1 Introduction

Starting in the mid-Cretaceous, the spread of the Western Interior Seaway divided North America in half, an event that should lend itself well to explorations of vicariance in terrestrial and freshwater taxa. However, such analyses are stymied by two separate taphonomic biases. First, the North American record is temporally biased, with spikes in diversity being known in the Aptian–Albian and the Campanian–Maastrichtian with few terrestrial sites in between (Jacobs and Winkler, 1998; Weishampel et al., 2004; Zanno and Makovicky, 2013). Secondly, what mid-Cretaceous sites we do have are geographically biased as well, concentrated on the western landmass of Laramidia (Ullmann et al., 2012; Krumenacker et al., 2016; Prieto-Márquez et al., 2016). Appalachia, to the east, has remained something of a mystery, but recent discoveries are starting to reveal aspects of the diversity of this understudied landmass (e.g. Adams et al., 2017; Brownstein, 2018; Adrian et al., 2019; Noto et al., 2019).

The Woodbine Group outcrops across north-central Texas and is situated within both this temporal and geographic gap. Dating to 96 Ma and situated on the western paleocoastline of Appalachia (Powell, 1968; Dodge, 1969; Kennedy and Cobban, 1990; Emerson et al., 1994; Lee, 1997a, 1997b; Jacobs and Winkler, 1998; Gradstein et al., 2004), the Woodbine long has provided tantalizing hints to Appalachian diversity. Unfortunately, fossils from this unit are often fragmentary and isolated, frustrating taxonomic identification beyond broad groupings of Cretaceous organisms (Lee, 1997a; Head, 1998; Jacobs and Winkler, 1998; Adams et al., 2011). The Arlington Archosaur Site (AAS) is an unusual outlier amidst other Woodbine localities. The quality of preservation and the density of recovered fossil material are both unusually high, providing a window into the paleoecosystem of the Cenomanian coastline (e.g. Adams et al., 2017; Brownstein, 2018; Adrian et al., 2019; Noto et al., 2019).

As its name suggests, the site is particularly rich in archosaurian fossils, with at least four crocodyliform (Adams et al., 2017; Noto et al., 2019) and five dinosaur taxa (Main et al., 2014; Noto, 2016) known from the locality. Among these taxa, the most common species recovered from the AAS is the large neosuchian crocodyliform *Deltasuchus motherali* (Adams et al., 2017). Originally described from a single, adult individual, ongoing research and collection of AAS materials have revealed numerous smaller-bodied specimens attributable to this taxon. Furthermore, searches of museum collections at Southern Methodist University (SMU) and the Witte Museum (WM) have resulted in the identification of additional *D. motherali* elements from Bear Creek (SMU Locality 245) near the south entrance to Dallas–Fort Worth

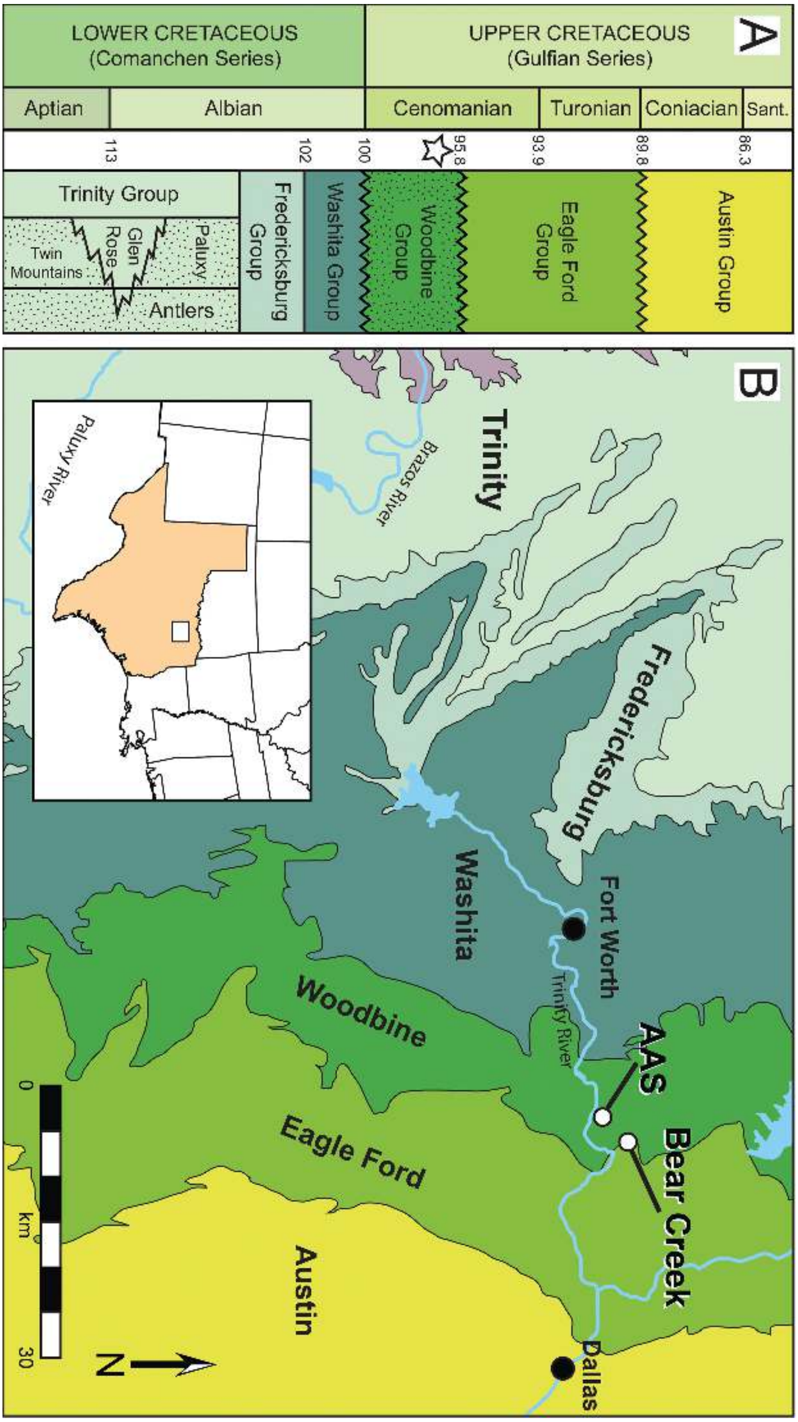
International Airport. Here we describe juvenile to adult *Deltasuchus* elements, emphasizing ontogenetic change seen across the group. We also expand the original phylogenetic analysis of *D. motherali* with new elements preserved in these additional specimens, and increase taxon sampling to further explore a seemingly endemic, Appalachian radiation of neosuchians.

Anatomical Abbreviations – Alveolar and dental positions are named with the first letter of the supporting bone (**p** for premaxilla, **m** for maxilla, **d** for dentary) and the number of the alveolus or tooth counting from mesial to distal along the toothrow; **ang**, angular; **ar**, articular; **ars**, articular sutural surface; **cqc**, cranio-quadrate canal; **d**, dentary; **ects**, ectopterygoid sutural surface; **fae**, foramen aëreum; **f**, frontal; **fio**, foramen intermandibularis oralis; **fs**, frontal sutural surface; **gf**, glenoid fossa; **ics**, intercondylar sulcus; **j**, jugal; **js**, jugal sutural surface; **lac**, lacrimal; **lac no**, lacrimal notch; **lac plp**, lacrimal posterolateral process; **lacs**, lacrimal sutural surface; lacrimal; **lac js**, lacrimal-jugal sutural surface; **lhc**, lateral hemicondyle; **mAME**, M. adductor mandibulae externus; **mhc**, medial hemicondyle; **mx**, maxilla; **mxs**, maxillary sutural surface; **nar**, naris; **nas**, nasal sutural surface; **op**, occlusal pit; **par**, parietal; **pars**, parietal sutural surface; **parops**, paroccipital process sutural surface; **pmx**, premaxilla; **pmx mxs**, premaxillary-maxillary sutural surface; **pob**, postorbital bar; **pos**, postorbital sutural surface; **prf**, prefrontal; **prfp**, prefrontal pillar; **prfs**, prefrontal sutural surface; **q**, quadrate; **qad**, quadrate anterodorsal process; **qat**, adductor tubercle of the quadrate; **qd**, quadrate dorsal process; **qjs**, quadratojugal sutural surface; **qpt**, quadrate pterygoid process; **qvf**, ventral fossa of the quadrate; **qs**, quadrate sutural surface; **ra**, retroarticular process; **roe**, external otic recess; **sp**, splenial; **sps**, splenial sutural surface; **sq**, squamosal; **sqj**, spina quadratojugalis; **sqs**, squamosal sutural surface; **sur**, surangular; **surs**, surangular sutural surface; **sym**, mandibular symphysis; **uef**, groove for upper ear valve.

Institution Abbreviation – **DMNH**, Perot Museum of Nature and Science, Dallas, Texas, USA; **SMU**, Southern Methodist University Shuler Museum of Paleontology, Dallas, Texas, USA; **WM**, Witte Museum, San Antonio, Texas, USA.

2 Age and Geologic Setting

The Upper Cretaceous (middle to upper Cenomanian) Woodbine Group of Texas represents a series of fully marine to terrestrial rocks deposited as a southward thinning clastic wedge in the Gulf Coast Basin (Figure 1) (Dodge, 1952, 1969; Oliver, 1971). Recent studies based on subsurface data


A
LOWER CRETACEOUS
(Comanchen Series)
UPPER CRETACEOUS
(Gulfian Series)
Aptian
Albian
Cenomanian
Turonian
Coniacian
Sant.
113
102
100
95.8
93.9
89.8
86.3
Trinity Group
Twin Mountains
Glen Rose
Paluxy
Antlers
Fredericksburg Group
Washita Group
Woodbine Group
Eagle Ford Group
Austin Group
B
Paluxy River
Brazos River
Trinity
Fredericksburg
Washita
Fort Worth
Trinity River
AAS
Bear Creek
Woodbine
Eagle Ford
Austin
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0
km
30
N

Caption for Figure 1 (cont.)

Figure 1 Location and geologic setting of the AAS and Bear Creek. **A**, stratigraphic column for the Upper Cretaceous of north-central Texas showing the position of the Woodbine Group relative to timescale and adjacent geologic units. Stippled intervals represent terrestrial deposits. Star indicates position of the AAS and Bear Creek sites. Time scale based on Gradstein et al. (2004). **B**, generalized map of geologic units in the Fort Worth Basin, showing enlarged area from white box of inset map of Texas. Modified from Barnes et al. (1972) and Strganac (2015).

classify the Woodbine as a third-order regressive sequence deposited over ~1.5 million years, with source sediments originating from the Ouachita and Arbuckle Mountains of Oklahoma and Arkansas (Ambrose et al., 2009; Adams and Carr, 2010; Blum and Pecha, 2014; Hentz et al., 2014). Its lower boundary is formed by an unconformity with the Grayson Marl (Washita Group) while its upper boundary is formed by an unconformity with the Eagle Ford Group (Dodge, 1969; Oliver, 1971; Johnson, 1974). Presence of the ammonite zonal marker *Conlinoceras tarrentense* in the upper Woodbine establishes a minimum age of early middle Cenomanian (~96 million years) (Kennedy and Cobban, 1990; Emerson et al., 1994; Jacobs and Winkler, 1998; Gradstein et al., 2004), with deposition ending no later than 92 million years (Ambrose et al., 2009).

Woodbine stratigraphy is complex, with differing interpretations arising from surface outcrop and subsurface core and wireline data, themselves derived from widely different locations within the depositional basin (Dodge, 1969; Oliver, 1971; Johnson, 1974; Ambrose et al., 2009; Adams and Carr, 2010; Hentz et al., 2014). In the Dallas–Fort Worth area four units are typically recognized (in ascending order): Rush Creek, Dexter, Lewisville, and Arlington (Dodge, 1969). The lower Rush Creek and Dexter represent marginal to fully marine deposits, while the upper Lewisville and Arlington represent terrigenous fluvio-deltaic environments all influenced by eustatic sea-level changes (Powell, 1968; Oliver, 1971; Johnson, 1974; Ambrose et al., 2009; Adams and Carr, 2010; Hentz et al., 2014).

The Arlington Archosaur Site (AAS) is situated within the upper Woodbine (Lewisville) and consists of a 200 m long, 5 m thick hillside exposure, with 50 m representing the main fossil quarry (Figure 1B). This outcrop preserves a coastal environment that includes a mixture of marine, freshwater, and terrestrial influences (Noto et al., 2012; Adams et al., 2017; Noto et al., 2019). The outcrop is divided into four distinct facies, recording a transition from primarily terrestrial to primarily marine deposition (Main, 2013; Adams et al., 2017). The majority of fossils are found in the lowermost facies, which most likely represents a freshwater or brackish wetland deposited within a lower delta plain system (Noto et al., 2012; Main, 2013; Adams et al., 2017). The AAS is remarkable for the sheer number and diversity of organisms recovered (at least 37 unique vertebrate taxa to date, as well as invertebrates and plants) and the quality of preservation of the material (Noto, 2015; Adams et al., 2017).

Bear Creek (SMU locality 245, Figure 1B) is positioned in the uppermost Woodbine (Arlington) and represents the transition phase of the Woodbine Formation into the deeper marine shale facies of the Eagle Ford Group (Lee, 1997a). This site has produced numerous fossil remains, including teeth and bone fragments of crocodyliforms and dinosaurs. The outcrop consists of a lower shaly sandstone unit and an upper sandy shale unit interbedded with thin fossiliferous sandstone that contain dark, lignitic, and carbonaceous layers. Thin units consist of very fine- to fine-grained sandstone with ferruginous cement, iron concretions, chert pebbles, and phosphatic nodules. A phosphatic pebble conglomerate surface, marking a transgressive lag deposit, is rich in reworked vertebrate teeth and small fragments including fishes, frogs, turtles, crocodiles, dinosaurs, and a mammal (Lee, 1997a). The uppermost Woodbine preserves a terrigenous coastal depositional system with fluvio-deltaic influences (Powell, 1968; Dodge, 1969; Lee, 1997a, 1997b; Jacobs and Winkler, 1998) and represents a low-stand sequence within an early transgressive system tract of the Greenhorn Cycle of Kauffman and Caldwell (1993).

The taphonomy of these sites is also complex, representing a largely time-averaged assemblage formed through a variety of taphonomic modes, including subaerial exposure, aqueous transport, and predation (Noto et al., 2012; Main et al., 2014; Noto, 2015; Adams et al., 2017). Within the fossil-rich layer of the AAS (Facies A sensu Adams et al., 2017), elements are generally well-preserved, if disarticulated. The presence of mixed marine, brackish, freshwater, and terrestrial taxa suggest a parautochthonous assemblage, sampled from across the paleodeltaic system, but common vertebrate coprolites, as well as the high quality of the fossil preservation and the minimal spread of associated skeletal elements, indicate that transport was low energy and fairly minimal (McNulty and Slaughter, 1968; Russell, 1988; Cumbaa et al., 2010; Adams et al., 2017; Noto et al., 2019).

Most fossils were collected in situ and these elements are a rich, chocolate brown color. The surface quality is high, and the remains are preserved in three dimensions, but a few exhibit minor compression and distortion (e.g. the left maxilla and the right dentary/splenial of DMNH 2013–07–1859). Elements that were collected at or near the surface have been exposed to more extensive weathering and mineral overgrowth, resulting in changes in color, texture, and overall preservational quality. These elements range from a light brown to light gray color, and take on a chalky appearance (e.g. right premaxilla DMNH 2013–07–1636 and left quadrate DMNH 2013–07–0733). A small number exhibit extensive gypsum overgrowth (e.g. DMNH 2014–06–01, a poorly preserved, left angular).

3 Systematic Paleontology

CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NEOSUCHIA Benton and Clark, 1988
PALUXYSUCHIDAE, clade nov.

Phylogenetic Definition – Branch-based clade comprising all taxa more closely related to *Paluxysuchus newmani* Adams, 2013, than to either *Goniopholis crassidens* Owen, 1841 or *Pholidosaurus schaumburgensis* Meyer, 1841.

Diagnosis – Members of this clade are mid- to large-sized neosuchian crocodylomorphs diagnosable not by autapomorphies, but instead by a unique combination of characters present in other clades (specifically Goniopholididae and Tethysuchia): platyrostral mesorostrine skull (shared with some goniopholidids); maxilla festooned, with well-defined anterior wave, projecting laterally and ventrally (shared with some goniopholidids); posterior ramus of prefrontal is long, reaching the median region of the orbits (shared with goniopholidids and pholidosaurids); lacrimal reaches the anteroventral margin of the orbit; jugal does not exceed the anterior margin of orbit (shared with tethysuchians); the posterior ramus of the jugal beneath the infratemporal fenestra is rod-shaped (shared with pholidosaurids); median process of the frontal extends anterior to the tip of the prefrontal (shared with tethysuchians); postorbital with anterolateral process present (shared with goniopholidids and pholidosaurids); contact between the descending process of the postorbital and the ectopterygoid; no external mandibular fenestra (shared with some goniopholidids and pholidosaurids); surangular extends to the posterior region of the retroarticular process; retroarticular process facing dorsally and paddle shaped (shared with pholidosaurids).

CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NEOSUCHIA Benton and Clark, 1988
PALUXYSUCHIDAE, clade nov.

DELTASUCHUS Adams et al., 2017
DELTASUCHUS MOTHERALI Adams et al., 2017

Holotype – DMNH 2013–07–0001, partial skull and mandible.

Referred Material – DMNH 2013–07–1859, partial skull and mandible; DMNH 2014–06–01, partial mandible; DMNH 2013–07–0079, right dentary and maxilla; DMNH 2013–07–0297, left premaxilla, right premaxilla; DMNH 2013–07–1888, right dentary; DMNH 2013–07–0239, left dentary; DMNH 2013–07–0218, right dentary; DMNH 2013–07–1984, right dentary; DMNH 2013–07–0240, left dentary; DMNH 2013–07–0322, left dentary; DMNH 2013–07–0228, left dentary; DMNH 2013–07–0312, right dentary; DMNH 2013–07–0802, right dentary; DMNH 2013–07–0219, left maxilla; DMNH 2013–07–1404d, left prefrontal; DMNH 2013–07–0733, left quadrate; DMNH 2013–07–0084, left lacrimal; DMNH 2013–07–1871, frontal; DMNH 2013–07–1992, left and right quadratojugals, left and right quadrates; DMNH 2013–07–1993, left lacrimal; DMNH 2013–07–1994, partial right exoccipital; DMNH 2013–07–1995, right prefrontal; DMNH 2013–07–1997, right quadrate; DMNH 2013–07–1975, right prefrontal, left jugal; DMNH 2013–07–0178, teeth; SMU 76810, articulated right surangular and angular; WM 2019–15 Ga, left premaxilla; WM 2019–15 Gb, tooth.

Revised Diagnosis – A member of Paluxysuchidae differing from other known neosuchians in having the following unique combination of characters and autapomorphies (* = additional characteristics relative to Adams et al., 2017): anterior premaxilla ventrally directed, overbites the dentary (shared with goniopholidids and tethysuchians); postnarial fossa present on the premaxilla; dual pseudocanines on both the dentary and maxilla; frontal excluded from the orbital margin (an autapomorphy for the group)*; anterolaterally facing margin on the dorsal portion of the postorbital; deep fossa on the ventral surface of the quadrate (shared with some pholidosaurids); medial quadrate condyle expands ventrally, separated from lateral condyle by deep intercondylar sulcus; the mandibular symphysis extends posteriorly to the level of the eighth dentary alveolus.

4 Description

4.1 General Description

The AAS is extremely rich in fossil crocodyliforms, with multiple individuals and at least four and perhaps five taxa known from the site (Adams et al., 2017; Noto et al., 2019). Of these, the best represented taxon is *Deltasuchus motherali*. The holotype of *D. motherali* (DMNH 2013–07–0001) includes associated, but disarticulated, craniomandibular elements ascribable to a large, adult neosuchian crocodyliform. The specimen is incomplete, including both premaxillae, maxillae, and nasals, a left postorbital, a left jugal, a right squamosal, both quadrates, a right otoccipital, the basioccipital, both ectopterygoids, and fragments of the pterygoids and dentaries. Based on a reconstructed cranial length of 800 mm, the total body length of the holotype animal is estimated at between 5.6 and 6 m in length. Unlike other large-bodied crocodyliforms known from the mid-Cretaceous of Texas, who exhibit more specialized slender snouts, e.g. *Terminonaris* and *Woodbinesuchus*, *Deltasuchus* has a robust, broadly triangular snout.

Multiple smaller-bodied individuals ascribable to *D. motherali* are also known from the AAS. By far the most complete specimen, other than the holotype (DMNH 2013–07–0001), belongs to an individual that, when articulated, is roughly half the size of the holotype (DMNH 2013–07–1859). Like the holotype (Adams et al., 2017), DMNH 2013–07–1859 includes associated, but disarticulated, cranial and mandibular elements (Figure 2). However, association of these elements to one individual is justified for the following reasons: adjacent elements articulate well along sutural surfaces, all elements were found in close physical proximity to one another within the same bedding plane, and there is no duplication of right and left elements within the skull. At 440 mm in cranial length (measured from the anteriormost tip of the premaxilla, along the midline, to the posteriormost margin of the skull table), this individual would have been between 3.08 and 3.30 m in total body length (sensu Schmidt, 1944; Bellairs, 1969; Adams et al., 2017).

DMNH 2013–07–1859 exhibits the following unique combination of characters that can diagnose it to Paluxysuchidae: enlarged supratemporal fenestrae; paired pseudocanines in the maxilla (m4 and m5), posterior process of the premaxilla overlaps anterodorsal surface of the maxilla anterolaterally, then transition to a butt joint posteromedially; anterior process of the frontal extends anterior to the tip of the prefrontal. It can be assigned to *D. motherali*, as opposed to *Terminonaris* and *Woodbinesuchus* also present in the Woodbine, based on its more robust, widely triangular snout shape, ventrally directed premaxilla, and the extremity of the expansion of the pseudocanines, as well as the associated bulging of the lateral margins of the maxilla which accommodate that enlarged dentition (Adams et al., 2017).

A second individual (DMNH 2014–06–01) is represented by a partial mandible; including left and right articulars, an articulated left angular and surangular and a disarticulated right angular, surangular, and a small portion of posterior dentary (Figure 3). In addition to the elements on each side articulating with one another, these elements were found in close physical proximity and exhibit matching sizes, though the elements from the left side of the jaw exhibit poorer

Figure 2 Subadult *D. motherali* (DMNH 2013–07–1859). Cranial elements in **A,** dorsal view and mandible in **B**, dorsal and lateral views. See text for anatomical abbreviations. Scale bar equals 5 cm.

quality surface preservation. This individual would have been of similar size to, and is morphologically indistinguishable from, DMNH 2013–07–1859, but duplication of elements signifies that they do represent two separate animals.

The second set includes a right maxilla and a right anterior fragment of a dentary that were found in direct association with one another (DMNH 2013–07–0079) (Figure 4A–D). This individual exhibits the paired pseudocanines on both maxilla and dentary expected of the clade, and other than being only slightly larger than the other two juveniles previously described, is morphologically similar to these other specimens. Duplication of elements further

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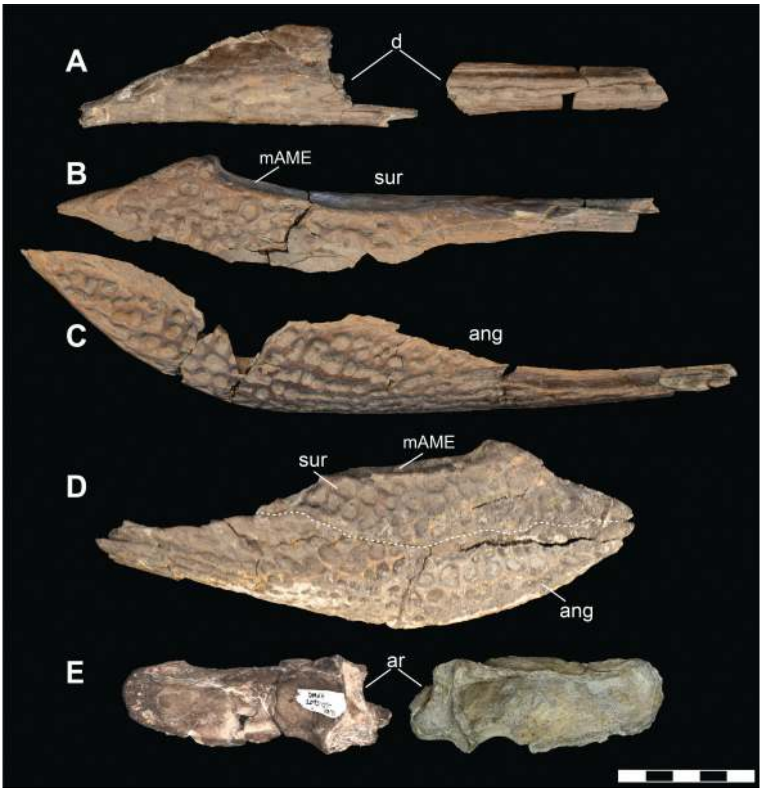

Figure 3 Mandible elements of *D. motherali* (DMNH 2014–06–01). Right dentary in **A**, lateral view; right surangular in **B**, lateral view; right angular in **C**, lateral view; left surangular and angular in **D**, lateral view, dashed line indicating sutural boundary between the angular and surangular; left and right articulars in **E**, dorsal views. See text for anatomical abbreviations. Scale bar equals 5 cm.

differentiates it from DMNH 2013–07–1859. As a comparison of size, the right dentary of DMNH 2013–07–0079 is 34.79 mm wide in ventral view at the level of the d4 alveolus while the right dentary of DMNH 2013–07–1859 is 31.10 mm wide in the same dimension. Scaling the length estimate based on these measurements yields an animal between 3.45 and 3.69 m in total length.

Three larger individuals are represented by isolated elements. DMNH 2013–07–0297 are paired premaxillae that articulate along their sutural margin (Figure 4E). The maximum width of the right premaxillae is 44.70 mm, at the level of p4. When compared to the more complete holotype, DMNH 2013–07–0001, which is 74 mm wide in this dimension, scaling between the two suggest an animal that would have been between 3.38 and 3.62 m in total length. WM