denne et al., 2016). Oysters (*Ostrea*) and gastropods are relatively rare in the upper part of the sandy zone at the spillway, but can be common in nearby exposures. *Ostrea* is an important marker fossil for the Lewisville Formation, helping differentiate this mostly marine part of the Woodbine Group from the terrestrially deposited Dexter Formation below it (Fig. 1B). The index ammonite *Conlinoceras tarrantense* is known from other sites in the Lewisville Formation, placing these sediments in the uppermost lower Cenomanian to lower middle Cenomanian (Cobban et al., 2006; Gale et al., 2020), corresponding to approximately 96 Ma in age (Denne et al., 2016).

MATERIALS AND METHODS

Phylogenetic analysis

We evaluated the systematic placement of the newly described specimen via phylogenetic analysis using maximum parsimony. We chose to use the recent matrix of Dieudonné et al. (2021), with a few modifications. We re-evaluated and changed the coding of four characters (characters 186, 194, 298, and 300) for *Convolosaurus marri*, a neornithischian from nearby Aptian–Albian sediments of north Texas (Andrzejewski et al., 2019). Those changes are listed in Supplementary Data 1, and are based on direct examination of *C. marri* material exhibited at the Perot Museum of Nature and Science.

In addition to the changed character codings for *Convolosaurus*, we made two more changes to the taxon-character matrix of Dieudonné et al. (2021). The first was to add a third character state to Character 139 to account for the greater diversity of predentary morphologies (or corresponding dentary morphologies) observed in many neornithischians. The second was to add a new character (Character 343 in the current analysis) to account for variation in the amount of separation between the predentary (or the dorsal facet for the predentary) and the first dentary alveolus. Scoring for the new character was determined from the literature except for *Ampelognathus coheni* and *Convolosaurus marri*, which were scored from direct examination of specimens. The final matrix consisted of 73 taxa and 343 characters. The lists of taxon and character changes are given in Supplementary Data 1, and a README file documenting the steps needed to replicate the analysis is provided as Supplementary Data 2. Electronic versions of the NEXUS and TNT files for the analysis are provided as Supplementary Data 3 and 4 respectively, and are also available at MorphoBank here: http://morphobank.org/permalink/?P4609.

Analyses were performed using the software TNT version 1.6 (Goloboff et al., 2008), made freely available through the website of the Willi Hennig Society. All characters were treated as unordered and equally weighted. The operational outgroup was *Herrerasaurus ischigualastensis*. We performed a heuristic 'new technology' search with 10 replications as the starting point for each hit, and a combination of random and constraint sectorial searches, five cycles of ratchet, five cycles of tree-drifting, and five rounds of tree-fusing (command line code in TNT: xmult = hits 100 replic 10 css rss ratchet 5 drift 5 fuse 5). Each search was carried out until reaching 100 hits of the same minimum tree length. The resulting set of most parsimonious trees (MPTs) were subjected to a round of TBR branch swapping. A strict Nelsen consensus tree was generated from the resulting set of MPTs. Nodal support was calculated for the consensus by running a standard bootstrap analysis with 1000 replicates (see Supplementary Data 5).

Institutional Abbreviations—**DMNH**, Perot Museum of Nature and Science (formerly Dallas Museum of Natural
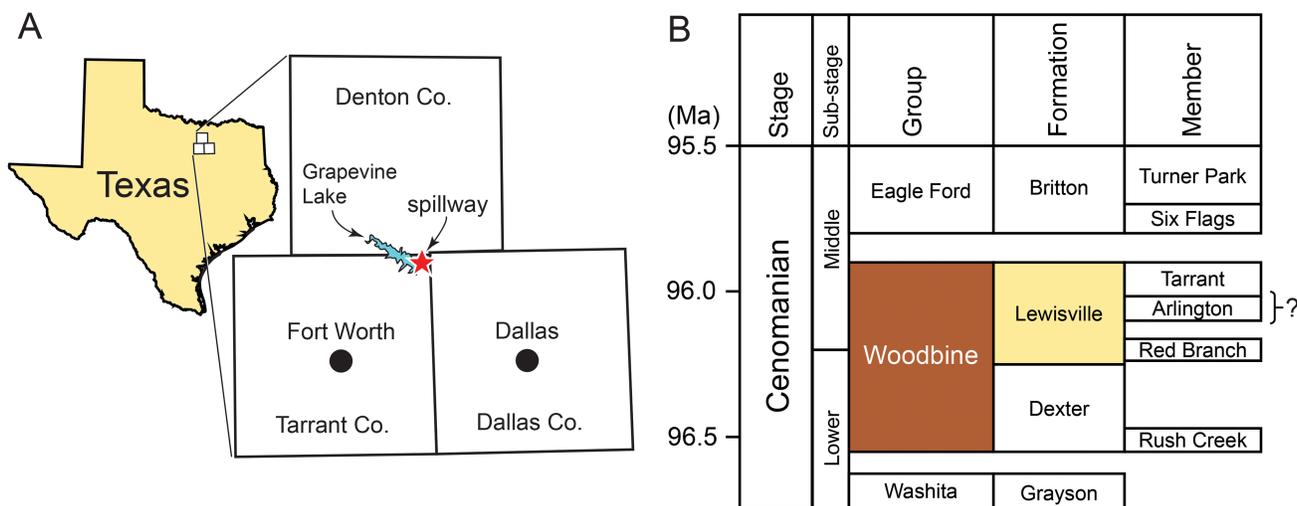
A

B

FIGURE 1. Location and stratigraphy. **A**, outline of Texas with call-out of Dallas, Tarrant, and Denton Counties. Grapevine Lake emergency spillway location indicated by star; **B**, stylized stratigraphy of the Woodbine Group as exposed in the Dallas-Fort Worth area of Texas, based on revisions of the Woodbine and Eagle Ford Groups by Denne et al. (2016). Bracket and question mark is estimated stratigraphic level of DMNH 2021-05-02.

History, and Museum of Nature and Science, Dallas), Dallas, TX, U.S.A.; **SMU**, The Shuler Museum–Southern Methodist University, Dallas, TX, U.S.A.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842, sensu Padian and May, 1993
ORNITHISCHIA Seeley, 1887, sensu Sereno, 1998
CERAPODA Sereno, 1986, sensu Butler et al., 2008
ORNITHOPODA Marsh, 1881, sensu Sereno, 1998
AMPELOGNATHUS COHENI, gen. et
sp. nov. (Fig. 2)

Holotype—DMNH 2021-05-02, an almost complete left dentary, missing a piece of its posterolateral corner, all dentition except the root of dentary tooth 6, and the medial walls of most alveoli dorsal to the replacement teeth foramina.

Etymology—'Ampelo-,' from Greek for grapevines in reference to its discovery in the emergency spillway for Grapevine Lake; 'gnathus' from Greek for jaw; 'coheni,' in honor of Murray Cohen, the avocational fossil enthusiast who found the specimen.

Type Locality—Grapevine Lake emergency spillway, extreme northern Tarrant County, TX, U.S.A. (Fig. 1A). The site is on land managed by the United States Army Corps of Engineers (USACE), and is legally accessible only by permission. The specimen was collected under USACE Lake Activity Permit Number GR-2020-01 issued to the Perot Museum of Nature and Science. More specific specimen locality information is on file at the Perot Museum, in Dallas, TX, U.S.A. and is available to qualified researchers upon request. The specimen was collected from a sequence of fine, millimeter-scale repetitive laminae of sand, silt, clay, and carbonaceous material. The fine-laminated sediments are consistent with deposition in a tidally influenced, back-island lagoonal setting.

Diagnosis—*Ampelognathus coheni* is distinguished from other, closely related ornithopod dinosaurs by: an approximately 45° counter-clockwise 'twist' or torsion of the middle and posterior sections of the dentary relative to the anterior part of the dentary, resulting in dorsomedial orientation of the axes of the posterior (distal) alveoli relative to the anterior (mesial) alveoli (autapomorphy); no diastema between predentary

contact and first dentary alveolus; coronoid process weak or low, so that dentary height at the process is less than 150 percent mandibular height under the mid-part of the tooth row.

Description—DMNH 2021-05-02 was surface-collected and subjected to weathering prior to discovery. Fine crystals of gypsum formed in places on the surface and in cavities within the bone, causing additional damage (Fig. 2). These geological processes degraded much of the bone exterior, destroying many fine details. However, the specimen does not show signs of extensive physical deformation. Dimensions of the specimen are given with graphical depiction of measurement points in the supplementary online file (Fig. S1, Supplementary Data 1).

The dentary is weakly sinuous in lateral view, and is anteroposteriorly short for its height (Fig. 2A). The alveolar (dorsal) and ventral margins of the bone converge toward the predentary contact. The dorsal border dips anteroventrally toward the predentary, but is nearly straight posterior to the fifth and sixth alveoli (Fig. 2A, B). The ventral profile of the dentary is weakly convex, with only a small, ventromedially deflected 'chin' that marks the dentary symphysis and ventromedial contact with the predentary (Fig. 2A–D). The coronoid process projects posterodorsally and constitutes approximately 30 percent of the dorsoventral height of the bone.

To enable the greatest exposure and views of the full range of alveoli, the dentary is described here with the coronoid process oriented dorsally (Fig. 2C, E, F). In this position, the anterior end of the dentary is rotated clockwise in anterior view relative to the rest of the bone to as far back as the fourth or fifth alveolus (Fig. 2E). This torsion directs the axes of the anterior-most alveoli dorsolaterally instead of dorsally (Fig. S1, Supplementary Data 1), and it laterally displaces the alveolar margin in anterior and dorsal views (Fig. 2C, E). The anterior end of the tooth row dips anteroventrally, placing the first three to four alveoli lower than the more posterior part of the tooth row. The anterior end of the dentary curves medially and ventrally to the dentary symphysis, which would have formed a spout-shaped tip of the mandible when combined with its counterpart right dentary. The symphyseal contact itself is a small, triangular surface along the medial edge of the in-turned dentary (Fig. 2B–E).

The anterior surface of the dentary bears two facets for receipt of the predentary bone. The clockwise rotation of the dentary angles the predentary facets approximately 40–45° from vertical
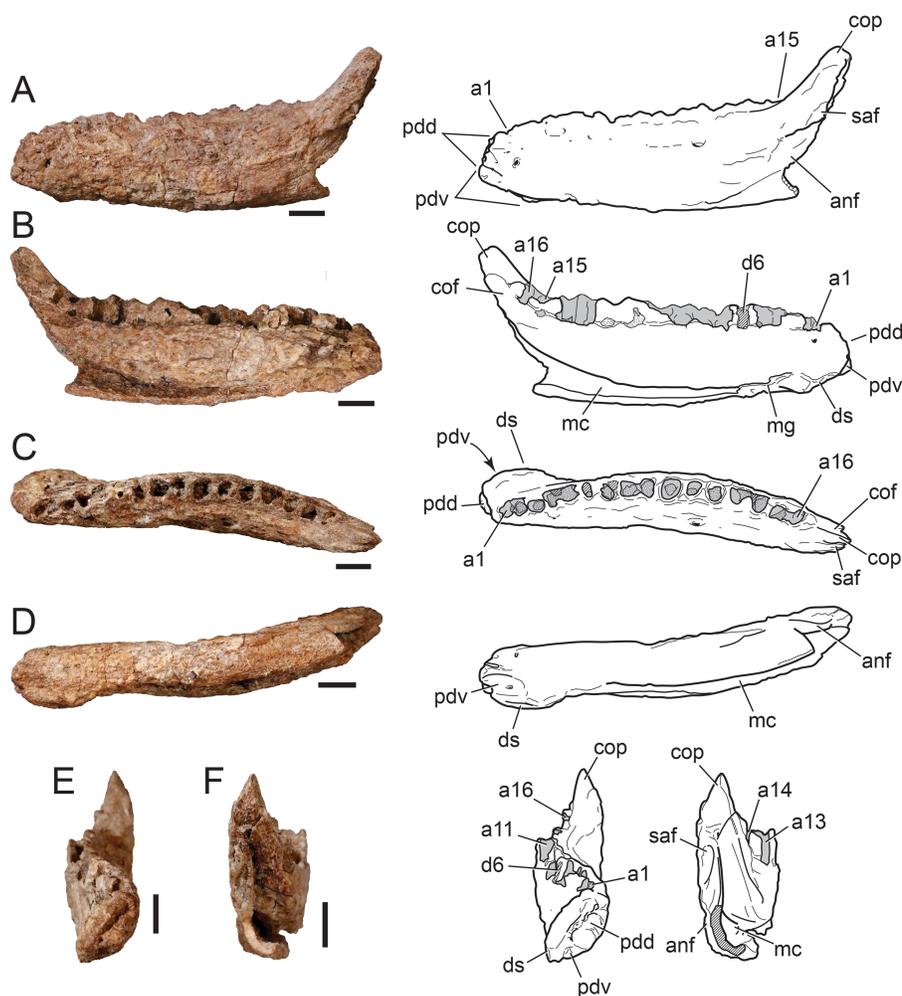
FIGURE 2. DMNH 2021-05-02, holotype left dentary of *Ampelognathus coheni*, photos and labeled outline drawings in **A**, lateral; **B**, medial; **C**, dorsal; **D**, ventral; **E**, anterior; and **F**, posterior views. **Abbreviations**: **a#**, alveolus and numerical position in tooth row; **anf**, angular facet; **cof**, coronoid facet; **cop**, coronoid process; **d6**, dentary tooth 6 base; **ds**, dentary symphysis; **mc**, Meckelian canal; **mg**, Meckelian groove; **pdd**, dorsal facet for predentary; **pdv**, ventral facet for predentary; **saf**, surangular facet. Gray fill indicates recessed surfaces. Stippling indicates visible sediment. Cross-hatching indicates broken bone surface. Scale bars equal 5 mm.

when the posterior (distal) part of the tooth row and coronoid process are dorsally oriented (Fig. 2E). The anterior-most tip of the dentary is at a level within the middle third of the overall height of the bone, and it marks the angular apex between the two facets for the predentary. From the apex of the anterior tip of the dentary, the dorsal predentary facet angles posterodorsally approximately 70° above horizontal in lateral and medial views, and is approximately 65 percent the length of the ventral facet (Fig. 2A, B; Fig. S1, Supplementary Data 1). The dorsal facet is deeply incised, making a sharp groove for the predentary articulation. There are multiple foramina in the lateral surface of the bone just posterior to the facet, including an anterior dentary foramen set in an anterodorsal to posteroventral-oriented groove that continues to the anterior border of the dentary. The ventral predentary facet is shallower and broader than the dorsal facet. From the apex of the anterior tip of the dentary, the ventral predentary facet angles posteroventrally approximately 20° below horizontal in lateral view (Figs. 2A, S1, Supplementary Data 1). The ventral facet extends posteriorly to a plane even with the second alveolus, and its dorsolateral edge is defined by a low ridge. The medial margin of the facet has a slightly raised edge along the dentary symphysis, but it cannot be determined if it received a single or bi-lobed ventral process of the predentary.

There are 16 tooth positions, which together form a tooth row that bows medially/lingually to form a weakly inset lateral 'cheek' region. The alveoli are smallest anteriorly, increase in size to the middle of the tooth row, then reduce in size in the posterior-most one or two tooth positions (Fig. 2C; Table S1, Supplementary Data 1). Small sections of the medial wall of the alveoli are preserved adjacent to the third, 10–12th, and 15th alveoli. A faint groove parallels the tooth row just lateral and ventral to the undulating alveolar margin of the bone, beginning at approximately the ninth alveolus and fading out after the 14th (Fig. 2A, C). A curved row of foramina on the lateral surface of the bone helps delineate the cheek region, with the largest foramen aligned with the septum between the 11th and 12th alveoli. There are several more foramina in the dentary surface near the predentary contact. A medial groove marks the base of the medial alveolar wall, and replacement tooth foramina are present where the wall is complete enough to preserve them (Fig. 2C).

PHYLOGENETIC RESULTS

The phylogenetic analysis resulted in 132 equally most parsimonious trees, each with a length of 1433 steps (C.I. = 0.296; R.I. = 0.614). A Strict Consensus of the trees is shown in Fig. 3. As expected, overall tree topology was consistent with that of Dieudonné et al. (2021), including the recovery of heterodontosaurs as the sister clade to pachycephalosaurs, and this more inclusive clade as the sister to Ceratopsia. *Ampelognathus coheni* was recovered within Ornithopoda, as the sister taxon to the clade consisting of *Thescelosaurus* and Iguanodontia (Fig. 3). This relationship was supported by the shared presence of a downturned anterior end of the dentary tooth row.
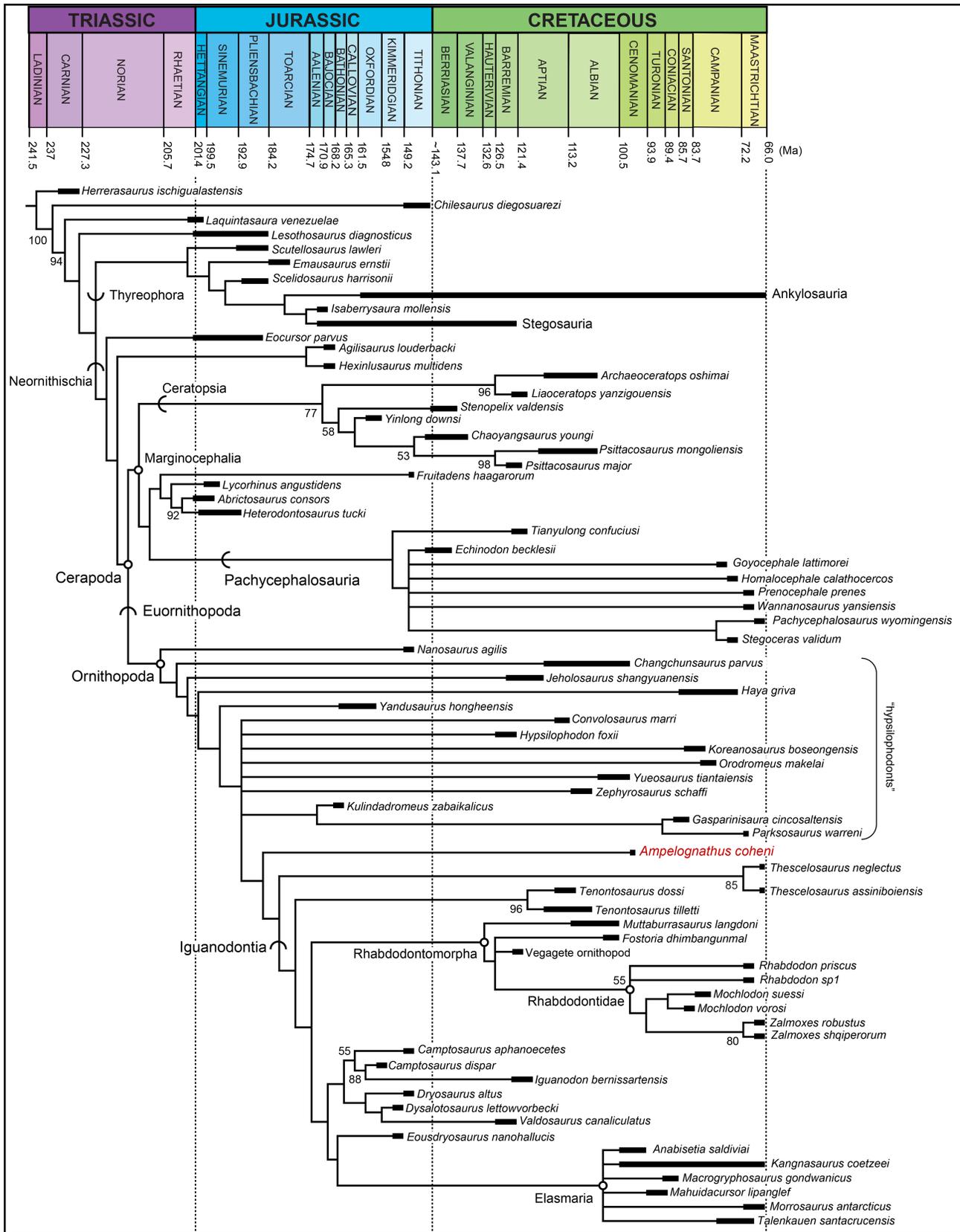
FIGURE 3. Strict consensus of 132 equally most parsimonious trees (length = 1433 evolutionary steps, C.I. = 0.296, R.I. = 0.614) recovered from the analysis, superimposed upon geological timescale. Thickened sections of branches indicate published geological ranges of taxa (including uncertainty). Arc sections on branches indicate stem-defined lineage names. Open circles at nodes indicate node-defined clade names. Bootstrap values shown at nodes with at least 50 percent bootstrap support. Geological timescale from Gradstein et al. (2020).

Ampelognathus coheni is supported by a single unambiguous character from the analysis: the presence of a low coronoid process so that depth of the dentary at the coronoid is less than 150 percent the depth of the mandible beneath the tooth row. Support for the position of *A. coheni* is low, and it takes only one additional step for *Ampelognathus* to become a 'wildcard' taxon. This is not surprising given the limited number of characters that can be scored for the taxon.

DISCUSSION

The newly described dentary is similar in overall form to those of non-iguanodontian ornithopods such as *Nanosaurus agilis*, *Hypsilophodon foxii*, *Changchunsaurus parvus*, and *Haya griva* (Barta & Norell, 2021; Carpenter & Galton, 2018; Galton, 1974; Jin et al., 2010; Makovicky et al., 2011). However, the combination of low coronoid process, number of dentary tooth positions, lack of diastema between predentary contact and first dentary alveolus, proportions and orientation of predentary facets, and torsion of the dentary on its long axis distinguish it from these other taxa. The dentary morphology is also clearly different from that of the contemporaneous hadrosauroid *Protohadros byrdi*, which besides being much larger also has a pronounced coronoid process, at least 28 dentary tooth files in a distinct battery, and greatly enlarged and ventrally expanded anterior end (Head, 1998).

The discovery of new neornithischian taxa and reassessment of long-known taxa in recent years prompted a resurgence in scrutiny of the base of the ornithischian stem, resulting in new hypotheses of relationships near the base of the ornithischian tree (Andrzejewski et al., 2019; Barrett et al., 2005; Barta & Norell, 2021; Boyd, 2014, 2015; Butler et al., 2011a; Dieudonné et al., 2016, 2021; Han et al., 2012; Jin et al., 2010; Makovicky et al., 2011; Ősi et al., 2012; Yang et al., 2020). While the amount of phylogenetically informative morphology preserved in DMNH 2021-05-02 is limited, we sought to test whether enough data were present to place it in a reasonably supported phylogenetic context.

Our analysis finds *Ampelognathus coheni* is more closely related to *Thescelosaurus*, *Tenontosaurus*, and Iguanodontia than to 'hypsilophodont-grade' ornithopods such as *Jeholosaurus*, *Haya*, *Hypsilophodon*, and *Convolosaurus* (Fig. 3). However, support for the relative positions of taxa in the ornithopod clade are not well supported (Fig. 3), as is also the case in other analyses of the group using differing morphological matrices and phylogenetic methods (Barta & Norell, 2021; Boyd, 2015; Dieudonné et al., 2021). Many of these ornithopod taxa are also based on limited fossil remains, which hinders a more robust understanding of their evolutionary relationships.

Comparison of *Ampelognathus* and *Convolosaurus*

The fossil record of small-bodied, North American, Cretaceous ornithischians is generally poor, with notable exceptions. *Convolosaurus marri* is known from multiple individuals of different sizes recovered from a single locality, offering an opportunity to study growth and morphological variation in a population of an Early Cretaceous, small-bodied ornithopod (Andrzejewski et al., 2019). It is appropriate to compare *C. marri* and *Ampelognathus* because their geographic proximity (northern Texas) and ages (Aptian–Albian and Cenomanian, respectively) give reasons to speculate whether these two ornithopod taxa may represent a case of anagenetic evolution within a clade or lineage in one area over time.

The dentary in *Convolosaurus* shows some similarities to *Ampelognathus*. Both taxa lack a distinct diastema between the predentary contact and the first dentary alveolus. The ventral articular surface for the predentary is longer than the lateral

articular surface for the predentary, and the ventral margin of the dentary can curve somewhat dorsally toward the predentary contact in both taxa. However, there are only from eight to 11 dentary tooth positions in dentaries of *Convolosaurus* depending on size and assumed ontogenetic status, compared with 16 in *Ampelognathus* (Andrzejewski et al., 2019). The difference in tooth number cannot be attributed to size-related variation, because the holotype of *Ampelognathus* and SMU 74087 (a dentary of *Convolosaurus*) are both approximately 52 mm in length but have alveolar counts of 16 and 11, respectively (Andrzejewski et al., 2019). The articular facets for the predentary and the dentary tooth row align almost dorsoventrally in anterior view in *Convolosaurus*, whereas the predentary facets angle approximately 45° from the mid and posterior alveoli in *Ampelognathus* because of the axial rotation of the dentary (Figs. 2E, S1, Supplementary Data 1). These differences and the results of the cladistic analysis suggest *Convolosaurus* and *Ampelognathus* do not represent anagenetic taxa arising within a single lineage.

Axial Torsion of the Dentary and Life Orientation

When the coronoid process is dorsally aligned as in the description above (Fig. 2E), the axes of the anterior dentary alveoli project dorsolaterally instead of dorsally (Fig. S1, Supplemental File 1). However, in this orientation the anterior teeth would also follow the alveolar axes and project dorsolaterally as well. The lateral (labial) occlusal surfaces of the anterior dentary teeth would then face ventrolaterally, impeding the ability to occlude with the medial (lingual) side surfaces of the opposing upper teeth.

It is likely that in life the mandibular ramus was normally oriented with the anterior dentary alveoli and teeth directed more dorsally, allowing labio/lingual occlusion with the upper teeth. This requires more medial-ward (counterclockwise in anterior view) rotation of the dentary on its axis relative to that depicted Figure 2E. This would orient the axes of the middle and posterior alveoli (and their respective teeth) more dorsomedially (Fig. S1, Supplemental File 1), and would more easily allow occlusion between the lateral (labial) sides of all the dentary teeth and medial (lingual) sides of the maxillary teeth. The amount of axial rotation needed to direct the anterior alveoli dorsally would also angle the coronoid process more medially, similar to the degree seen in hadrosaurids (Nabavizadeh, 2014).

Relevance of the Curved Ventral Margin of the Dentary

The ventral margin of DMNH 2021-05-02 is curved and convex ventrally (Fig. 2A, B), a character noted in the phylogenetic analysis of Dieudonné et al. (2021) (character #143 of our analysis here). However, we chose to code this character as missing data ("?") for *Ampelognathus coheni* in our dataset. There are other neornithischian taxa in which the profile of the ventral margin of the dentary varies through ontogeny. This was noted in specimens of the Late Jurassic neornithischian *Nanosaurus agilis*, in which smaller, ontogenetically younger specimens exhibit ventrally curved dentary margins, whereas the margin of the dentary is straighter in larger individuals (Carpenter & Galton, 2018). Similar patterns may be present in taxa such as *Haya griva*, in which the ventral edge of figured dentaries appear more curved in smaller individuals than in large individuals (Barta & Norell, 2021; Makovicky et al., 2011). The same pattern of curved versus straighter ventral margins of the dentaries is also present in smaller versus larger specimens of *Jeholosaurus shangyuanensis* (Barrett & Han, 2009), and a curved dentary margin is present in the holotype of *Changmiania liaoningensis* (Yang et al., 2020).

The variability in the curvature of the ventral margin of the dentary in these relatively small-bodied ornithopods was treated as a phylogenetically informative character in the taxon-character matrices of Dieudonné et al. (2021). However, the pattern of the dentary ventral margin straightening with increasing size opens the possibility that this character is at least partly dependent on ontogeny, and is not a clear-cut phylogenetic signal. Until a non-iguanodontian ornithopod taxon is represented by enough specimens to establish the pattern of morphological changes in the dentary through ontogeny, it may be tenuous to assume the preserved anatomy in a given specimen is phylogenetically informative.

Characters that are dependent and correlated with attaining certain ontogenetic stages for their expression should be coded as missing data in phylogenetic analyses for taxa or specimens of unknown or insufficient ontogenetic development to have expressed them. The dentary DMNH 2021-05-02 is: (1) the only element known for *Ampelognathus coheni* at this time; (2) the specimen is small; and (3) it exhibits a morphological feature that may be typical in ontogenetically immature individuals of small-bodied, non-iguanodontian ornithopods. Therefore, the ontogenetic status of DMNH 2021-05-02 is uncertain. Coding an ontogenetically variable character as unambiguously present or absent in a taxon for which we are uncertain of the mature morphology, or the point in ontogeny at which that character expresses, may introduce an element of assumption error into the data resulting in misleading results. Instead, it is prudent to code this character as "missing data" in the analysis at this time (Campione et al., 2013; Choiniere et al., 2014; Gates et al., 2007; Kammerer, 2010; Poole, 2022; Tykoski, 2005).

Paleoecology and Biogeographic Implications

The discovery of *Ampelognathus* adds a small, but important, piece to our growing understanding of the vertebrate fauna of the Lewisville Formation. Prior to this only two ornithischians, *Protohadros* and an un-named nodosaur, were known from the formation (Head, 1998; Lee, 1997b). Evidence of small ornithischians was largely absent despite the presence of other small-bodied vertebrate taxa in the formation (Adrian et al., 2019, 2021; Lee, 1997b; Main, 2013; Noto et al., 2017, 2020, 2022; Ostrowski & Noto 2017; Tykoski & Fiorillo, 2010). There are three potential explanations for the dearth of small ornithischians in the Lewisville Formation: (1) actual absence of these taxa from the ecosystem, (2) taphonomic filters against small body sizes, or (3) ecological displacement by other herbivorous taxa. We may reject the first explanation by examining similar assemblages.

The lower to middle Cenomanian Mussentuchit Member of the Cedar Mountain Formation of Utah hosts a vertebrate fauna similar to that in the Lewisville Formation, including an early diverging euornithopod and multiple morphotypes of small ornithischian teeth, though ornithischians make up a very small proportion of the total faunal diversity (Avrahami et al., 2018; Garrison et al., 2007). Older deposits, such as the Blackleaf, Twin Mountains, and Cloverly formations each preserve at least one small-bodied ornithopod (Andrzejewski et al., 2019; Oreska et al., 2013; Ullman et al., 2012). In the second case, the abundance of small-bodied vertebrate taxa from several Lewisville localities, good quality *in situ* preservation, and general absence of high-energy depositional environments in these exposures argues against a strictly size-biased taphonomic explanation for the absence of small ornithischians (Adams et al., 2017; Hacker & Shimada, 2021; Lee, 1997b; Noto, 2015; Tykoski & Fiorillo, 2010). The last option is most plausible, where the limited diversity of small-bodied herbivorous ornithischians is due to competitive pressure from the juveniles

and adults of larger taxa, particularly hadrosauroids (Codron et al., 2013; Wyenberg-Henzler et al., 2021).

Protohadros byrdi is the most common and widespread herbivorous dinosaur taxon known in the Lewisville Formation, with numerous remains and tracks attributed to it. Remains include juvenile and subadult specimens with estimated body lengths ranging from approximately 2 meters to 7 or more meters recovered from multiple localities (Head, 1998; Main et al., 2014; Noto et al., 2013; Noto, 2015). Like most hadrosauroids, *Protohadros* possessed a wide oral margin, a sign of low diet selectivity, whereas *Ampelognathus* had a relatively narrow beak as seen in more specialized or selective herbivores (Mallon & Anderson, 2014; Wyenberg-Henzler et al., 2021). Among early-diverging ornithopods each dentary was capable of long-axis rotation during jaw adduction, whereas the unusual dorsolateral orientation of the anterior alveoli in *Ampelognathus* may reflect a more specialized feeding mechanism (Nabavizadeh & Weishampel, 2016). Therefore, *Ampelognathus* may have been a minor component of the community, consuming a more restricted diet to decrease competition from similar sized juveniles of the more numerous *Protohadros*. In this case, the structure of the Lewisville ecosystem reflects broader trends in the structure of dinosaur-dominated communities throughout the Mesozoic (Codron et al., 2013; Wyenberg-Henzler et al., 2021).

Interpretation of the biogeographic history of the Woodbine Group is intimately tied to the development of the Western Interior Seaway (WIS). Throughout the Early Cretaceous, North America was a single landmass that maintained a relatively cosmopolitan, low diversity flora and fauna (Suarez et al., 2021; Zanno & Makovicky, 2011). Beginning in the Albian, pulses of tectonic activity and eustatic sea level changes led to temporary, large-scale marine incursions into the continental interior (Slattery et al., 2015). The earliest documented continuous seaway separating Laramidia and Appalachia occurred in the latest Albian ("Skull Creek Seaway"), and lasted at least a few million years (Slattery et al., 2015). This was followed by a brief regression in the early Cenomanian that reconnected the landmasses for 2–3 million years; however, most of the area that would one day be Texas remained underwater during this time (Slattery et al., 2015; Winkler et al., 1995). By the middle Cenomanian, the Greenhorn Transgression completed the WIS and isolated both landmasses, a condition which remained in place until the Maastrichtian (Slattery et al., 2015).

Previous studies noted a near-complete lack of faunal overlap between the Lewisville and earlier Aptian–Albian assemblages in Texas, suggesting a major faunal transition occurred in the interim (Jacobs & Winkler, 1998; Winkler et al., 1995). More recent work supports a transitional nature for the Lewisville assemblage. The fauna had a strong similarity with coeval Laramidian assemblages as expected given this part of Appalachia had only recently isolated from a formerly cosmopolitan fauna, and it included the descendants of a few immigrant taxa that had just begun to evolve independently (Adams et al., 2017; Adrian et al., 2019, 2021; Noto et al., 2020, 2022). *Ampelognathus* further reflects this biogeographic pattern. The current analysis places it as more derived than *Convolosaurus* and more closely related to *Tenontosaurus*, both taxa known from the Trinity Group (Aptian–Albian) of north Texas. Yet *Convolosaurus* is currently known from only one locality, while *Tenontosaurus* was widespread across North America (Andrzejewski et al., 2019; Weishampel et al., 2004). This relationship suggests *Ampelognathus* may be derived from a member of the Early Cretaceous cosmopolitan fauna, and evolved as a result of one of the transgressive events that separated Laramidia and Appalachia during the Cretaceous, similar to other Lewisville Formation taxa. However, this hypothesis is tentative because of the

limited information available from the specimen and its unstable phylogenetic position.

CONCLUSIONS

Ampelognathus coheni is a new, non-iguanodontian ornithopod dinosaur established on DMNH 2021-05-02, a mostly complete left dentary from the Lewisville Formation (Woodbine Group) of Tarrant County, Texas. The dentary of *A. coheni* generally resembles those in other non-iguanodontian ornithopods. It is distinguished from them and the much larger-bodied contemporaneous hadrosauroid *Protohadros byrdi* by axial torsion of the anterior end of the dentary that directs the anterior alveoli dorsolaterally instead of dorsally, little to no separation or diastema between the predentary facet and first dentary alveolus, a low coronoid process so overall dentary height is less than 150 percent mandible height at the mid-point of the dentary, and relatively high dentary tooth count for its size. A phylogenetic analysis based on the dataset of Dieudonné et al. (2021) places *A. coheni* as the sister taxon to a clade comprised of *Thescelosaurus* and Iguanodontia, a relationship weakly supported by the shared presence of a downturned anterior end of the dentary tooth row.

Ampelognathus is the first small-bodied ornithischian taxon known from the Lewisville Formation, and the Woodbine Group as a whole. Its presence adds to the diversity of fossil organisms known from the lower middle Cenomanian deposits of southwestern Appalachia, a time and place with an otherwise poor record of terrestrial ecosystems. The increasing knowledge of paleo-diversity along the west coast of the Appalachian landmass shortly after the final separation of Laramidia and Appalachia by incursion of the WIS should facilitate more comparisons and contrasts with similar-aged paleo-ecosystems preserved in units such as the Cedar Mountain Formation and Naturita Formations of Laramidia. This should provide a better understanding of the pattern and timing of floral and faunal divergence, and the resulting tempo of evolution on both sides of the WIS through the remainder of the Late Cretaceous.

DATA AVAILABILITY STATEMENT

The holotype specimen of *Ampelognathus coheni*, DMNH 2021-05-02 is reposited in the collections of the Perot Museum of Nature and Science in Dallas, TX, U.S.A., and is available for study by appointment by qualified researchers.

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AUTHOR CONTRIBUTIONS

RST prepared the specimen, created figures, gathered and scored data, and composed parts of the manuscript. DLC conducted the phylogenetic analysis and composed parts of the manuscript. CN composed parts of the manuscript. All authors edited the manuscript.

SUPPLEMENTARY FILES

Supplementary Data 1.docx: character list used in phylogenetic analysis, list of taxa with changed coding, Figure S1, and Table S1.

Supplementary Data 2.txt: parameters and specifications used to run phylogenetic analysis.

Supplementary Data 3.nex: nexus file of taxon-character matrix used in phylogenetic analysis.

Supplementary Data 4.tnt: TNT file of taxon-character matric used in phylogenetic analysis.

Supplementary Data 5.tre: tree file with complete set of trees generated by phylogenetic analysis.

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