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ARTICLE

USING POSITIONAL HOMOLOGY IN AETOSAUR (ARCHOSAURIA: PSEUDOSUCHIA) OSTEODERMS TO EVALUATE THE TAXONOMIC STATUS OF *LUCASUCHUS HUNTI*

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ABSTRACT—The Otis Chalk quarries in the Upper Triassic Dockum Group of West Texas have produced aetosaur material that most workers have suggested represents two distinct morphotypes. We use characters from aetosaur specimens with articulated or semi-articulated carapaces in which the anteroposterior placement of osteoderms can be established with certainty to compare homologous osteoderms in the Otis Chalk material. This study confirms that the genera *Longosuchus* and *Lucasuchus* are distinct morphotypes, which differ in that the former taxon has paramedian osteoderms with random pitted ornamentation and low pyramidal bosses that contact the posterior margin, and spines on the lateral osteoderms that are posteriorly emarginated, whereas the latter taxon has paramedians with a strongly radial ornamentation and large conical eminences, and spines on the lateral osteoderms that are not posteriorly emarginated. Both taxa also have paramedians that are overlapped anteriorly by the laterals, a character that may be a synapomorphy of desmatosuchine aetosaurs. The arguments that these morphotypes represent ontogenetic stages or sexual dimorphs of a single biological species cannot be corroborated using either comparisons with modern pseudosuchians, other aetosaur taxa, or stratigraphic ranges. *Longosuchus* is known only from the type area and has no utility as an index taxon of the Otischalkian land-vertebrate faunachron, although *Lucasuchus* suggests a tentative correlation between part of the Dockum Group of Texas and the Pekin Formation of North Carolina.

INTRODUCTION

Aetosaurs are a monophyletic group of pseudosuchian archosaurs characterized by an extensive carapace of osteoderms (often referred to in the literature as 'plates' or 'scutes') with a variety of distinctive features, including dorsal eminences (or 'bosses') and ornamentation patterns, which are used to diagnose aetosaur taxa (e.g., Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 1999, 2000; Parker, 2007).

Aetosaur osteoderms of the dorsal carapace form two inner anteroposterior columns (termed paramedian osteoderms) and two outer columns (termed lateral osteoderms) (Fig. 1). Thus, each mediolateral row of osteoderms is formed by two paramedians and two laterals. These rows are assigned to specific body regions based upon the type of vertebrae the row covers (e.g., cervical, dorsal, caudal) (Long and Ballew, 1985). Differences have been recognized in osteoderm morphology and ornamentation between body regions (e.g., Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 1999), and these have been detailed for particular taxa (e.g., Martz, 2002; Parker, 2003, 2007, 2008; Martz and Small, 2006; Schoch, 2007).

Due to the abundance of material and the taxonomic utility of isolated osteoderms, aetosaurs have been utilized as index taxa for Late Triassic non-marine biostratigraphy and biochronology (Long and Ballew, 1985; Lucas and Hunt, 1993; Lucas and Heckert, 1996; Heckert and Lucas, 2000; Heckert et al., 2007; but see Langer 2005; Rayfield et al., 2005, 2009; Martz and Small, 2006; and Parker, 2006, for reservations about the utility of aetosaur osteoderms for this purpose).

Previous Work

Sawin (1947) described aetosaur cranial and postcranial material from the Upper Triassic Otis Chalk quarries in the Dockum Group of Howard County, west Texas, and identified two morphotypes, both of which he assigned to the genus *Typothorax*. Sawin (1947:202) assigned several of the paramedian plates to the type species *Typothorax coccinarum* (Cope, 1875) because they possessed "conical eminences referable to" that taxon (Huene, 1915). In addition, Sawin (1947:202) assigned much material of the other recognized morphotype from the quarries, most notably the "associated remains of two relatively complete specimens" (TMM 31185-84a, TMM 31185-84b), to a new species, *Typothorax meadei*.

Sawin (1947:202) assigned this latter material to *Typothorax* based on the presence of "sigmoidal femora and dermal plates resembling those of the type of *Typothorax*," arguing that the only other North American genus available at the time, *Desmatosuchus*, "represents a larger reptile with more completely developed dermal armor." However, Sawin (1947:233) considered *Typothorax meadei* distinct from *T. coccinarum* in that the former (*T. meadei*) possesses "bluntly pyramidal, posteriorly placed eminences . . . [which] cannot be a growth phase of the conical shapes (*T. coccinarum*)." It is important to note that in separating the material into two distinct morphotypes, Sawin (1947) also made use of information (field notes and quarry maps) that cannot be located, and were therefore not available to subsequent workers.

Sometime after Sawin's description, all of this material in the Texas Memorial Museum (TMM) collections was re-catalogued as either *Typothorax meadei* or *Desmatosuchus haplocerus* (the latter including some of the plates with conical eminences that Sawin assigned to *Typothorax coccinarum*). However, none of the material is actually referable to either genus (Long and Ballew, 1985; Small, 1989; Hunt and Lucas, 1990; Parker, 2003). These catalogued misidentifications have caused confusion (e.g., Desojo and Baez, 2005; Kubo and Benton, 2007), most notably Elder's (1978) hypothesis that *Typothorax* and *Desmatosuchus* are congeneric due to their alleged similarities. Moreover, Elder (1978) considered the Otis Chalk '*Desmatosuchus*' material to possibly represent a sexual dimorph of "*Typothorax*"

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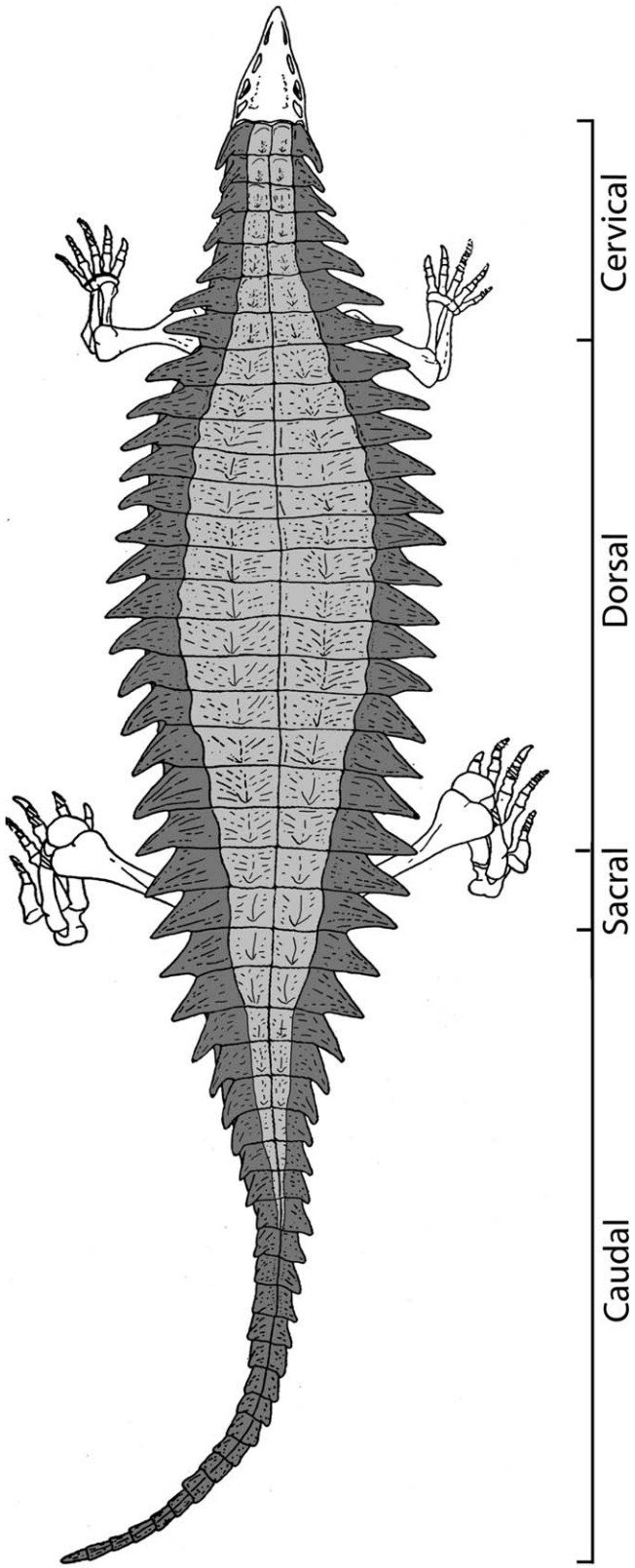

FIGURE 1. Reconstruction of *Longosuchus meadei* showing osteoderm columns and body regions. Lateral plates are shaded dark gray, whereas paramedian plates are shaded light gray. Modified from Sawin (1947). Note that the loss of paramedian plates in the caudal region is probably incorrect.

meadei. This was subsequently shown to be unlikely by Small (1989); however, it is notable that Elder (1978) recognized the same two aetosaur morphotypes in the Otis Chalk material identified by Sawin (1947), although she interpreted them differently.

As a result of the recognition that osteoderm morphology is diagnostic for aetosaur taxa, it became apparent to some workers that "*Typothorax*" *meadei* and *Typothorax coccinarum* were not congeneric (Long and Ballew, 1985; Small, 1989; Murry, 1989) and a new genus, *Longosuchus*, was subsequently proposed by Hunt and Lucas (1990) for "*Typothorax*" *meadei*. However, Hunt and Lucas (1990) referred all of the Otis Chalk aetosaur material to *Longosuchus*, including the plates with conical eminences, with no explanation for why they recognized only a single taxon as being present.

Long and Murry (1995) followed Sawin (1947) and Elder (1978) in considering the plates with the conical eminences to be morphologically distinct from *Longosuchus*, and assigned this material, as well as all of the other material in the TMM collections from the Otis Chalk Quarries catalogued as '*Desmatosuchus*,' to a new genus and species, *Lucasuchus hunti*. However, Lucas and Heckert (1996) and Heckert and Lucas (1999, 2000) followed Hunt and Lucas (1990) in considering all of the material to belong to a single taxon. They regarded *Lucasuchus hunti* to be a junior synonym of *Longosuchus meadei*, although Heckert and Lucas (2000:1562) admitted that "some of the material" referred to *L. hunti* may represent a different species.

Heckert and Lucas (1999:62) attempted to substantiate the synonymy of *Longosuchus* and *Lucasuchus* by noting that in a phylogenetic analysis a "strict consensus ... bore out our initial suspicions" that they were congeneric (presumably because they were sister taxa), and they therefore removed *Lucasuchus* from their final analysis. This approach was questioned by Harris et al. (2003), mainly because as *Longosuchus* and *Lucasuchus* are not coded identically in Heckert and Lucas' (1999) data matrix, they do not represent taxonomic equivalents, and therefore neither can be safely removed without affecting the analysis (Wilkinson, 1995). Furthermore, re-analysis of the data set of Heckert and Lucas (1999) by Harris et al. (2003) did not recover *Lucasuchus* and *Longosuchus* as sister taxa. Parker (2003, 2007) also did not recover the two as sister taxa in his phylogenetic analysis and argued for the validity of *Lucasuchus*. The same study found *Lucasuchus* to be closer to *Desmatosuchus* and *Acaenasuchus* than to *Longosuchus* (Parker, 2003, 2007).

Here we re-address the validity of *Lucasuchus* by determining whether or not two similar but distinct morphotypes truly exist in the Otis Chalk aetosaur material. We also present revised diagnoses for *Longosuchus* and *Lucasuchus*, consider the question of whether or not these morphotypes represent sexual dimorphs, and re-consider the utility of these taxa for biochronology.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque; **TMM**, Texas Memorial Museum, Austin.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA sensu Gauthier, 1986
PSEUDOSUCHIA sensu Gauthier, 1986
AETOSAURIA sensu Parker, 2007
DESMATOSUCHINAE sensu Parker, 2007
LONGOSUCHUS MEADEI (Sawin, 1947)
(Figs. 1, 2A–B, 3A–B, 4)

Typothorax meadei: Sawin, 1947:201, figs. 1–13, 15a, 15b1, 15b2, pl. 34.

Typothorax meadei: Gregory, 1953:11.
Typothorax: Walker, 1961:177, fig. 24c.
Typothorax meadei: Krebs, 1976:78, fig. 20.
Typothorax: Bonaparte 1978:300, fig. 136d.
Typothorax meadei: Murry, 1986:123, fig. 9.12b.
Typothorax meadei: Parrish, 1986:11, fig. 12g, 13d, 33h.
Typothorax meadei: Small, 1989:301, fig. 1a.
Longosuchus meadei: Hunt and Lucas, 1990:317, figs. 2c–f, 3i–j.
Longosuchus meadei: Parrish, 1994:196, figs. 1–6.
Longosuchus meadei: Long and Murry, 1995:67, figs. 58–63.
Longosuchus meadei: Heckert and Lucas, 2000:1561.
Typothorax meadei: Kubo and Benton, 2007:1523.

Lectotype—The former TMM 31185–84b, includes TMM 31185–97, partial postcranial skeleton, and TMM 31185–98, skull.

Paralectotype—31185–84a, partial postcranial skeleton and fragmentary skull.

Comments—One confusing aspect of *Longosuchus meadei* is the status of the type materials. Sawin (1947) did not assign a holotype, but instead explicitly designated two specimens (TMM 31185–84a and TMM 31185–84b) as syntypes. Hunt and Lucas (1990) subsequently designated TMM 31185–84b as the lectotype in accordance with the International Code of Zoological Nomenclature (2000; ICZN hereafter) Article 74.1 and made TMM 31185–84a a referred specimen. However, as a previous cosyntype, TMM 31185–84a automatically becomes a paralectotype according to ICZN Article 74F.

The lectotype (TMM 31185–84b) was subsequently renumbered 31185–97 by curatorial staff. Long and Murry (1995) argued that TMM 31185–97 contains material from more than one individual and restricted the type designation to the skull (renumbered as 31185–98), which they referred to as the holotype. However, a holotype may only be designated in the original publication (ICZN Article 73.1.3 and Recommendation 73F), and the lectotype designation for the specimen by Hunt and Lucas (1990) therefore remains valid. Moreover, Long and Murry (1995) diagnosed *Longosuchus meadei* solely on characters of the osteoderms even though they restricted the type to the skull. Thus, we prefer to follow Hunt and Lucas (1990) in retaining nearly all the material originally assigned to TMM 31185–97 (formerly TMM 31185–84b) within the lectotype designation.

Referred Specimens—see Long and Murry (1995) for a complete list.

Occurrence and Distribution—Colorado City Member (= lower portion of Cooper Canyon Formation), Dockum Group, Texas (Lehman, 1994; Lucas et al., 1994; Martz, 2008).

Age—Latest Carnian or early-mid Norian (Late Triassic).

Revised Diagnosis—Desmatosuchine aetosaur with the following unique combination of characters: paramedian plates with a random pattern of circular pits, a raised anterior bar, and a dorsal pyramidal eminence that contacts the posterior plate margin; differs from aetosaurines in possessing seven thickened cervical paramedian plates that are longer than wide and cover the entire cervical vertebral series; and possessing lateral plates in which the dorsal flange is larger than the lateral flange; also differs from aetosaurines in that the lateral osteoderm overlaps the anterior part of the articular surface of the paramedian osteoderm as in other desmatosuchines; possesses well-developed lateral spines that differ from those of *Desmatosuchus* in being faceted, increasing in size from the cervical to the dorsal regions, and lacking distinct extremely elongate recurved shoulder horns; differs from *Lucasuchus* in that the lateral spines are posteriorly emarginated and lack a strong radial ornamentation of grooves and ridges; differs from *Sierritasuchus* in that the cervical vertebrae lack ventral keels and the lateral spines are faceted and not recurved.

LUCASUCHUS HUNTI Long and Murry, 1995
(Figs. 2C–D, 3C–D, 5, 6)

Typothorax coccinarum: Sawin, 1947:233, figs. 15b2, b4.
Desmatosuchus haplocerus: Elder, 1978.
Typothorax haplocerus: Elder, 1978.
Longosuchus meadei: Hunt and Lucas 1990:321, figs. 2a–b, 3a–h.
Lucasuchus hunti: Long and Murry, 1995:73, fig. 64.
Longosuchus meadei: Heckert and Lucas, 1999:62.
Lucasuchus hunti: Harris et al., 2003:250.
Lucasuchus hunti: Parker, 2007:57.

Holotype—TMM 31100–257, posterior dorsal paramedian plate.

Key Referred Specimens—TMM 31100–503, cervical paramedian plate; TMM 31100–469, cervical paramedian plate; TMM 31185–66, articulated posterior cervical/anterior dorsal paramedian and lateral plates; TMM 31100–361, dorsal paramedian plate; AMNH 2799, right posterior cervical or anterior dorsal paramedian plate. See Long and Murry (1995) for other osteoderm material.

Comments—Long and Murry (1995) assigned postcranial material to *Lucasuchus*, which is very similar to that of *Longosuchus*. Because *Longosuchus* occurs in the same quarries and the original association of the material is lost, we refrain at this time from assigning any non-armor material to *Lucasuchus*.

Occurrence and Distribution—Colorado City Member (= lower portion of Cooper Canyon Formation), Dockum Group, Texas (Lucas et al., 1994; Lehman, 1994; Martz, 2008); Pekin Formation, North Carolina.

Age—Latest Carnian or early-mid Norian (Late Triassic).

Revised Diagnosis—Desmatosuchine aetosaur that differs from all others in possessing paramedian plates with a distinct tall, conical eminence that does not contact the posterior plate margin; differs from all aetosaurines by possessing lateral plates with dorsal flanges that are longer than the lateral flange, and that the lateral osteoderm overlaps the anterior part of the articular surface of the paramedian osteoderm as in other desmatosuchines; differs from *Longosuchus*, *Desmatosuchus*, and *Sierritasuchus* in possessing a radial patterning of grooves and ridges on the paramedian and lateral plates; differs from *Longosuchus* in possessing lateral spines that lack facets and a posterior emargination; differs from *Sierritasuchus* in that the lateral spines are conical and straight, not dorsoventrally flattened and recurved.

POSITIONAL ANALYSIS OF THE OTIS CHALK AETOSAUR OSTEODERMS

Both the paramedian and lateral osteoderms of aetosaurs show considerable anteroposterior morphological change within columns. When comparing different specimens, it is therefore absolutely essential to establish which osteoderms come from the same region of the carapace and are therefore more or less homologous. Otherwise, apparent differences in osteoderm morphology may represent anteroposterior variation rather than taxonomic (or intraspecific) differences. In this study we identify and compare homologous osteoderms in the Otis Chalk material to determine whether or not there are indeed two distinct morphotypes as postulated by some previous workers.

This study makes use of the guidelines provided by Long and Ballew (1985), Martz and Small (2006), and Parker (2007), in which anteroposterior variation in osteoderm morphology is established from articulated or semi-articulated specimens, then applied to disarticulated specimens of other taxa to determine osteoderm placement on the carapace. We refer to this endeavor here as 'positional analysis,' and it allows comparisons between osteoderms from equivalent regions of the carapace in different specimens. Although most of these reference specimens are aetosaurines (sensu Parker, 2007), *Desmatosuchus* and *Longosuchus* specimens in which osteoderms were found

associated with vertebrae from different parts of the column or other postcranial elements (Case, 1922; Sawin, 1947; Parker, 2008) demonstrate that most aetosaurine patterns hold true for desmatosuchines (sensu Parker, 2007). We will also identify additional characters with possible taxonomic relevance.

Using articulated and semi-articulated specimens, the following observations important to this study can be made regarding paramedian osteoderms in aetosaur carapaces, as outlined previously by Long and Ballew (1985), Long and Murry (1995), Heckert and Lucas (1999), and Parker (2007, 2008): (1) The unornamented raised bar or depressed lamina extending the length of the osteoderm lies along its anterior edge; (2) width-length ratios for plates increase from the cervical to the dorsal regions and then decrease from the pelvic through the caudal regions; (3) dorsal eminences become more pronounced posteriorly through the carapace; (4) in desmatosuchines, cervical plates are anteroposteriorly elongate, with the anterior end being narrower than the posterior end, rather than being wider than long as they are in aetosaurines; and (5) anterior dorsal plates are dorsoventrally thickened, and more posterior plates become progressively thinner. These guidelines are applied to the Otis Chalk material below.

One difficulty encountered in this particular study is that many of the osteoderms of the type materials of *Longosuchus* have been incorporated in a mount that is on display at the Texas Memorial Museum (TMM), and many are partially concealed by plaster reconstruction, limiting our ability to examine them. Fortunately, there are also many loose plates in the TMM collections that were not used in the reconstruction.

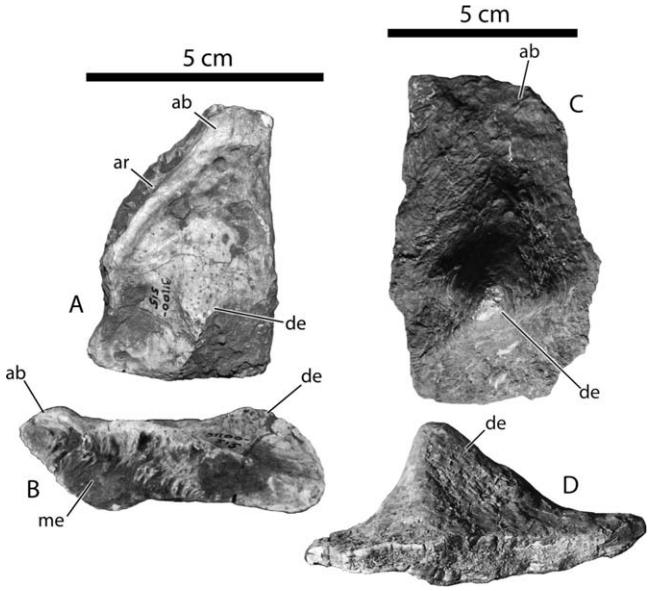

FIGURE 2. Comparisons of anterior cervical paramedian osteoderms of *Longosuchus meadei* and *Lucasuchus hunti*. Anterior cervical paramedian osteoderm of *L. meadei* (TMM 31100–515) in **A**, dorsal and **B**, medial views. Anterior cervical paramedian osteoderm of *L. hunti* in **C**, dorsal and **D**, anterior views. The height of the boss can be compared in B and D. **Abbreviations**: **ab**, anterior bar; **ar**, articular surface for lateral osteoderm; **de**, dorsal eminence or 'boss'; **me**, medial edge.

Anterior Cervical Paramedian Osteoderms

Paramedian plates interpreted by Sawin (1947) as anterior cervical paramedians, and placed as such in the mounted specimen of *Longosuchus* (TMM 31185–84a), are longer than wide, with anterior ends that are narrower than the posterior ends, and having bosses that are more weakly developed than in other paramedians. This morphology is similar to the anterior cervical paramedians of *Desmatosuchus*, which can be identified as such based on their association with cervical vertebrae (Case, 1922; Parker, 2008), and supports Sawin's (1947) identification. There is also an isolated left paramedian plate (TMM 31100–515; Fig. 2A–B) that is identical and shows greatly thickened 'tongue and groove' (sensu Long and Ballew, 1985) articular surfaces for the adjacent right paramedian and left lateral plate. Such articular surfaces are a synapomorphy of desmatosuchines (Parker, 2007).

Long and Murry (1995) referred two osteoderms (TMM 31100–503, TMM 31100–469; Fig. 2C–D; Long and Murry, 1995:fig. 65A–B) with a similar morphology to *Lucasuchus hunti*. These anterior cervical paramedians differ from those of *Longosuchus* in having a conical eminence that is more raised.

Posterior Cervical or Anteriormost Dorsal Paramedian and Lateral Osteoderms—An articulated set of paramedian and lateral plates of *Longosuchus* (TMM 31185–97; Fig. 3A–B; Long and Murry, 1995:fig. 60 G–I), are thickened compared to other paramedian osteoderms in the same specimen and wider than the anterior cervical paramedians. This morphology is consistent with plates from the posterior cervical and anteriormost dorsal regions in *Desmatosuchus* (Long and Murry, 1995; Parker, 2008). The dorsal boss is low (though slightly more prominent than in the anterior cervical paramedians), pyramidal, and contacts the posterior plate margin. The ornamentation is pitted and not distinctly radial. The lateral plate consists of dorsal and lateral flanges that meet at the base of an elongate, laterally projecting spike, the posterior face of which is deeply emarginated.

A similarly thickened right paramedian plate and articulated right lateral plate (TMM 31185–66; Fig. 3C–D) referred to *Lucasuchus hunti* by Long and Murry (1995) comes from the same region of the carapace; however, unlike *Longosuchus* the dorsal boss is conical and tall, and centralized on the plate, not contacting the posterior margin, and the spine of the lateral plate is more robust and not emarginated. Unfortunately, overpreparation has obscured the nature of the ornamentation in this plate.

Dorsal Paramedian Osteoderms

A right paramedian of *Longosuchus* that is articulated with a lateral plate (TMM 31185–97; Fig. 4C) is wider than long, and is dorsoventrally thinner than the cervical paramedians. Thus, it is probably from the dorsal region, but posterior to the osteoderms just described. This is also supported by the presence of a scapula that is diagenetically fused to the ventral margin of these plates. Moreover, the lateral edge articulating with the lateral osteoderm is sinuous, as is the case with paramedians associated with dorsal vertebrae in *Desmatosuchus* (Parker, 2008).

The medial edge of a left paramedian from TMM 31185–97 (Fig. 4A–B) fits with that of a right paramedian so perfectly, they were almost certainly articulated in life. The adjacent lateral plate for the left paramedian is missing, demonstrating that the anterior portion of lateral articular surface of the paramedian was overlapped by the anteromedial part of the lateral plate.

Another right paramedian plate with this morphology from TMM 31185–97 (Fig. 4D–F; Long and Murry, 1995:fig 60C–D) has part of lateral osteoderm attached. Comparing the shape of the articular surface on the dorsal and ventral sides (Fig. 4D–E) confirms that the anterior part of the articular surface of the paramedian is partially overlapped by the lateral osteoderm. This character is also seen in *Desmatosuchus* and is probably a desmatosuchine synapomorphy differing from the condition in aetosaurines, where the anterolateral portion of the anterior bar of the paramedian plate overlaps the anteromedial surface of the lateral plate.

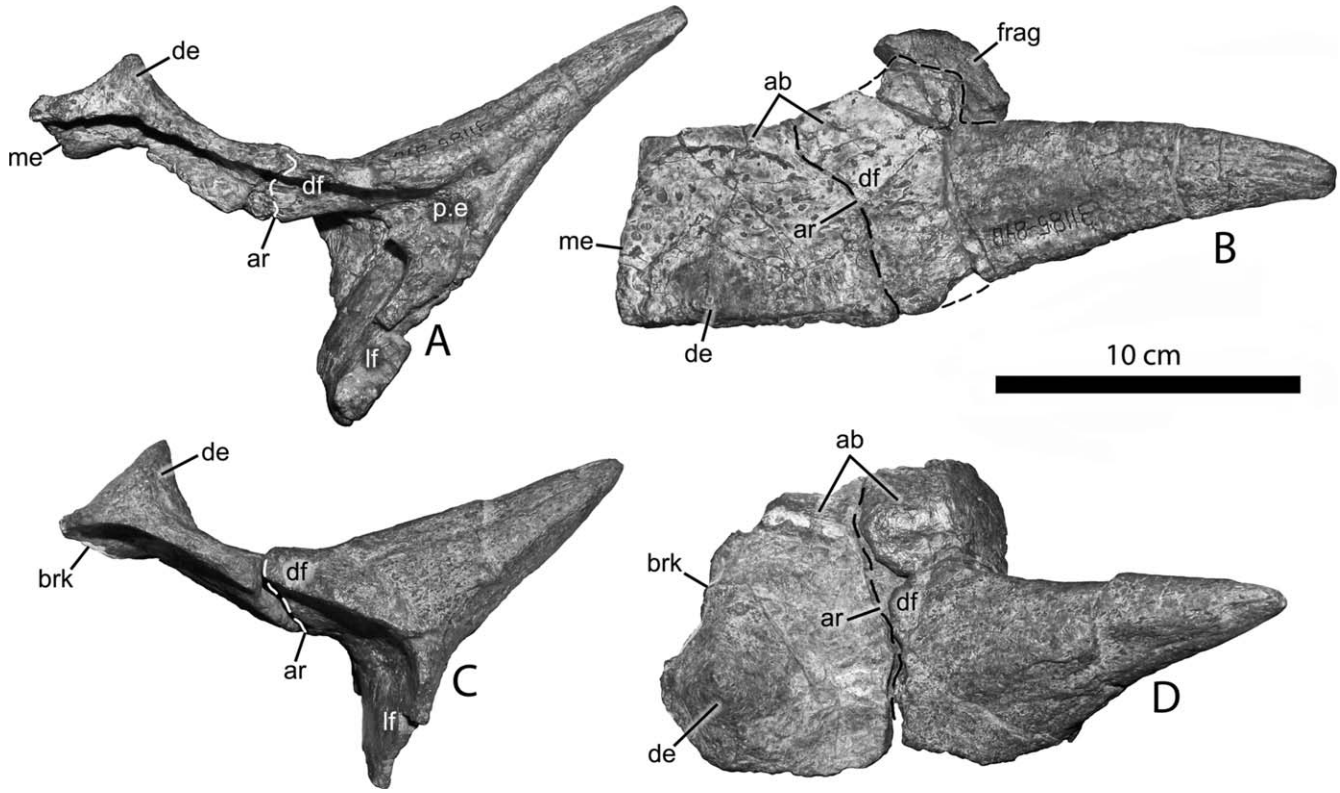

FIGURE 3. Comparisons of posterior cervical or anteriormost dorsal paramedian osteoderms of *Longosuchus meadei* and *Lucasuchus hunti*. Right paramedian osteoderm of *L. meadei* (TMM 31185–84b) in **A**, dorsal view and **B**, posterior view; right paramedian of *L. hunti* (TMM 31185–66) with articulated fragment of lateral osteoderm in **C**, dorsal view and **D**, posterior view. **Abbreviations**: **brk**, broken edge; **df**, dorsal flange of lateral osteoderm; **frag**, unidentified bone fragment; **lf**, lateral flange of lateral osteoderm; **pe**, posterior emargination.

A paramedian plate of *Lucasuchus* (TMM 31100–361; Fig. 5A–B; Long and Murry, 1995:fig. 64A–C) is similar in general form, including having a lateral articular surface that was clearly overlapped anteriorly by the lateral osteoderm, and is probably from the same region. However, this plate differs from those of *Longosuchus* in possessing a very large conical central dorsal eminence, and the plate ornamentation consists of elongate radial grooves and small pits. Both of these features differ from the dorsal paramedians of TMM 31185–97, which have lower, pyramidal eminences that contact the posterior edge, and more random and pitted ornamentation.

The holotype paramedian osteoderm of *Lucasuchus* (TMM 31100–257, Fig. 5C–D; Long and Murry, 1995:fig. 64F–G) is similar in form to TMM 31100–361 except that it is wider, and the lateral articular surface is not as strongly sinuous and does not show evidence of overlap by the lateral osteoderm. Thus, it most likely represents a slightly more posteriorly situated dorsal paramedian.

DISCUSSION

The Presence of Two Morphotypes

We have been able to compare homologous osteoderms from the cervical and anterior dorsal regions of the carapace in different individuals, and thus have been able to substantiate the existence of two morphotypes. These differences clearly demonstrate that the tall, conical, centrally placed eminences, and more radial ornamentation on osteoderms assigned to *Lucasuchus* are not simply due to positional changes (as also argued by Sawin, 1947), but consistently differ in equivalent regions of the carapace from the lower, pyramidal, more posteriorly placed bosses, and more randomly pitted ornamentation of *Longosuchus*. Our study supports, and replicates, the hypothesis of Sawin (1947), Elder (1978), and Long and Murry (1995) that two morphotypes can be differentiated in the Otis Chalk aetosaur material by distinctive characters.

Furthermore, osteoderms referred to *Longosuchus* and *Lucasuchus* are of similar size. This rules out ontogeny as a plausible explanation for the morphological differences, although sexual dimorphism (discussed below) is still a plausible explanation.

Sexual Dimorphism

Elder (1978) suggested that the Otis Chalk aetosaur morphotypes may represent males and females of the same biological species. However, the hunt for osteological means of distinguishing males and females in extant crocodylians has generally failed to identify dramatic differences, other than average size (e.g., Grigg and Gans, 1993; Erickson et al., 2005; Ziegler and Olbort, 2007; Bonnan et al., 2008). Powell (2000) found subtle differences in the morphology of the pelvis and chevrons in *Alligator mississippiensis*, but these elements are not known for *Lucasuchus*, and are poorly preserved in *Longosuchus*. Although this does not rule out the possibility that dramatic and easily identifiable differences between males and females existed in non-crocodylian pseudosuchians, it does mean that the hypothesis of Elder (1978) cannot draw support from comparison with extant pseudosuchians (crocodylians).

The only other evidence for sexual dimorphism is the fact that the *Longosuchus* and *Lucasuchus* morphotypes co-occur in the same quarries, and therefore coexisted both geographically

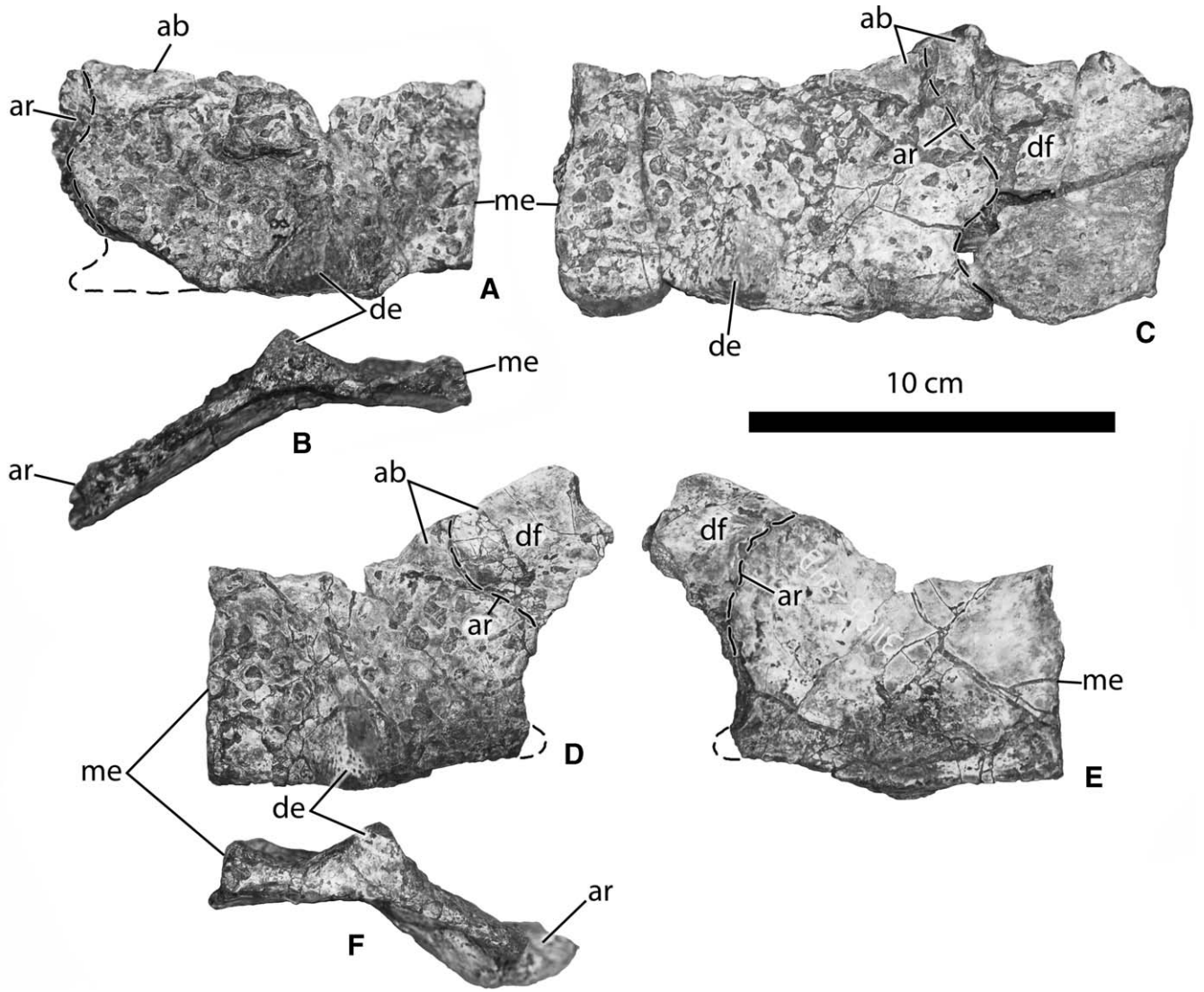

FIGURE 4. Dorsal paramedian osteoderms of the holotype of *Longosuchus meadei* (TMM 31185–84b). Isolated left dorsal paramedian in **A**, dorsal view and **B**, posterior view; **C**, right dorsal paramedian with articulated dorsal flange of lateral osteoderm in dorsal view. Isolated paramedian osteoderm with articulated dorsal flange lateral osteoderm in **D**, dorsal view, **E**, ventral view, and **F**, posterior view. Dashed lines show edge of articular surface for lateral osteoderm, and reconstructed broken posterolateral corners. **Abbreviations**: **ab**, anterior bar; **ar**, articular surface for lateral osteoderm; **de**, dorsal eminence or 'boss'; **me**, medial edge.

and (presumably) temporally, as was used to argue for sexual dimorphism in the phytosaur taxa *Pseudopalatus buceros* and *P. pristinus* (Colbert, 1947; Zeigler et al., 2002). Long and Murry (1995) pointed out that the majority of the *Longosuchus* and *Lucasuchus* material was recovered from different quarries, *Longosuchus* from TMM 31185 and *Lucasuchus* from TMM 31100; however, both taxa are represented in both quarries, demonstrating that they were clearly contemporaneous. Unfortunately, because neither taxon is known in western North America outside of the Otis Chalk localities, it is impossible to demonstrate if they consistently co-occur stratigraphically, as should be expected for sexual dimorphs. Moreover, osteoderms referable to *Lucasuchus* (e.g., AMNH 2799; Fig. 6) have been recovered from Upper Triassic rocks in North Carolina where *Longosuchus* is not currently known (Long and Murry, 1995).

Additionally, other Upper Triassic vertebrate quarries contain multiple aetosaur taxa with strong morphological differences that are not considered by any workers to represent sexual dimorphs, such as *Desmatosuchus* and *Calyptosuchus* from the *Placerias* Quarry, and *Desmatosuchus*, *Paratypothorax*, and *Typothorax* from the Post Quarry (Small, 1989; Long and Murry, 1995), and *Typothorax* and *Rioarribasuchus* from the Snyder Quarry (Heckert et al., 2003). Therefore, the stratigraphic co-occurrence of aetosaur morphotypes does not necessarily indicate sexual dimorphism.

In summary, there is no direct morphological or stratigraphic evidence that *Longosuchus* and *Lucasuchus* are sexual dimorphs, and this possibility must be considered strictly speculative. We prefer at this time to simply say that they are distinct morphological taxa with their own unique character suites.

Referred Material and Biochronology

The lithostratigraphic and biostratigraphic correlation of the Dockum Group in Howard County, West Texas, has been controversial. Lucas and Hunt (1993) and Lucas (1998b)

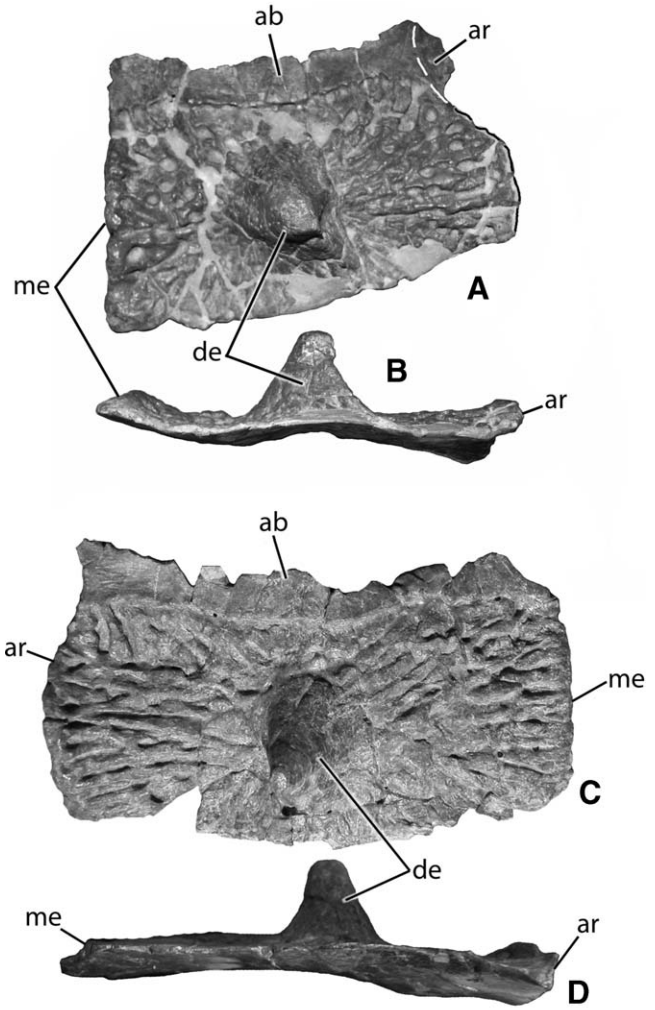

FIGURE 5. Paramedian osteoderms of *Lucasuchus hunti*. Dorsal paramedian osteoderm (TMM 31100–361) in **A**, dorsal view and **B**, posterior view; holotype dorsal paramedian (TMM 31100–257) in **C**, dorsal view and **D**, anterior view. **Abbreviations**: **ab**, anterior bar; **ar**, articular surface for lateral osteoderm; **de**, dorsal eminence or 'boss'; **me**, medial edge.

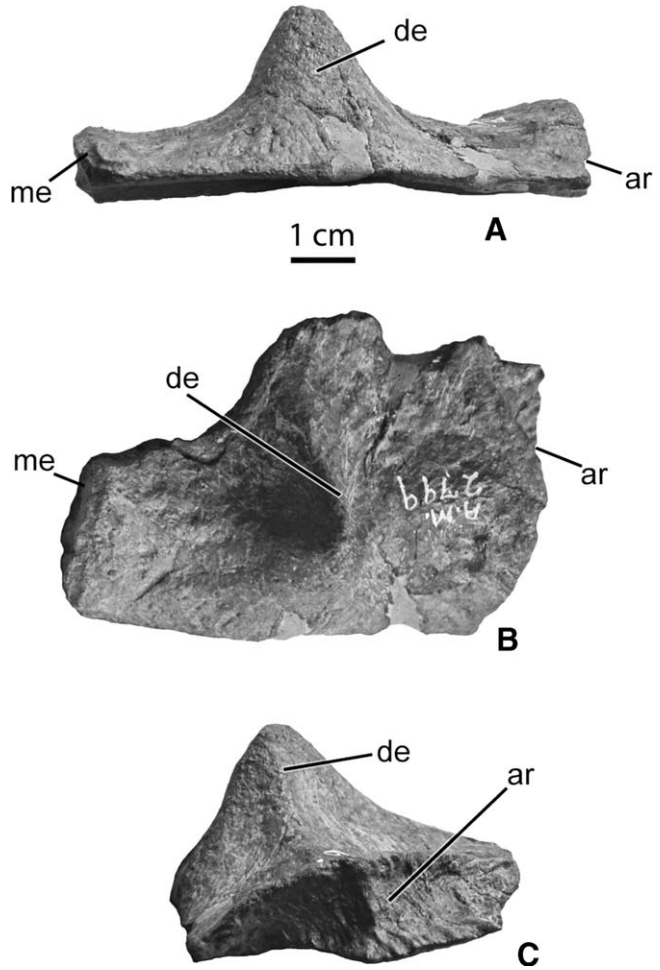

FIGURE 6. Right paramedian osteoderm of *Lucasuchus hunti* (AMNH 2799) in **A**, posterior, **B**, dorsal, and **C**, lateral views. **Abbreviations**: **ab**, anterior bar; **ar**, articular surface for lateral osteoderm; **de**, dorsal eminence or 'boss'; **me**, medial edge.

considered these strata, which they called the Colorado City Member, to be contemporaneous with the vertebrate faunas in the very lowermost strata of the Chinle Formation and Dockum Group elsewhere in the western United States as part of the Otischalkian land-vertebrate faunachron. However, Lehman (1994) and Lehman and Chatterjee (2005) assigned these strata to the Cooper Canyon Formation, which they correlated lithostratigraphically to strata in eastern New Mexico (the Bull Canyon Formation) containing the type assemblage of the younger Revueltian land vertebrate faunachron (Lucas and Hunt, 1993; Lucas, 1998b). Recently, Martz (2008) concluded that only the upper part of the Cooper Canyon Formation is Revueltian; and that the 'Colorado City Member,' although probably correlating with the lower part of the Cooper Canyon Formation, is probably equivalent to strata containing Otischalkian or slightly younger Adamanian faunas elsewhere.

Longosuchus is considered an index taxon of the Otischalkian (Hunt and Lucas, 1993; Lucas, 1998; Lucas et al., 2007; but also see Langer, 2005; Martz, 2008; and Rayfield et al., 2005, 2009), with referred specimens used to correlate eastern and western North America to North Africa (Lucas, 1998a, 1998b); however, our revisions of *Longosuchus* and *Lucasuchus* require a reexamination of this material.

Hunt and Lucas (1990) referred a fragmentary osteoderm (NMMNH P-11005) from the Salitral Shale Member of the Chinle Formation of New Mexico to *Longosuchus*. Lucas et al. (2003) later referred this specimen to *Desmatosuchus haplocerus*. However, the specimen does not possess any clear characters of either taxon (Long and Murry, 1995; Parker, 2003, 2008), and may in fact represent a paratypothoracisine aetosaur (Irmis, 2008:166–167).

Hunt and Lucas (1990) also referred several osteoderms (e.g., AMNH 2799; Fig. 6) from the Pekin Formation of North Carolina to *Longosuchus*. These referrals provided a hypothesized correlation between the Pekin Formation and the Dockum Group of Howard County, West Texas (the '*Longosuchus* biochron' of Hunt and Lucas, which is effectively equivalent to the Otischalkian). Long and Murry (1995) considered the AMNH specimens to belong to *Lucasuchus hunti*, which is supported by the presence of distinct conical eminences. However, because *Lucasuchus* co-occurs with *Longosuchus* at the Otis Chalk quarries, this re-identification does not nullify the proposed correlation of Hunt and Lucas (1990) and Lucas and Hunt (1993), just the use of

Longosuchus as the index taxon as noted by Lucas and Heckert (1996).

Lucas (1998a) referred several lateral osteoderms from Morocco to *Longosuchus*, arguing for global utility as an index taxon. However, the Moroccan material consists of osteoderms with dorsoventrally compressed, slightly recurved lateral horns, which are more consistent with paratypothoracisine aetosaurs than with *Longosuchus* (Parker, 2007). The occurrence of either *Longosuchus* or *Lucasuchus* outside of North America cannot be substantiated at this time.

In summary, *Longosuchus* is currently restricted to a single, small geographical area (the Otis Chalk quarries in the Dockum Group of Howard County, West Texas), and currently has no utility as an index taxon for biochronology. However, *Lucasuchus* is known from both the Dockum Group of Howard County and the Pekin Formation of North Carolina, suggesting possible biochronologic correlation between these units as advocated by Lucas and Heckert (1996) and Heckert and Lucas (2000).

CONCLUSIONS

Reexamination demonstrates that there are two distinct morphotypes in the Otis Chalk aetosaur material and differences in homologous osteoderms from *Longosuchus* and *Lucasuchus* strongly suggest that they are distinct taxa (Sawin, 1947; Long and Murry, 1995; contra Hunt and Lucas, 1990; Lucas and Heckert, 1996; Heckert and Lucas, 1999, 2000). Although the possibility exists that the two taxa represent sexual dimorphs (as postulated by Elder, 1978), it cannot be supported using either comparisons with modern pseudosuchian archosaurs or comparable stratigraphic ranges; therefore we treat the differences between these aetosaurs as being taxonomic.

Because occurrences of *Longosuchus* are restricted to a small, geographical area, it is not suitable as an index taxon for biochronology. *Lucasuchus* is known from two distinct localities and therefore may be of limited biochronological use between eastern and western North America (Heckert and Lucas, 2000).

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