

A NEW SPECIES OF *DESMATOSUCHUS* (ARCHOSAURIA: AETOSAURIA) FROM THE UPPER TRIASSIC OF THE CHAMA BASIN, NORTH-CENTRAL NEW MEXICO

KATE E. ZEIGLER, ANDREW B. HECKERT and SPENCER G. LUCAS

New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104-1375

Abstract—We describe a new species of the aetosaur *Desmatosuchus*, *D. chamaensis*, from the Upper Triassic Snyder quarry, Petrified Forest Formation of the Chinle Group, Chama basin of north-central New Mexico. *D. chamaensis* is also present in the Bull Canyon Formation of east-central New Mexico. *D. chamaensis* is distinguished from the type and only other species of *Desmatosuchus*, *D. haplocerus*, by the presence of long recurved spikes on the dorsal scutes as well as small recurved spikes that are pyramidal in cross-section on the lateral scutes. *Desmatosuchus* is now a more robust index fossil, as *D. haplocerus* ranges from Otischalkian to earliest Revueltian, whereas *D. chamaensis* is an index fossil of the Revueltian. The evolution of *D. haplocerus* into the more spinous *D. chamaensis* is most parsimoniously interpreted as anagenetic.

Keywords: Aetosaur, *Desmatosuchus*, anagenesis, Petrified Forest

INTRODUCTION

The Late Triassic Snyder quarry, located in north-central New Mexico near Ghost Ranch, has produced a remarkable array of fossil vertebrates (Heckert et al., 1999, 2000). This locality, in the Petrified Forest Formation of the Chinle Group in the Chama River basin (Fig. 1), is the richest and most diverse Chinle bonebed discovered in the last 50 years. Tetrapod taxa recovered from the quarry include the aetosaur *Typhothorax coccinarum*, *Pseudopalatus*-grade phytosaurs, the theropod *Eucoelophysis*, and a species of the aetosaur *Desmatosuchus* that is distinctly different from the species *D. haplocerus* first identified by Cope (1892). Here, we describe this new species of *Desmatosuchus*. NMMNH = New Mexico Museum of Natural History, Albuquerque, and UCM = University of Colorado Museum, Boulder.

SYSTEMATIC PALEONTOLOGY

Superorder ARCHOSAURIA Cope, 1869

Order CROCODYLOTARSI Benton and Clark, 1988

Suborder AETOSAURIA Nicholson and Lydekker, 1889

Family STAGONOLEPIDIDAE Lydekker, 1887

Subfamily DESMATOSUCHINAE Huene, 1942

Genus *Desmatosuchus* (Cope, 1892)

Desmatosuchus chamaensis, new species

(Fig. 2)

1985 *Desmatosuchus* sp.: Carpenter and Parrish, p. 197-198

1986 *Desmatosuchus* sp.: Parrish and Carpenter, p. 152, fig. 11.3

1994 *Desmatosuchus* sp.: Hunt, p. 278, fig. 37A.

Holotype: NMMNH P-32793 (Fig. 2D), an incomplete right presacral paramedian scute.

Paratypes: NMMNH P-32795 (Fig. 2A-B), a nearly complete right presacral paramedian scute; NMMNH P-32797 (Fig. 2E), a right presacral paramedian scute; NMMNH P-31295 (Fig. 2F), a right lateral scute; NMMNH P-32796 (Fig. 2G), a left lateral scute; NMMNH P-33099, an incomplete left cervical or presacral paramedian (Fig. 2J); and NMMNH P-33100, a third lateral cervical horn (Fig. 2K-L); NMMNH P-29045, an incomplete right? cervical lateral scute.

Type horizon and locality: Petrified Forest Formation of

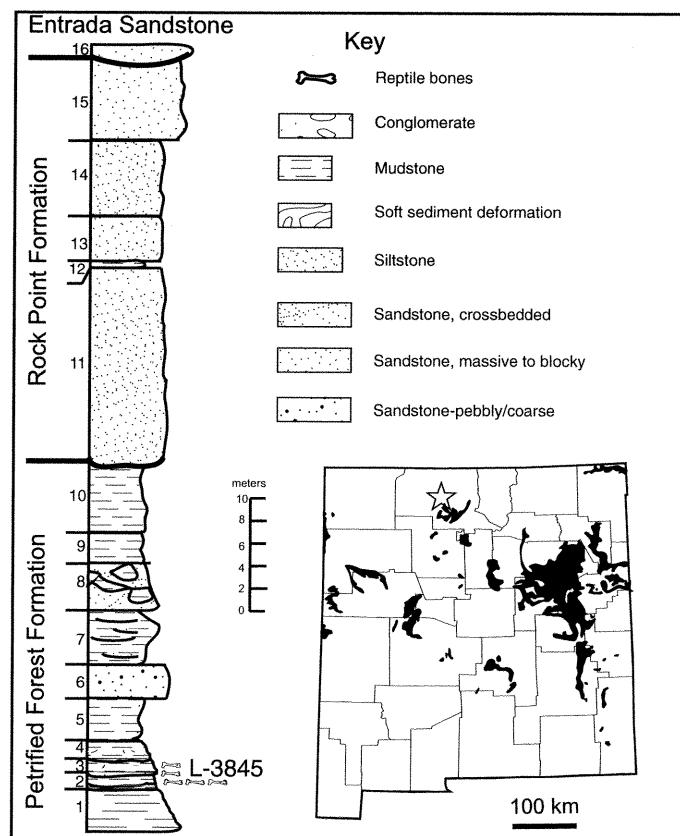


FIGURE 1. Index map and measured stratigraphic section of the type locality of *D. chamaensis*. Shading on state map is Triassic outcrops.

the Chinle Group at NMMNH locality 3845, northwest of Abiquiu in Rio Arriba County, New Mexico. The quarry is approximately 60 m below the base of the Entrada Sandstone and 28 m below the Rock Point Formation of the Chinle Group (Fig. 1). The locality is mid- to late Norian in age (~215 Ma) and is within the Revueltian faunachron based on the presence of the index fossils *Typhothorax coccinarum* and *Pseudopalatus* (Lucas, 1998).

Referred specimens: From the Bull Canyon Formation in

east-central New Mexico: UCM-47725, a right cervical paramedian scute (Parrish and Carpenter, 1986, fig. 11.3; Hunt, 1994, fig. 37A) (Fig. 2I-H); NMMNH P-4894, an incomplete recurved spike from a cervical scute (Fig. 2C).

Diagnosis: *D. chamaensis* is distinguished from *D. haplocerus* by differences in the morphology of the paramedian and lateral scutes. The paramedian scutes in *D. chamaensis* possess a long, strongly recurved spike, whereas the same scutes in *D. haplocerus* lack a recurved spike, though they possess a boss at the same place on the scute body. The recurved spike on the lateral scutes of *D. chamaensis* are gracile compared to the size of the scute body, whereas the lateral spikes in *D. haplocerus* are robust. The lateral cervical scutes of *D. chamaensis* are relatively gracile compared to those of *D. haplocerus*.

Etymology: Named for the Chama River basin in north-central New Mexico where the Snyder quarry is located.

DESCRIPTION

The holotype, NMMNH P-32793 is a nearly complete right presacral paramedian scute with a small, posteriorly recurved spike and an ornamentation pattern of deep pits and ridges radiating from the spike (Fig. 2D). The posterior edge of the specimen is missing. The scute is 8.3 cm long and 18.4 cm wide. The spike is 6.5 cm long, with the tip missing, and it is broken at the base and crushed down into the scute body. This spike is smooth in the basal region and bears small foramina and a groove towards the tip. The spike is also sharply recurved, and its shape is approximately conical. The ventral aspect of this scute is smooth and relatively flat and has a small depression corresponding to the dorsal spike.

NMMNH P-32795 is a mostly complete presacral paramedian scute from the right side of the body (Fig. 2A). It has a long, sharply recurved spike projecting from the right half of the scute body with a strong ridge-and-groove pattern radiating from the spike. The scute is 10.5 cm long, and 8.8 cm wide with a spike measuring 11.0 cm, minus the tip. The spike is smooth in the basal region and bears small foramina towards the tip, together with a thin groove on the dorsal surface of the spike. The spike is sharply recurved, with a conical shape. The posterior margin is broken and missing the medial portion. The ventral surface is smooth, has a very low degree of curvature, and has a small depression where the spike projects from the dorsal side (Fig. 2B).

NMMNH P-32797 is a right presacral paramedian that is nearly complete (Fig. 2E). This specimen does not have a recurved spike, but instead has a low boss with a very rugose surface near the center. This boss does not contact the posterior margin of the scute. The ornamentation consists of irregular, shallow pits and long, similarly irregular grooves and ridges radiating from the boss. The scute is 7.0 cm long and 14.1 cm wide. The ventral surface is flat and smooth and lacks a depression corresponding to the boss.

NMMNH P-31295 is a nearly complete right lateral scute with a small, recurved spike in the center of the scute body (Fig. 2F). The ornamentation is less distinct than on the dorsal scutes, consisting of shallow ridges and grooves radiating from the spike. The scute body has a greater degree of curvature than any of the paramedian scutes, but is still flatter than those of any other spiked

aetosaur. The scute is 7.5 cm long and 8.9 cm wide. The spike is 5.5 cm long and is small and very sharply recurved. The surface of the spike is heavily pitted, and the shape is pyramidal due to the presence of a thin ridge along the anterodorsal surface of the spike. The ventral surface of the scute is flat and smooth with only a very faint depression corresponding to the spike. The scute has an obtuse angle of curvature.

NMMNH P-32796 is a well-preserved left lateral scute (Fig. 2G) that is slightly smaller than NMMNH P-31295. Like NMMNH P-31295, it is slightly angled and possesses a sharp anterior edge on the spike. The scute also has a small, recurved spike and a faint ornamentation of ridges and grooves. The scute body is 7.9 cm long and 8.3 cm wide. The spike is 4.5 cm long, although it has been broken in several places. The surface is lightly pitted compared to NMMNH P-31295, but also has the same pyramidal shape due to the anterodorsal ridge. The ventral surface of the scute is very smooth with a faint depression, and the scute body has a wide angle of curvature.

NMMNH P-33099 is a partial left cervical or presacral paramedian scute possessing a long recurved spike that has been crushed down into the scute body (Fig. 2J). This scute possesses a flat base and has the distinct irregular ridge-and-groove pattern seen on the other paramedian scutes. The scute is 14.1 cm long and 10.6 cm wide, with a preserved spike length of 9.0 cm (the tip is missing). The spike is also smooth in the basal region, with foramina and a faint groove developed near its end. The spike is nearly conical in shape, but has been depressed down against the body of the scute. The ventral surface is smooth, with a small pit corresponding to the dorsal spike.

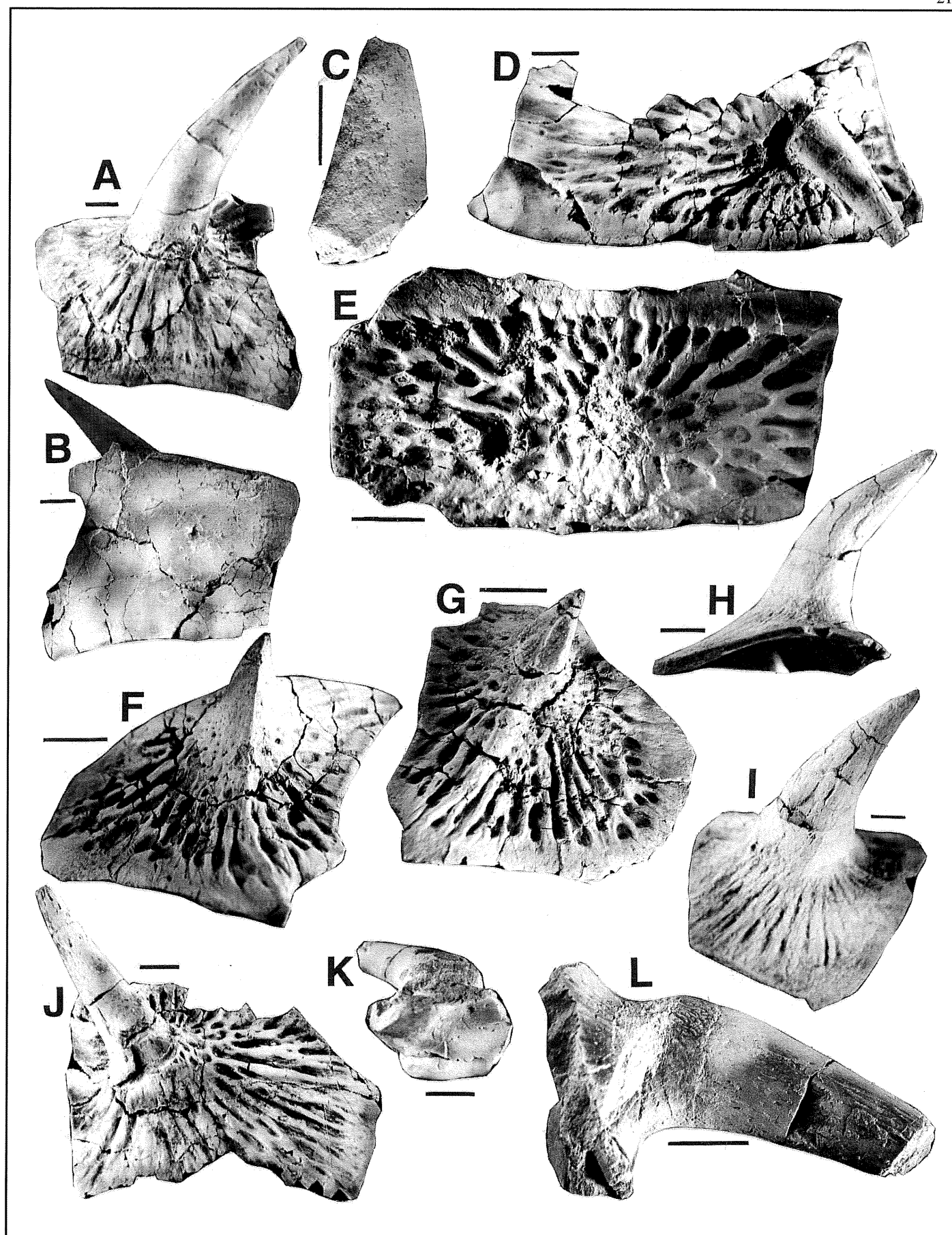
NMMNH P-33100 is a third lateral cervical spike that is missing the scute body and the tip of the spike (Figs. 1K-L). The horn is 7.3 cm long, minus the tip, and is smooth, although the base is quite rugose. Very faint grooves are present along the dorsal and ventral sides of the spike. The bone surface itself is in poor shape and flakes off easily, obscuring surficial morphology. The spike is generally oval in cross-section.

The final paratype specimen we identify here, NMMNH P-29045 is an incomplete right? cervical scute. The preserved portion of the spike measures 6.4 cm in length. The scute is broken anteriorly and posteriorly, and measures approximately 2.9 cm tall. The spike is oval in cross-section. There is a small foramen on the ventral surface corresponding to the spike.

We interpret UCM-47725 as a right paramedian scute (Fig. 2I), in excellent condition, with a sharply recurved spike (Fig. 2H). This spike is slightly shorter than that of NMMNH P-32795. The irregular ridge and groove pattern is less distinct than NMMNH P-32795, but is still apparent. The scute is 9.7 cm long and 8.5 cm wide with a 9.5 cm-long recurved spike with an essentially flat base. The spike is smooth in the basal region with foramina developing towards the tip of the spike and is conical in cross-section. The ventral surface is smooth with a faint depression below the spike. Parrish and Carpenter's (1986, fig. 11.3) drawing of this scute misrepresents the degree of curvature of the spike and its size relative to the scute body.

NMMNH P-4894 is a portion of a recurved spike from a paramedian scute (Fig. 2C). The spike has a ridge along the anterior side, creating an oval to triangular cross-section. This fragment is 5.5 cm long and is missing both the tip and the body of

FIGURE 2. (Opposite page) Dorsal paramedian and lateral scutes from *D. chamaensis*: **A-B**, Paratype, NMMNH P-32795, right paramedian scute in **A**, dorsal and **B**, ventral views; **C**, Referred specimen, NMMNH P-4894, portions of recurved spike from a cervical scute in lateral view; **D**, Holotype, NMMNH P-32793, right presacral paramedian scute, in dorsal view; **E**, Paratype, NMMNH P-32797, right presacral paramedian scute in dorsal view; **F**, Paratype, NMMNH P-31295, right lateral scute in dorsal view; **G**, Paratype, NMMNH P-32796, left lateral scute in dorsal view; **H-I**, Referred specimen UCM-47725, right paramedian scute, in **H**, lateral and **I**, dorsal views; **J**, Paratype, NMMNH P-33099, left paramedian scute in dorsal view; **K-L**, Paratype, NMMNH P-33100, third lateral cervical horn in **K**, ventral and **L**, dorsal views. Scale bars = 2 cm.



In general, the scutes of *D. chamaensis* display the same pattern of ornamentation and overall shape as the scutes of *D. haplocerus* (Case, 1920, 1922, figs. 7-20, pl. 5-10; Gregory, 1953, figs. 1-14; Long and Ballew, 1985 p. 47-50, figs 2-7, pl. 1; Long and Murry, 1995, p. 89-99, fig. 88; Heckert and Lucas, 2000, p. 1555-1561, fig. 6a-c). In particular, the lateral scutes have a very low angle of curvature as they wrap around the body of the animal. The scutes of both species are ornamented with a pattern of ridges that radiates from the spike in the lateral and cervical scutes and from the boss on the presacral dorsal scutes. The width-to-length ratio of the presacral paramedian scutes is approximately 2:1 in both species, and the scutes lack the prominent anterior bar seen in all other aetosaur genera. They do, however, have anterior laminae, an autapomorphy of *Desmatosuchus*. Therefore, the scutes of *D. chamaensis* are justifiably assigned to *Desmatosuchus*.

These scutes lack the strong anterior bar and random pitting ornamentation as well as the mediolateral expansion of the dorsal scutes seen in *Typothorax*. The lateral scutes of *Typothorax* are acute in their angle of curvature and lack the prominent recurved spikes seen in *Desmatosuchus* (Long and Murry, 1995, p. 99-108, fig. 100). The scutes of *D. chamaensis* differ from those of *Paratypothorax* in that they do not have the long ray-like ornamentation and lack the large eminences seen on the posterior dorsal sacral and anterior caudal scutes of *Paratypothorax*. Further, eminences of *Desmatosuchus* do not contact the posterior margin of the scute, unlike those of *Paratypothorax* or *Stagonolepis*. The scutes of *Desmatosuchus* are also not expanded mediolaterally (Long and Murry, 1995, p. 108-114, fig. 113; Heckert and Lucas, 2000).

The most distinctive features of *D. chamaensis* lie in the paramedian scutes and in the presacral lateral scutes. As we have discussed previously, no other aetosaur has such prominent spikes on its paramedian scutes. These spikes are largest on scutes we interpret as anterior paramedian scutes, and are more reduced on wider scutes, such that there is an inverse ratio of absolute spike height to scute width. The presacral lateral scutes in both species of *Desmatosuchus* possess recurved spikes. However, the spikes on the lateral scutes of *D. chamaensis* are pyramidal in shape, with an edge along the anterior side of the spike, whereas the lateral scutes of *D. haplocerus* are round or ovoid in cross-section.

The ornamentation on the scutes of *D. chamaensis* is also different from that of *D. haplocerus*. Scutes of *D. chamaensis* possess a strongly radial, deep ridge-and-groove pattern, whereas those of *D. haplocerus* have deep semi-circular pits that are only faintly radial in arrangement. While the anterior paramedian scutes and the dorsal lateral scutes differ significantly from those of *D. haplocerus*, the posterior presacral paramedian scutes show no immediately obvious differences. The paramedian scutes of both species have a faint boss near the medial edge of the scute, making identification of species difficult based solely on a presacral paramedian scute.

The scutes of *D. chamaensis* from the Snyder quarry are part of an extensive Upper Triassic bonebed that consists primarily of disarticulated, partially associated fossil material. Seven of the scutes described here were removed from an area approximately one square meter in size. Given that these seven scutes were found in close association with one another, we assume that they be-

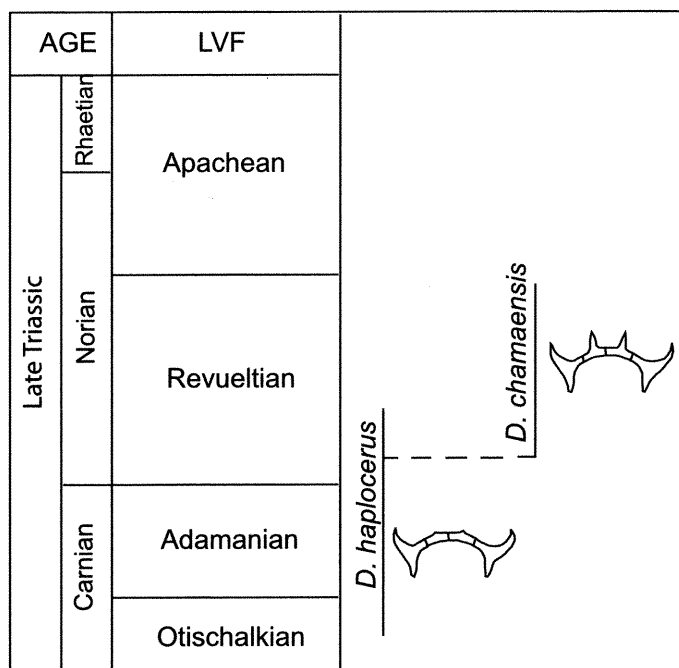


FIGURE 3. Species-level phylogenetic tree of *Desmatosuchus* with pectoral cross-sections through both species. Note temporal overlap of *D. haplocerus* (Otischalkian to early Revueltian) with *D. chamaensis* (early to late Revueltian).

longed to a single individual that was disarticulated by decay and scavenging prior to burial. Indeed, evidence of scavenging is present on specimen NMMNH P-32797 in the form of two subcircular puncture marks, probably caused by a phytosaur or similar predator biting down onto the scute (Fig. 2E).

D. haplocerus is most abundant in strata of Adamanian (latest Carnian) age. Some isolated scutes of *D. chamaensis* were previously reported from Revueltian strata and simply assigned to *Desmatosuchus* sp. (Carpenter and Parrish, 1985; Parrish and Carpenter, 1986; Hunt 1994). Upon re-examination of these specimens, it is clear that they belong to *D. chamaensis*. The *Desmatosuchus* scutes that were discovered at the Snyder quarry in previous seasons of excavation were initially assigned to *D. haplocerus*. We incorrectly described their occurrence in these mid-Revueltian strata as an age-range extension for *D. haplocerus*, although we did recognize the possibility that they represent a new species (Zeigler et al., 2000).

Small (1985, 1989) described specimens he assigned to *D. haplocerus* from the early Revueltian Post quarry in the Bull Canyon Formation of West Texas. We agree that this early Revueltian occurrence is of *D. haplocerus*, so this is the youngest record of the species. With an age range from the Otischalkian through Revueltian (Carnian through mid-Norian), *D. haplocerus* made a very poor index fossil. However, with further excavation of the Snyder quarry this past summer, scutes were discovered that are distinct from *D. haplocerus*.

Therefore, we now recognize the occurrence of two successive species of *Desmatosuchus* in the fossil record, *D. haplocerus* (Otischalkian-early Revueltian) and *D. chamaensis* (early to mid-Revueltian) (Fig. 3). *Desmatosuchus* developed a more spinous carapace in the Revueltian, although the reasons for this adaptation are not immediately evident. In *D. haplocerus*, recurved spikes occur along the lateral margins of the animal's body, with a series of much larger lateral recurved spikes occurring in the cervical region, particularly on the fourth and fifth lateral scutes. As *D. haplocerus* evolved into *D. chamaensis*, the genus added sharply

recurved spikes to the dorsal cervical scutes as well as shifted the shape of the lateral spikes from conical to pyramidal by adding a distinct ridge to the anterior edge of the spike. The discovery of this new species provides us with a unique view of a species-level transition in the fossil record of aetosaurs. Indeed, most other aetosaur genera are monotypic. The exceptions, *Stagonolepis* and *Aetosaurus*, consist of two or more species that co-occur and which are readily distinguished by size (Heckert and Lucas, 2000).

D. haplocerus records in the Chinle Group range in age from Otischalkian to early Revueltian; *D. chamaensis* records range from early to late Revueltian (Fig. 3). The simplest interpretation of this pattern is to argue that *D. haplocerus* and *D. chamaensis* form an ancestor-descendant lineage in which there is a short interval (early Revueltian) of temporal overlap. Superficially, this fits the pattern of punctuated equilibrium, but the fossil records of *D. haplocerus* and *D. chamaensis* are not extensive enough to document morphological stasis of either species. What is more signifi-

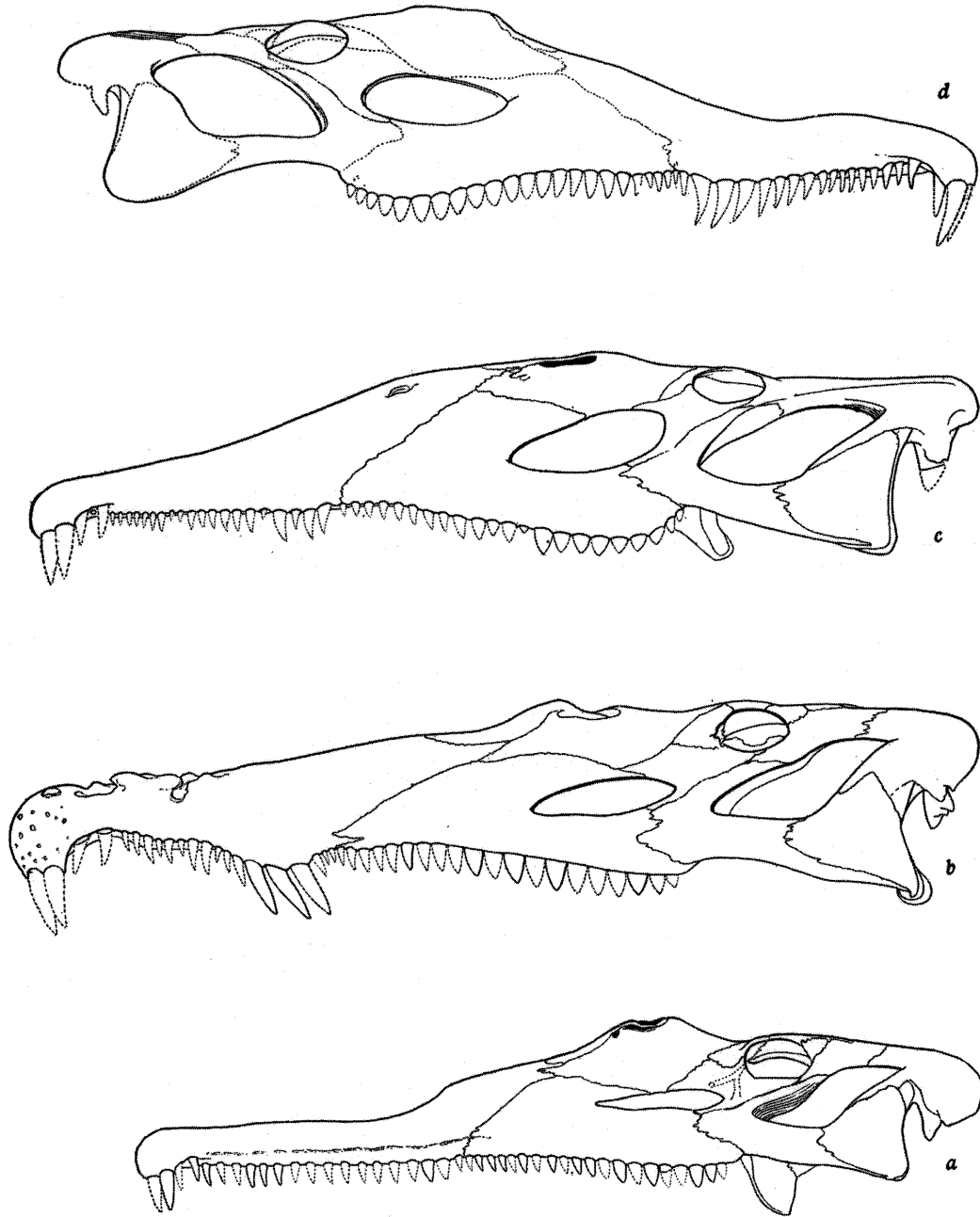
cant is that the record suggests anagenetic evolution in an aetosaur species lineage. Indeed, the data do not support cladogenesis in the species-level evolution of *Desmatosuchus*.

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Adult *Machaeroprotopus* skulls of four species, x1/9. a. *M. adamanensis* (type), 7038/26699. b. *M. gregorii*, (type) A270/27200. c. *M. lithodendrorum* (type), 7034/26688. d. *M. tenuis* A257/27149 (from Camp, 1930, fig. 11, p. 40).