A NEW AETOSAUR (ARCHOSAURIA, SUCHIA) FROM THE UPPER TRIASSIC PEKIN FORMATION, DEEP RIVER BASIN, NORTH CAROLINA, U.S.A., AND ITS IMPLICATIONS FOR EARLY AETOSAUR EVOLUTION

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ABSTRACT—Aetosaurs are an extinct clade of quadrupedal, heavily armored archosaurs that had a worldwide distribution during the Late Triassic. Aetosaur fossils from the Upper Triassic Pekin Formation in the Deep River Basin of North Carolina (U.S.A.) consist primarily of isolated osteoderms and, rarely, more associated material. Here we describe a new genus and species, Gorgetosuchus pekinensis, based on an associated incomplete anterior carapace, consisting of a total of 19 nearly complete paramedian and lateral osteoderms from the first 10 rows of armor as well as some associated fragments. An important feature of Gorgetosuchus is that an articulated fifth row of cervical osteoderms almost encloses the neck, with prominent spines on both the dorsal and lateral osteoderms. This is a novel configuration among aetosaurs. Otherwise, NCSM 21723 preserves a mosaic of character states found in Longosuchus, Lucasuchus, or both taxa while simultaneously preserving several more plesiomorphic character states, such as cervical osteoderms that are wider than long. Our reevaluation of other Pekin Formation specimens that various authors have assigned to Desmatosuchus, Longosuchus, or Lucasuchus confirms that some possess characteristics of Lucasuchus, whereas others are not generically determinate. Incorporating Gorgetosuchus into existing phylogenies of aetosaurs results in a reshuffling of basal aetosaur relationships, but a variety of analyses consistently place Gorgetosuchus as a basal desmatosuchine. Using current taxonomic practices, there are at least three aetosaur genera in the Pekin Formation: Lucasuchus, Cotiosuchus, and Gorgetosuchus.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The aetosaurs are a group of moderate- to large-sized quadrupedal herbivorous to omnivorous archosaurs found in Upper Triassic strata from every modern continent except Australia and Antarctica (Heckert and Lucas, 2000; Desojo et al., 2013). Long and Ballew (1985) described carapaces in terms of paramedian, lateral, ventral, and appendicular osteoderms. The aetosaur carapace consists of paired longitudinal columns of paramedian and lateral osteoderms, as well as, in at least some taxa, multiple columns of polygonal ventral osteoderms as well as more irregularly shaped and distributed appendicular osteoderms (see reviews by Heckert and Lucas, 2000; Desojo et al., 2013). Long and Ballew (1985) documented the taxonomic utility of aetosaur osteoderms, citing diagnostic ornamentation patterns, and since that time various authors have established numerous aetosaur taxa, often based largely or entirely on osteoderms (e.g., Hunt and Lucas, 1991; Long and Murry, 1995; Lucas et al., 2002, 2007; Zeigler et al., 2002; Martz and Small, 2006; Parker et al., 2008), and osteosaur characters are used extensively in phylogenetic analyses of the group (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999, 2000; Parker, 2007). There are complications related to understanding positional variation and identifying homologies in osteoderms, especially in taxa with more plesiomorphic armor (recently reviewed by Small and Martz, 2013). However, even those who have criticized identifications based on armor, especially isolated osteoderms (e.g., Martz and Small, 2006; Parker, 2007), have also erected and/or recognized many taxa based largely to entirely on the distinctiveness of paramedian and lateral osteoderms when these complications are suitably addressed (e.g., Martz and Small, 2006; Parker, 2007; Parker et al., 2008; Parker and Martz, 2010). Indeed, Parker and Martz (2010) have demonstrated that osteoderm features can be used to distinguish between co-occurring desmatosuchine taxa (Longosuchus and Lucasuchus) even when one of them (Lucasuchus) is known almost exclusively from osteoderms.

Here we describe a new genus and species of aetosaur, based on an associated anterior carapace consisting of 10 paramedian and nine lateral osteoderms, as well as several other more fragmentary osteoderms, from the Pekin Formation of North Carolina, U.S.A. In so doing we attempt to place this genus in a phylogenetic context, comment on its evolutionary significance, and review the aetosaur record from the Pekin Formation. This work supersedes preliminary descriptions provided by Fraser et al. (2006), Schneider et al. (2011), and Heckert et al. (2012).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; NCSM, North Carolina Museum of Natural Sciences, Raleigh; TMM, Texas Memorial Museum, Austin.
GEOLOGIC SETTING

All Triassic strata in North Carolina are part of the Newark Supergroup, sediments deposited in a series of rift basins extending from the present-day Gulf Coast to Canada. Olsen (1997; Weems and Olsen, 1997) referred all Triassic sedimentary rocks in North Carolina to the Chatham Group of the Newark Supergroup. In North Carolina, the easternmost of these basins exposed at the surface is the Deep River Basin, which is subdivided into the northern Durham, the central Sanford, and the southern Wadesboro sub-basins (Olsen et al., 1991: Fig. 1A). The locality, NCPALEO 1902, is in the northernmost portion of the Sanford sub-basin, just south of the Colon cross-structure, a basement feature that separates it from the Durham sub-basin to the north (Olsen et al., 1991; Fig. 1B). Sanford sub-basin stratigraphy includes, in ascending order, the Pekin, Cumnock, and Sanford formations (Campbell and Kimball, 1923). Both the Pekin and Sanford formations are predominantly red sandstone–dominated units sandwiched around the middle, predominantly gray and fine-grained, Cumnock Formation. Reinemund (1955) mapped the area surrounding NCPALEO 1902 as Pekin Formation (Trp), which he described as 1750–1800 feet (533–548 m) of reddish-brown mudstones, siltstones, and fine- to medium-grained sandstones that are locally conglomeratic in this area.

The specimens described here were collected from large blocks in a brick quarry in southeastern Chatham County, North Carolina (detailed locality data are on file at NCSM as locality NCPALEO 1902; Fig. 1A). The brick operation is focused on mining clay and other fine-grained materials from a thin (<50 m thick) portion of the Pekin Formation, and as part of that operation large (~1–5 m diameter) boulders of coarse-grained strata are pushed out of context and left to weather. The specimens described here were found in these isolated blocks, as were dicynodonts (Green et al., 2005; Green, 2012) and traversodont cynodonts (Liu and Sues, 2010), so precise stratigraphic data for the material are missing. The majority of these blocks are probably derived from a single persistent bed near the floor of current quarry operations that we interpret as channel and/or alluvial fan deposits derived from the nearby rift margin. As mapped by Reinemund (1955), the quarry appears to be stratigraphically high in the Pekin Formation, but the quarry sediments lack calcareous nodules (caliche) characteristic of the uppermost Pekin Formation (P. Olsen, pers. comm.). Thus, the specimens are clearly derived from the upper half of the Pekin Formation, but their exact position within the Pekin Formation is unknown.

MATERIALS AND METHODS

The specimens described here were found associated in large quarry blocks, consisting primarily of crossbedded sandstone, siltstone, and conglomerate. After using a rock saw to remove fossiliferous blocks, they were transported to the NCSM. There, preparation consisted of removing matrix with tungsten-carbide pins and air scribes, and specimens are consolidated using polyvinyl acetate (PVAC; VINAC B-15, McGean Company, Cleveland, Ohio, USA). The specimens were photographed using a Nikon D60 digital camera, with images manipulated in Adobe Photoshop and drawings accomplished using Adobe Illustrator.

The systematic paleontology follows Nesbitt (2011) for all groups more inclusive than ‘Aetosauria’ and Desojo et al. (2013) for less inclusive taxa. The data matrix (21 taxa and 37 characters) was modified from Parker (2007) following Parker et al. (2008), Desojo et al. (2012), and our own observations of the new taxon and some others (see below), entered into Mesquite (Maddison and Maddison, 2011) and analyzed using TNT 1.1 (Goloboff et al., 2008). The analyses utilized the maximum parsimony criteria in an implicit search. Strict consensus trees were then calculated together with the consistency (CI), retention (RI), and Bremer decay indices, and absolute frequency and
frequency difference (GC) bootstrap values (details provided in Phylogeny). We used PAUP 4.0b10 for 32-bit Microsoft Windows (Swofford, 2003) to check some of the results obtained, but all analyses reported and illustrated here were executed in TNT.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
ARCHOSAURIA Cope, 1869
SUCHIA Krebs, 1974
AETOSAURIA Marsh, 1884
STAGONOLEPIDIDAE Lydekker, 1887
GORGETOSUCHUS, gen. et sp. nov.

Type and Only Species—Gorgetosuchus pekinensis, gen. et sp. nov.

Diagnosis—As for the type and only species.

Etymology—The genus name comes from ‘gorget,’ a piece of armor worn as a collar encircling the neck dating back to medieval times, and ‘suchus,’ Greek for crocodile.

Distribution—As for the type and only species.

GORGETOSUCHUS PEKINENSIS, gen. et sp. nov. (Figs. 2, 3)

Holotype—NCSM 21723, an incomplete carapace consisting of all or parts of 10 paramedian and nine lateral osteoderms from the first 10 rows of the carapace and some associated osteoderm fragments (Figs. 2, 3).

Referred Specimens—None at this time, although some other osteoderms from the Pekin Formation may pertain to Gorrowitosuchus (see “Comparisons with other Pekin Formation aetosaurs”).

Etymology—The species name comes from the Pekin Formation, the stratigraphic unit encompassing the type locality.

Type Locality—NCPALEO 1902, a brick quarry stratigraphically high in the Pekin Formation of southeastern Chatham County, North Carolina (precise locality data, to the extent possible, are on file at NCSM).

Age—Most workers have assigned the Pekin Formation and equivalent strata an early Late Triassic (Carnian) age based primarily on palynology and vertebrate biostratigraphy (Olsen et al., 1991; Cornet, 1993; Huber et al., 1993; Litwin and Ash, 1993; Olsen, 1997; Weems and Olsen, 1997; Lucas and Huber, 2003). More recent work demonstrates that many stratigraphic sections historically considered to be Carnian may in fact be Norian in age because the base of the Norian stage is approximately 228 Ma (Muttoni et al., 2004; Furin et al., 2006). However, Whiteside et al. (2011:table S2) provided an age estimate of 231 Ma for the Pekin Formation and considered that to be a Carnian age, whereas younger strata, such as the Cumnooak (225 Ma) and Sanford (223 Ma) formations are 223–225 Ma and of early Norian age.

Diagnosis—Aetosaur distinguished from all other taxa by possession of cervical armor consisting of strongly flexed paramedian and lateral osteoderms forming distinct hexagonal cross-section in anteroposterior view, with the paramedians wider than long, possessing a pronounced boss, and ornamented by a few weakly incised, randomly arrayed pits; possesses the following unique combination of character states: prominent bosses at or near (but not overlapping) posterior margin of cervical dorsal paramedians; cervical paramedians arched or flexed and wider than long; paramedians with minimal pattern of randomly distributed shallow, ovoid pits; anterior bars on osteoderms; medially offset boss; laterally thickened articulation of paramedian osteoderms overlapped by lateral osteoderms; paramedian osteoderms sinuous in medial view; and lateral flanges of lateral osteoderms directed ventrally.

DESCRIPTION

The holotype was discovered as a closely associated jumble in a single block that had fallen off one of the large boulders at the site. The close association of osteoderms in that block, with many disarticulated but still touching each other (Fig. 2C, D), leaves no doubt that all the osteoderms pertain to a single individual, as illustrated in Figure 2A, B. Table 1 shows our interpretation of the position of each of the preserved specimens, and we provide measurements in Tables 2 and 3. Only the fifth row of osteoderms is complete, but at least one paramedian and one lateral osteoderm is preserved from rows 2–4 and 7–8 (and there are no laterals in the first row; Fig. 2A), so we can completely reconstruct all the rows except 6, 9, and 10 with confidence (Fig. 2B).

All of the osteoderms except the first paramedian possess an anterior bar (sensu Long and Ballew, 1985), although it is not generally strongly developed. The bosses (paramedians) or spines (laterals) dominate the external side of all osteoderms such that only a few, relatively shallow pits adorn the rest of the surface (Fig. 3). These pits are ovoid, not deeply incised, and randomly distributed (Fig. 3A, E, F, I–J). The bosses and spines are faceted to varying degrees, and therefore are pyramidal, not conical or ovoid, in cross-section, and possess numerous fine pits (Fig. 3). The bosses on the paramedian osteoderms are medially offset and contact, but do not overlap, the posterior margin. The spines on the lateral osteoderms are strongly developed and begin as somewhat flattened horns anteriorly that gradually become more elongate and faceted posteriorly. All of the paramedian osteoderms are sinuous in medial view (Fig. 3C, D, G, H) and substantially thickened by a prominent transverse ventral keel.

In the configuration we advocate (Figs. 2A, B, E, F, N), the cervical dorsal paramedians are wider than long, especially anteriorly, with a prominent boss (dorsal eminence of some workers, e.g., Parker, 2007) that is medially offset and situated close to, but not overlapping, the posterior margin. The left paramedian representing the first row is more irregularly shaped, especially laterally, and lacks both an anterior bar and an articulation for a lateral osteoderm (Fig. 2H–J). We therefore interpret it as a nuchal osteoderm that rests on the back of the skull in contact with the parietal (Walker, 1961). Throughout the paramedian series, the boss is pyramidal, with ridges emanating from the tip; some of these ridges reach the medial margin of the osteoderm. Bosses increase in height posteriorly through the eight preserved rows. The first two paramedians are gently arched (Fig. 2H) and the others are strongly flexed (Fig. 2E, F, K, N) in anteroposterior view, such that relatively little of the osteoderm is flat and the wider lateral surfaces of the osteoderm are directed dorsolaterally (Fig. 2E, F, K, N). In medial view, the paramedians are thickened and sinusoidal—dorsally concave anteriorly and convex posteriorly (Fig. 3C, D, G, H). In dorsal view, the anterior portion of the lateral margin is embayed, accepting the anteromedial corner of the associated lateral osteoderm (Fig. 2L), identical to the condition described in Longosuchus and Lucusuchus by Parker and Martz (2010). The osteoderms increase in length from the first (~20 mm) to the sixth row, stabilizing at approximately 50 mm length (Table 2), but are universally wider than long.

Lateral osteoderms are not present in the first row of aetosaur carapaces (Sawin, 1947; Walker, 1961; Desojo and Báez, 2005; Schoch, 2007). Thus, the first row of laterals corresponds to the second row of paramedians (Fig. 2A, B; Table 1), and the only row not preserved is the sixth row (fifth lateral osteoderm), although there is a single fragment of a large, spinose osteoderm recovered from the same block that may represent a portion of a large lateral from this row because its cross-section is larger than that of any other preserved osteoderm (labeled ‘6?’ on Fig. 2B).
FIGURE 2. Photographs (A, C–E, G–N) and sketches (B, F) of the holotype of *Gorgetosuchus pekinensis*, NCSM 21723, from NCPALEO 1902, Pekin Formation of North Carolina. A, entire specimen shown as rearticulated in somewhat flattened dorsal view; B, interpretive sketch of A with restored osteoderms shaded; C, D, after initial preparation but before specimens were rearticulated; E, articulated ring of fifth row of osteoderms in posterior view; F, interpretive sketch of E, G, first left lateral osteoderm in lateral view; H–J, first dorsal paramedian in posterior (H), dorsal (I), and ventral (J) views; K–M, third dorsal paramedian in posterior (K), dorsal (L), and ventral (M) views; N, articulated third paramedian and lateral osteoderms in posterior views. **Abbreviations:** ab, anterior bar; af, articular facet for lateral osteoderm; b, boss; df, dorsal flange of lateral osteoderm; ldpm, left column of dorsal paramedian osteoderms; lf, lateral flange of paramedian osteoderms; ls, lateral spike; mf, medial flange of paramedian osteoderm; rdpm, right column of dorsal paramedian osteoderms; rlc, right column of lateral osteoderms; vf, ventral flange of lateral osteoderm; vk, ventral keel. Numbers refer to osteoderm rows. Scale bars equal 5 cm (A–F) and 2 cm (H–N).
All lateral osteoderms are strongly flexed, with a spine that increases in height posteriorly in the preserved osteoderms (Fig. 2A, B). In the most posterior osteoderms, this increase in height makes up for the overlap of each osteoderm, so that when reconstructed all of the preserved spines project essentially the same distance laterally. The spines are dorsoventrally compressed (Fig. 2E, F, N). The dorsal side typically bears a strong ridge that separates two concave surfaces. The ventral side is more convex. Another pronounced ridge runs anteroposteriorly along the flexed surface, separating the dorsal and ventral flanges—this ridge is even present on the anterior bar. The spine projects dorsolaterally from the osteoderm in the fashion of Desmatosuchus, Longosuchus, and Lucasuchus (e.g., Long and Murry, 1995; Parker, 2008), but in reality this is laterally in the reconstructed carapace due to the flexure of the paramedians (e.g., Fig. 2E, F, N). The posterior margin of the spine is straight (Fig. 3I, J), so that the spine does not curve or bend, unlike homologous osteoderms in Desmatosuchus and Sierritasuchus. Flexure between the dorsal and lateral flanges in the lateral osteoderms is typically ~90° when viewed posteriorly (Fig. 2E, F, N). When measured along the posterior margin, the lateral flange (which we advocate calling the ‘ventral flange’) is wider than the dorsal flange (Fig. 2E, F; Table 3).

Comparisons with Previously Named Taxa

The following comparisons are based on firsthand observations of Gorgetosuchus and the holotype specimens of each species of the listed genera. The most distinctive feature of Gorgetosuchus is that the cervical paramedian and lateral osteoderms are strongly flexed so that the distal edges of the lateral osteoderms lie beneath the center of the paramedians, resulting in a distinctive, narrow, hexagonal cross-section, with the spines on the lateral osteoderms projecting laterally and lying below

### Abbreviations

- DPM: dorsal paramedian
- X: present
- N/A: not applicable because there are no laterals on first (nuchal) row.
- ab: anterior bar
- as: articular surface for overlapping lateral osteoderm
- b: boss
- df: dorsal flange of lateral osteoderm
- lf: lateral flange of paramedian osteoderm
- ls: lateral spike
- mf: medial flange of paramedian osteoderm
- vf: ventral flange of lateral osteoderm

### Table 1. Distribution of osteoderms in NCSM 21723, the holotype of Gorgetosuchus pekinensis.

| Row | Left lateral | Left DPM | Right DPM | Right lateral |
|-----|--------------|----------|-----------|--------------|
| 1   | N/A          | X        |           | X            |
| 2   | X            | X        | X         |              |
| 3   | X            | X        |           |              |
| 4   | X            | X        | X         |              |
| 5   | X            | X        |           |              |
| 6   | X            |           | X         | X            |
| 7   | X            | X        |           |              |
| 8   | X            | X        |           |              |
| 9   | X            |          |           |              |
| 10  | X            |          |           |              |

Scale bars equal 2 cm.
the midline of the hexagon (e.g., Fig. 2E, F). This is unique among aetosaurs, although the proportionately narrower osteoderms of Longosuchus could be reconstructed to yield a more hexagonal cross-section (e.g., Parker and Martz, 2011:fig. 3a) that will still not put an appreciable portion of the lateral osteoderm ventral to the paramedian, as we reconstruct in Figure 2E, F. The presence of strongly flexed lateral osteoderms that bear prominent knobs or spikes separates Gorgetosuchus from basal aetosaurs, including Aetosaurus, Aetosauroides, Apachesuchus, Coahomasuchus, Neoaeotosauroidea, Aetobarbakinoides, Calyptosuchus, and Siagonolepis, all of which possess less strongly flexed lateral osteoderms with, at most, a low knob or keel. Only one lateral osteoderm has been reported for Adamanauchus eisenhardiae (Lucas et al., 2007), but that osteoderm is more gently flexed and reminiscent of Siagonolepis (Walker, 1961) and Calyptosuchus (Long and Ballew, 1985; Long and Murry, 1995), not Gorgetosuchus. The presence of strong dorsal bosses on the paramedians of Gorgetosuchus further separate it from Aetosaurus, Coahomasuchus, Neoaeotosauroidea, Adamanauchus, Apachesuchus, Aetosauroides, Siagonolepis, Typothorax, and Redondasuchus. The lateral osteoderms of Gorgetosuchus differ from those of typhootyphoceratines (including paratypotyphoceratines) sensu Parker (2007) in that the dorsal flange is not reduced, and none of the laterals of Gorgetosuchus are as strongly flexed (~45°) as seen in the lateral osteoderms of these taxa (e.g., Paratypothythorax, Rioarrhabasuchus, Tecovasuchus, and Typothythorax). The posterior location of the bosses distinguishes Gorgetosuchus from Desmatosuchus, Lucasuchus, and Acaenasuchus. The absence of pronounced pitting and the more or less random orientation of the few pits evident on the paramedians of Gorgetosuchus distinguish it from Longosuchus (which possesses a more dense and deeply incised array of random pits) and Lucasuchus (which possesses more deeply incised, radially orientated pits) (Parker and Martz, 2010). The faint, ovoid pits are distinct from the more deeply incised and irregular pits of Desmatosuchus (Case, 1922; Long and Murry, 1995; Parker, 2005) and Sierriotasuchus (Parker et al., 2008). The external surface of the bone is well preserved, so there is no reason to consider the shallow pitting of Gorgetosuchus a taphonomic artifact.

Based on the preserved osteoderms, Gorgetosuchus appears most similar to the aetosaurs Longosuchus (Sawin, 1947; Hunt and Lucas, 1990; Long and Murry, 1995), Lucasuchus (Long and Murry, 1995; Parker and Martz, 2010), and Desmatosuchus (Case, 1922; Long and Murry, 1995; Parker, 2008), which are all desmatosuchine aetosaurs sensu Heckert and Lucas (2000) and Parker (2007). Indeed, the overlap of the anteromedial corner of the lateral osteoderms onto the cervical paramedians is a desmatosuchine characteristic (Parker and Martz, 2010). However, unlike desmatosuchines sensu Parker (2007), the lateral (ventral) flanges of the lateral osteoderms are wider than the dorsal flanges, which is an ‘aetosaurine’ (~ basal aetosaurs of this analysis—see Phylogeny, below) characteristic (Parker and Martz, 2010). In the following paragraphs, we compare Gorgetosuchus with these desmatosuchine aetosaurs and other taxa to demonstrate its distinctiveness even further.

Gorgetosuchus is similar to Longosuchus (as rediagnosed by Parker and Martz, 2010) in that the dorsal eminence is not centrally located but instead contacts the posterior margin of the osteoderm, although the dorsal eminence is situated more posteriorly in Longosuchus (e.g., Parker and Martz, 2010:fig. 4c, d) than in Gorgetosuchus (Fig. 3A, B, E, F, I, J). The relatively complete preservation of the cervical series of Gorgetosuchus indicates that this is not an artifact of positional variation because no osteoderm of Gorgetosuchus matches the proportions of Longosuchus cervical osteoderms (Parker and Martz, 2010). It is also similar in that the size of the lateral spines increases, and those spines are faceted, not conical, and not recurved (e.g., Figs. 2E, F; 3I, J). However, it differs from Longosuchus in that the cervical paramedian osteoderms are wider than long, with much higher bosses than Longosuchus, and the lateral spines of Gorgetosuchus are not obviously emarginated as they are in Longosuchus (compare Fig. 3 with Parker and Martz, 2010:fig. 3a). Furthermore, the pitting in Longosuchus is deeper and larger, and the longest lateral spines preserved in

| Specimen | Length (max) | Length (flex) | Width dorsal flanges | Width lateral flange | Height spine |
|----------|-------------|---------------|----------------------|---------------------|-------------|
| LL2      | 30.4 (AP)   | —             | 15.3 (AP)            | 20.0 (AP)           | 12.1        |
| LL3      | 39.1        | 39.3          | 21.9                 | 22.3                | 15.1        |
| LL4      | 49.5        | 45.6          | 29.4                 | 30.8                | 20.4        |
| LL5      | 54.7        | 53.0          | 32.5                 | 40.0                | 24.6        |
| RL5      | 54.8        | 51.1          | 26.8                 | 44.7                | 27.3        |
| RL7      | 59.7        | 57.4          | ~34.3                | ~45.3               | Cut         |
| LL8      | 58.9        | 37.5          | 45.5                 | 28.9                |             |
| LL9      | 57.9 (AP)   | 41.6          | 47.2                 | 30.8                |             |
| LL10     | 64.2        | 62.0          | 39.1                 | 42.4                | 36.3        |

**Table 2.** Longitudinal measurements (in mm) of NCSM 21723, the holotype of Gorgetosuchus pekinensis.

The laterally observed measurements (in mm) of NCSM 21723, the holotype of Gorgetosuchus pekinensis.

| Specimen | Width | Mediodateral length | Width from medial edge to boss | Width from boss to lateral edge | Thickness |
|----------|-------|---------------------|--------------------------------|--------------------------------|-----------|
| LDPM1    | ~34   | 20.2 (est)          | 15.3                           | 20.0                           | 10.1      |
| LDPM2    | 31.3  | 25.5 (AP)           | 19.3                           | 23.3                           | 11.6      |
| LDPM3    | 34.5  | 36.7                | 23.7                           | 25.9                           | 14.5      |
| LDPM4    | 42.9  | 34.8                | 23.8                           | 30.2                           | 20.1      |
| RDPM4    | 37.8  | 43.9                | 21.9                           | 29.9                           | 19.6      |
| LDPM5    | 44.6  | 47.7                | 23.8                           | 37.0                           | 21.5      |
| RDPM5    | 44.9  | 48.9                | 24.8                           | 33.8                           | 20.0      |
| RDPM6    | 52.9  | 50.8                | ~23.0                          | 37.0                           | 25.5      |
| RDPM7    | 56.1  | 50.6                | 28.1                           | 41.7                           | 26.1      |
| LDPM8    | 64.2  | 49.8                | ~32.8                          | 46.9                           | 25.2      |

**Table 3.** Lateral osteoderm measurements (in mm) of NCSM 21723, the holotype of Gorgetosuchus pekinensis.

**Abbreviations:** AP, as preserved—measurement is incomplete; est, estimated from broken surfaces; LDPM, left dorsal paramedian; RDPM, right dorsal paramedian.
Lucasuchus in Daeosaur in A Pipe Pit B. (lower fragment) to show it is a single left lateral osteoderm of in dorsal view. Scale bars equal 2 cm.

FIGURE 4. Isolated aetosaur osteoderms from the Pekin Formation of North Carolina. A–I from NCPALEO 1902; J–L from Pomona Pipe Pit B. A–C, NCSM 19025, left caudal(?) paramedian of cf. Lucasuchus in A, dorsal, B, anterior, and C, lateral views; D, E, NCSM 21625, caudal(?) paramedian osteoderm of a desmatosuchine aetosaur in D, dorsal and E, anterior views; F, G, NCSM 23170, left (?) paramedian osteoderm of an indeterminate desmatosuchine aetosaur in F, dorsal and G, lateral(?) views; H, I, spine of a caudal(?) paramedian(?) osteoderm in H, dorsal and I, posterior views; J, K, AMNH 2799, paramedian osteoderm of Lucasuchus in J, dorsal and K, medial views; L, AMNH 2809 (upper fragment) and AMNH 2798 (lower fragment) to show it is a single left lateral osteoderm of Lucasuchus in dorsal view. Scale bars equal 2 cm.

Comparisons with Other Pekin Formation Aetosaurs

We have recovered several other osteoderms of aetosaurs from NCPALEO 1902. Some could conceivably pertain to Gorgetosuchus (Fig. 4A–I). However, all were found in different blocks, frequently of different lithologies, so it is extremely unlikely that any represent the same individual as the holotype, or even each other. Furthermore, all appear to be from a more posterior position in the carapace, so we cannot directly compare them with homologous elements in Gorgetosuchus. We describe these osteoderms briefly to facilitate future comparisons as well as our discussion of the aetosaur record of the Pekin Formation, which includes previously published specimens from the Pomona Pipe quarry (Baird and Patterson, 1967; Hunt and Lucas, 1990; Huber et al., 1993; Parker and Martz, 2010). We provide a summary of our interpretations of these specimens in Table 4. The following paragraphs document the observations on which those interpretations are based.

The best-preserved osteoderm, NCSM 19025 (Fig. 4A–C), was recovered as an isolated specimen in a pebbly conglomerate. We interpret it as a left dorsal paramedian, probably from the sacral to caudal portion of the carapace because it is relatively narrow (width:length < 2:1), spinose, and the anterolateral expansion of the anterior bar suggests that the next most anterior osteoderm was wider. The most prominent feature is the elongate, spinose boss that begins as a low, ridge-like knob near the anterior bar...
and extends posteriorly, and somewhat laterally, to a sharp point that nearly overhangs the posterior margin (Fig. 4A, C). This spine is strongly ridged, and those ridges help to provide some indication of a radial pattern to the ovoid pits that dominate the flatter surfaces. The knob is offset slightly medially, and the anterolateral corner of the anterior bar is anteriorly expanded. The entire osteoderm is strongly flexed, with the lateral portion downturned ~30° relative to the medial surface (Fig. 4B). In side view, the osteoderm is sinuousoid in the same manner as described for *Gorgetosuchus* paramediands. As preserved, it is slightly wider (~55 mm) than long (~41 mm). In overall configuration, it is quite similar to *Lucasuchus* as well, especially because the boss is very similar in shape to TMM 31100-312, so we consider it best referred to cf. *Lucasuchus*.

The largest isolated osteoderm, NCSM 21265 (Fig. 4D, E), was recovered from a light-colored sandstone and is somewhat similar to NCSM 19025 except that the eminence is more pyramidal and does not extend as far anteriorly. The ornamentation is also more radial, especially on the medial side, where the pits are more elongate and groove-like. It is similar to osteoderms of *Longosuchus* and *Gorgetosuchus* in having a pyramidal boss that contacts the posterior margin, but the radial pattern is more similar to *Lucasuchus* or even *Calyptosuchus*, although the latter has more knob-like bosses (e.g., Long and Murry, 1995:fig. 69). Very little of the lateral margin is preserved, hindering further identification. We tentatively consider this a desmatosuchine osteoderm that most likely represents *Lucasuchus* or *Gorgetosuchus*, but is generically indeterminate.

Of the other two specimens, NCSM 23170 (Fig. 4F, G) is a more fragmentary osteoderm that is otherwise identical to NCSM 21265 in that it possesses a ridged, pyramidal boss and a prominent anterior bar. What patterning is preserved appears radial, and the boss is situated posteriorly. It is probably a left dorsal paramedian of a desmatosuchine aetosaur, possibly *Lucasuchus*, but is best identified as (?)desmatosuchine.

The most fragmentary specimen, NCSM 25063 (Fig. 4H, I), is an incomplete, isolated spine lacking the tip that could pertain to either a lateral osteoderm or a caudal paramedian, because these are the two regions of the aetosaur carapace most likely to bear long spines (Zeigler et al., 2002; Heckert et al., 2003; Parker, 2007; Desojo et al., 2013). The spine is more strongly faceted and more posteriorly projecting than the laterals of *Gorgetosuchus*, with some pitting on the lateral (ventral) surface, but the specimen is too incomplete to assign to a genus. Both of these osteoderms are best assigned to Desmatosuchinae indet.

There are two other noteworthy occurrences of osteoderms from the Pekin Formation. One of these is the first occurrence of the aetosaur *Coahomasuchus* in the Newark Supergroup (Fraser et al., 2006), also from NCPALEO 1902 and currently under study by the authors (Schneider et al., 2011; Heckert et al., 2012), and the second is a fragmentary assemblage of osteoderms from the Pomona Pipe B locality that are repositioned at AMNH.

The Pomona Pipe B locality is situated in the upper portion of the Pekin Formation, approximately 17.7 miles (28.5 km) farther to the west-southwest of NCPALEO 1902 (Reinemund, 1955), and was collected by R. Patterson in the late 1960s (Baird and Patterson, 1967). The most identifiable of these osteoderms, now at the AMNH, have been identified as *Typhothorax* (Baird and Patterson, 1967), *Longosuchus* (Hunt and Lucas, 1990; Huber et al., 1993), and, most recently, *Lucasuchus* (Long and Murry, 1995; Parker and Martz, 2010). These specimens consist of nine osteoderms of varying completeness in 10 pieces, most of which are too fragmentary to assign to a genus. Hunt and Lucas (1990: fig. 3c–h), Huber et al. (1993: fig. 4a–h), and Parker and Martz (2010:fig. 6) illustrated some of these specimens, which are cataloged as AMNH 2795–2799, 2803–2805, and AMNH 2809, although part of AMNH 2809 is a smaller fragment of AMNH 2797 (see below). AMNH 2799 (Fig. 4J, K) and AMNH 2797 (Fig. 4L; including the small fragment from AMNH 2809) are illustrated here. The specimens with preserved lateral spikes have very well developed cylindrical spines, as in *Lucasuchus* or other derived desmatosuchines (*Sierritasuchus, Desmatosuchus*) but unlike *Longosuchus*. In the following paragraphs, we describe the AMNH specimens in more detail.

The most diagnostic specimen, AMNH 2799 (Parker and Martz, 2010:fig. 6; Fig. 4J, K), is a right paramedian that is probably from the anterior dorsal portion of the column, because it possesses an extremely robust articulation for the corresponding lateral osteoderm (Fig. 4K). Parker and Martz (2010) illustrated, but did not describe, the specimen other than as a cervical or anterior dorsal right paramedian. It is wider (~92 mm) than long (~57 mm) and not flexed or arched at all, so we consider it an anterior dorsal, and it is significantly larger than any preserved osteoderm of *Gorgetosuchus*. The boss is slightly more medially situated than is apparent in Parker and Martz’s (2010:fig. 6b) illustration, so it appears that the osteoderm was photographed at a slight angle in their figure. The ornamentation is subdued but somewhat radial. After comparison with casts (e.g., TMM 31100-361) and photographs, we accept the identification of Parker and Martz (2010) that this is *Lucasuchus*.

During our examination of AMNH specimens, we determined that one of the pieces labeled AMNH 2809 is actually a fragment of AMNH 2797 (Fig. 4L), a lateral spike typically referred to *Longosuchus* (Hunt and Lucas, 1990:fig. 3e, f; Huber et al., 1993: fig. 4a, b). Reattaching the AMNH 2809 fragment to this specimen allows us to identify the combined specimen as a left lateral cervical osteoderm possessing a definite anterior bar and thickened articulation that overlapped the lateral edge of the corresponding paramedian osteoderm. The spine is elongate, much more so than in *Gorgetosuchus*. Although the base is striated, the cross-section of the spine where it is broken is more ovoid than polygonal, and the posterior margin is not emarginated, supporting assignment to *Lucasuchus*.

Of the other AMNH osteoderms, AMNH 2798 is more fragmentary than AMNH 2797 but generally similar and may be from the opposite (right) side, but with a spine that is also conical and not emarginated. The main piece of AMNH 2809 is a relatively complete paramedian with a very prominent, but broken, dorsal eminence that was an elongate knob or spike. The osteoderm is missing the anterior articulation; thus, we are not comfortable assigning it to a taxon more definitive than Desmatosuchinae indet. AMNH 2796 is an incomplete dorsal paramedian that is broken laterally and medially and possesses a low boss near the posterior margin. It is extremely incomplete, but what is preserved is more similar to *Longosuchus* than *Lucasuchus*, but it is not diagnostic to genus. Specimens AMNH 2804 and AMNH 2805 are both just broken knobs of lateral or paramedian osteoderms of indeterminate aetosaurs.

**PHYLOGENY**

The most recent phylogenetic analyses of aetosaurs (Parker, 2007; Parker et al., 2008; Desojo et al., 2012) recognize many more taxa, but utilize fewer characters, than did the analysis of Heckert and Lucas (1999, 2000). Although we reserve doubts about some of these taxa, and feel that some characters should have been retained, especially given the recent identification of *Revueltosaurus* as a possible sister taxon to the aetosaurs (e.g., Parker et al., 2005; Nesbitt, 2011), a complete reanalysis of the phylogeny of the aetosaurs is beyond the scope of this contribution. Accordingly, we sought to add *Gorgetosuchus* to an existing phylogeny (Parker, 2007), much as Parker et al. (2008) did with *Sierritasuchus* and Desojo et al. (2012) did with *Aetobarbakinoides* (Fig. 5A). Our results are provided in Figure 5B–D and discussed in the following paragraphs.

In addition to incorporating *Aetobarbakinoides*, Desojo et al. (2012) rescored several character states in *Aetosauroides*,
TABLE 4. Taxonomic assignment of isolated osteoderms from the Pekin Formation of North Carolina.

| Specimen   | Position                        | Assignment                       | Illustration                          |
|------------|---------------------------------|----------------------------------|---------------------------------------|
| NCSM 19025 | Left paramedian (sacrocaudal?)  | cf. *Lucasuchus*                 | Fig. 4A–C                             |
| NCM 21265  | Right paramedian                | *Desmatosuchinae aff. Lucasuchus*| Fig. 4D–E                             |
| NCM 23170  | Left? paramedian                | Desmatosuchinae indet.           | Fig. 4F–G                             |
| NCM 25065  | ?lateral or ?caudal paramedian  | Desmatosuchinae indet.           | N/A                                   |
| AMNH 2795  | Left? lateral spine             | Aetosauria indet.                | N/A                                   |
| AMNH 2796  | Incomplete paramedian           | *Lucasuchus*                     | Hunt and Lucas, 1990:fig. 3g–h        |
| AMNH 2797  | Left lateral                     | ?*Lucasuchus*                    | Fig. 4J–K; Hunt and Lucas, 1990:fig. 3g|
| (and 2809b)|                                 | N/A                              | Parker and Martz, 2010:fig. 6          |
| AMNH 2798  | Right? lateral                   | *Lucasuchus*                     | N/A                                   |
| AMNH 2799  | Left anterior paramedian         | N/A                              | N/A                                   |
| AMNH 2804  | Paramedian boss or lateral spine fragment | Aetosauria indet. | N/A                                   |
| AMNH 2805  | Paramedian boss or lateral spine fragment | Aetosauria indet. | N/A                                   |
| AMNH 2809a | Dorsal paramedian                | *Lucasuchus*                     | N/A                                   |
| AMNH 2809b | Left lateral                     | *Lucasuchus*                     | Fig. 4L; Hunt and Lucas, 1990:fig. 3e–f|

Aetosaurus, Neoaetosauroides, and Stagonolepis robertoni. We have accepted these modifications and made several others based on our studies of aetosaurs in the Pekin Formation. Specifically, we updated scorings of one character for *Lucasuchus* and four for *Longosuchus* based on the descriptions and illustrations contained in Parker and Martz (2010), as well as our own observations of casts of these taxa. We also updated two character states of *Coahomasa- chus* based on our ongoing study of the Pekin Formation specimen briefly described by Fraser et al. (2006; Schneider et al., 2011; Heck- ert et al., 2012) and corrected or updated three character-state cod- ings of *Typothorax* based on specimens described by Heckert et al. (2010). We changed one character state for *Redondasuchus* based on our knowledge of that taxon. Full discussion and justification of these changes are provided in the Supplementary Data 1 and the actual matrix used is in Supplementary Data 2. Subsequently, we coded *Gorgetosuchus* for as many (15; see Appendix 1) of the 37 characters as possible and added it to the resulting matrix. We con- sider *Adamanasuchus eisenhardtii* Lucas, Hunt, and Spielmann (2007) and *Apachesuchus heckerti* Spielmann and Lucas (2012) too fragmentary to include in the analysis, as have Parker et al. (2008) and Desojo et al. (2012) in the case of *Adamanasuchus*. We have not been able to evaluate *Stenonyt huangae* Small and Martz (2013) and thus did not include it, either. The matrix therefore includes 21 taxa (including *Gorgetosuchus*) and the 37 characters enumerated by Parker (2007), with *Postosuchus* used as an out- group. For reference, we have reproduced the strict consensus of the Desojo et al. (2012) analysis in Figure 5A.

Given the relatively small size of the matrix (fewer than 25 taxa; <40 characters), we chose to perform an exhaustive (implicit) search, rather than the branch-and-bound or heuristic (traditional) algorithms used by previous authors (Parker; 2007; Parker et al., 2008; Desojo et al., 2012). Otherwise, we followed almost exactly the same procedures listed by Desojo et al. (2012:26) to maximize consistency with their analysis, first with the updated data matrix but excluding *Gorgetosuchus*. The ‘rauisuchian’ *Postosuchus kirkpatricki* was used to root the recovered most parsimonious trees (MPTs), and the same 10 characters Parker (2007) ordered were kept as additive (ordered) characters. The data matrix was analyzed under equally weighted maximum parsimony using TNT 1.1 (Goloboff et al., 2008). Zero-length branches among any of the recovered MPTs were collapsed per rule 1 of Coddington and Scharff (1994). The analysis of the updated matrix resulted in four MPTs, the strict consensus of which is shown in Figure 5B. Statistics for this tree are a tree length of 70 steps, CI of 0.657, and RI of 0.832. The key difference we note in this tree is the continued loss of resolution among ‘aetosaurine’ (basal aetosaur) relationships. Similarly, rescoring *Longosuchus* and *Lucasuchus* following Parker and Martz (2010) shuffles their positions within the Des- matosuchinae, moving *Longosuchus* to a more basal position than recovered by previous authors.

We then added *Gorgetosuchus* and conducted analyses using the same search criteria. This resulted in three MPTs, the strict consensus of which is illustrated (Fig. 5C) and has a tree length of 71 steps, CI of 0.648, and RI of 0.832. Clearly, the six-taxon polytomy at the base of Stagonolepididae is the primary feature, which was somewhat surprising because both the poorly known *Redondasuchus* and much better known *Longosuchus* were pulled outside of the derived clades *Typothoraciscinae* and Des- matosuchinae, respectively, into this polytomy.

We suspected that this result was at least in part due to the poorly known *Aetobarbakinoides*, which lacks coding for most osteo- derm characters, including all lateral osteoderm characters. The lack of significant overlap between coded characters in *Aetobar- bakinoides* and taxa known solely from osteoderms (e.g., *Gorgetosuchus*, *Serritassuchus*, *Redondasuchus*, and *Acaenasau- chus*) necessarily renders those relationships ambiguous. In an attempt to resolve this in an unbiased manner, we employed safe taxonomic reduction (Wilkinson, 2003), but this only pruned one species of *Desmatosuchus* from the tree, with no alteration of topology otherwise, therefore resulting in no greater resolution of ingroup relationships. Accordingly, we ran a TNT script for iterative PCR, or iterative positional congruence (reduced) (Pol and Escapa, 2009), on the entire matrix, determining that there were three nodes where *Aetobarbakinoides* could be placed without upsetting parsimony. We pruned *Aetobarbakinoides* a posteriori (retaining information it provided for the most parsimonious arrangement of the remaining taxa). The result was a single MPT (Fig. 5D), with a tree length of 69 steps, a CI of 0.667, and a RI of 0.839. Importantly, even though the tree is well resolved, Bremer supports are very low, and only the dichot- omous splitting the *Typothoraciscinae* and the Desmatosuchinae requires more than one step to collapse.

**DISCUSSION**

The discovery of a distinctive aetosaur superficially similar to both *Longosuchus* and *Lucasuchus* from strata where each had been identified previously has implications for the paleobiodiversity of the Pekin Formation specifically and studies of aetosaurs generally. Although there are similarities of *Gorgetosuchus* to both *Longosuchus* and *Lucasuchus*, we are confident that the these taxa are indeed distinct, and that the similarities are not due to sexual dimorphism, ontogeny, or other intraspecific sources of variation. Indeed, the presence of an aetosaur with osteoderm morphology more or less intermediate between
the two taxa strengthens the arguments against interpreting *Longosuchus* and *Lucasuchus* as sexual dimorphs presented by Parker and Martz (2010).

We reject the hypothesis that *Gorgetosuchus* is a sexual dimorph of another taxon, such as *Lucasuchus* or *Longosuchus*, on multiple grounds. First, *Gorgetosuchus* has a fundamentally different plate arrangement than do these or other superficially similar taxa. *Gorgetosuchus* is unique among desmatosuchines in possessing cervical paramedian osteoderms that are clearly wider than long. Other desmatosuchines (as well as *Typothorax coccinarum*; see Heckert et al., 2010) have decoupled the 1:1 ratio of osteoderm rows to vertebrae (Long and Murry, 1995); this is possible but appears less likely in *Gorgetosuchus*, and we consider it highly unlikely that the different configuration of cervical plates would be a sexually dimorphic characteristic. Although some features of *Gorgetosuchus* relative to other taxa could easily be seen as dimorphic display features (the difference in cervical spine length relative to *Longosuchus* and *Lucasuchus*, for example), the subtle difference in ornamentation and the difference in paramedian proportions, which are similar to other, more plesiomorphic aetosaurs, are more parsimoniously explained by taxonomic differences. Finally, accepting Parker and Martz’s (2010) arguments that *Longosuchus* and *Lucasuchus* are distinct taxa for *Gorgetosuchus* to be a dimorph of either of those genera (presumably *Lucasuchus*, with which it co-occurs) would indicate that it was the first occurrence of such a dimorph in spite of the many fossils variously ascribed to *Longosuchus* and/or *Lucasuchus*.

FIGURE 5. Phylogenetic hypotheses of aetosaurs. A, strict consensus of Desojo et al. (2012), who incorporated *Aetobarbakinoides* and other updated character scorings into Parker’s (2007; Parker et al., 2008) matrix; B, reanalysis of that matrix with updates to character scorings of *Coahomasuchus*, *Typothorax*, *Redondasuchus*, *Longosuchus*, and *Lucasuchus*, as described in the text and Supplementary Data; C, strict consensus of the updated matrix after scoring and including *Gorgetosuchus*; D, strict consensus of the updated matrix with *Gorgetosuchus* but removing *Aetobarbakinoides* a posteriori from the analysis. Closed circles denote node-based taxa; open circles denote stem-based taxa. See text for additional discussion. Numbers are Bremer support values \( \equiv 1 \). Abbreviations: A, Aetosauria; D, Desmatosuchinae; P, Paratypothoracisini; T, Typothoracisinae; all as defined in Parker (2007).
At the local scale, we recognize at least three genera of aetosaurs from the Pekin Formation—Gorgetosuchus, Lucasuchus, and Coahomasuchus. At least two of these (Gorgetosuchus and Coahomasuchus) are both known from NCPALEO 1902, and Lucasuchus may be represented there as well (e.g., Fig. 4A–C). Given the paucity of available outcrop and limited study dedicated to the Pekin Formation relative to the Upper Triassic strata of the American Southwest, this qualitatively suggests that the Pekin Formation is at least as diverse as comparable stratigraphic units there. Extrapolating from this, in general we expect that Newark Supergroup basins should yield comparable diversity as the Chinle Group basins, and that workers arguing otherwise will have to account for the difference in outcrop exposure and collecting effort.

Accepting the occurrence of Lucasuchus and Coahomasuchus in the Pekin Formation strengthens correlation of the Pekin to the lowermost Chinle (Dockum) unit, the Colorado City Formation as used by Lucas et al. (2001 and references therein) or the ‘pre-Tecovas horizon’ of Long and Murry (1995). This correlation has been argued on the basis of the AMNH specimens from the Pomona Pipe locality, originally assigned to Longosuchus by Hunt and Lucas (1990) but referred to Lucasuchus by Long and Murry (1995), who did not accept the correlation, and Parker and Martz (2010), who did. Because the Pekin Formation continues to be identified as Carnian in age (e.g., Whiteside et al., 2011), this suggests that at least some strata in the American Southwest are Carnian in age regardless of acceptance or rejection (e.g., Lucas et al., 2012) of the ‘long Norian’ of Muttoni et al. (2004).

The very close similarity of Gorgetosuchus to Longosuchus and Lucasuchus underscores that great care must be taken in identifying, let alone naming, isolated osteoderms to specific taxa. Parker and Martz (2010), for example, argued this and went to great lengths to demonstrate the homology of osteoderms they referred to Longosuchus and Lucasuchus. In so doing, they provided the most compelling diagnosis of the two taxa—indeed, if Long and Murry (1995) had demonstrated the distinctiveness of Longosuchus and Lucasuchus as thoroughly and convincingly as Parker and Martz (2010), then much nomenclatural argument about the validity of both taxa and assignment of specimens to either genus (e.g., Long and Murry, 1995; Heckert et al., 1996; Heckert and Lucas, 1999, 2000; Parker, 2007) could have been avoided. However, it is also incumbent upon authors to clearly state the implications of their taxonomic work relative to existing phylogenies. As documented in the Supplementary Data, Parker and Martz’s (2010) work results in four scoring changes for Longosuchus and one for Lucasuchus, none of which were explicitly addressed by them, but which appear responsible for changing the topology of desmatosuchine aetosaurs (e.g., Fig. 5B). Given the relatively weakly resolved phylogenies of aetosaurs (see below), these changes are significant.

Our phylogenetic analysis clearly demonstrates that our understanding of the phylogenetic relationships within Aetosauria remains highly unstable. We interpret the tree in Figure 5D to represent uncertainty caused by the mosaic of characters present in Gorgetosuchus, some of which are similar to some thyrothracines (e.g., random pitting, cervical paramedians wider than long, ventral keels), whereas others are clearly desmatosuchine (prominent lateral osteoderms overlapping relatively narrow paramedians). Many taxa are too poorly known to contribute much to our understanding of ingroup relationships, and the relationships of basal aetosaur taxa in particular are highly labile. The fact that relatively few coding additions and changes can produce the different trees seen here, especially those in Figure 5A–B, indicates that discoveries of more complete specimens of existing taxa are likely to result in dramatic rearrangements of aetosaur phylogeny. Intuitively, this was already known based on the low support values reported by Harris et al. (2003) and still found in recent analyses (e.g., Desojo et al., 2012), but the extensive alterations to tree topology brought about by a few coding changes and addition of a relatively poorly known taxon that otherwise bridges the gap from basal aetosaurs to more derived desmatosuchines highlight the fact that the topology is far from settled.

CONCLUSIONS

The holotype specimen of Gorgetosuchus, although comprising only 19 associated osteoderms, is distinct from any known aetosaur, including Longosuchus and Lucasuchus, which it most closely resembles. A particularly novel feature of Gorgetosuchus is the morphology of the cervical osteoderms, which nearly encircle the neck. The presence of cervical lateral osteoderms that overlap paramedians that are wider than long suggests placement of Gorgetosuchus as basal to a clade of aetosaurs more closely related to Desmatosuchus than to Typothorax or Paratypothorax. Other specimens from the same locality may pertain to Gorgetosuchus, Lucasuchus, Coahomasuchus, or other aetosaurs and together indicate that the diversity of the Pekin Formation is nearly as high as that of any stratigraphic unit known to yield aetosaurs. The presence of Lucasuchus and Coahomasuchus in the Pekin Formation, which most workers have continued to consider Carnian in age, suggests that strata bearing these taxa in West Texas are also Carnian in age.

Our phylogenetic analyses bear out the placement of Gorgetosuchus as basal to a clade of desmatosuchine aetosaurs (Fig. 5C, D). It is also evident that the armor of some taxa, such as Aetobarbakinoides, is so poorly known that their contribution to our understanding of aetosaur phylogeny is minimal in a clade where many taxa are known largely to solely from osteoderms and existing phylogenetic hypotheses rely on numerous characters based on armor. Perhaps most importantly, the analyses we report here further demonstrate that correcting and updating the scoring of known aetosaur taxa can result in significantly different tree topologies and warrant caution in accepting past results, as well as our own. Additional discoveries, especially those that will facilitate comparisons of non-osteoderm characters across taxa presently known largely or entirely from osteoderms, are badly needed.

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APPENDIX 1. Scoring of NCSM 21723, the holotype of *Gorgetosuchus*, for 15 characters following the Parker (2007) matrix as modified by Parker et al. (2008) and Desojo et al. (2012) and described in the text and Supplementary Data.

| Character | 5 | 10 | 15 | 20 | 25 | 30 | 35 |
|-----------|---|----|----|----|----|----|----|
| *Gorgetosuchus pekinensis* | ???? | ???? | ???2?0 | 11011 | 1111 | ???? | ???? | 0? |