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Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*

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A new specimen of *Desmatosuchus* from northeastern Arizona (MNA V9300) preserves almost the entire vertebral column, the pelvis, and the majority of the armor carapace, allowing for an unprecedented detailed description of the taxon. Articulation and reconstruction of the armor carapace demonstrates that previous reconstructions of *Desmatosuchus* are erroneous in the orientation and position of the lateral armor. Lateral plates of the anterior dorsal region possess low rounded knobs instead of developed spines. The dorsal flange of the lateral plates of the dorsal region is longer than the lateral or ventral flange making the carapace transversely wider than previously thought. As a result, previous reconstructions articulate the lateral armor not only backwards but also on the wrong sides of the body. Posterior presacral vertebrae are extremely robust and possess fused ribs and the last presacral vertebra has been fused to the sacrum, a character that may be taxonomically useful. A prefrontal bone is also present in *Desmatosuchus*, contrary to previous descriptions. Reinvestigation of the genus *Desmatosuchus* suggests that there are only two valid species, *D. spurensis* and *D. smalli*. The lectotype of *Episcoposaurus haplocerus* is referable to *Desmatosuchus* but indeterminate at the species level, and therefore represents a nomen dubium. Accordingly, *D. spurensis* is reinstated as the type species of *Desmatosuchus* and the new Arizona specimen is assigned to this taxon. *Acaenasuchus geoffreyi*, a purported juvenile form of *Desmatosuchus*, is not referable to *Desmatosuchus*.

INTRODUCTION

Aetosauria is a monophyletic clade of quadrupedal, heavily armored, suchian archosaurs known exclusively from Upper Triassic strata worldwide. Aetosaurs are characterized by their elaborate armor carapace that consists of four columns of plates covering the dorsal surface of the animal. In addition, ventral and appendicular armor is also present in at least some members of this clade. The dorsal armor consists of two paramedian columns of osteoderms (plates) on either side of the midline of the animal, each of which is flanked by an adjacent column of lateral plates. Plates are highly ornamented and the lateral plates of several aetosaur taxa possess pronounced dorsal eminences that sometimes develop into spines. Although first noted by Gregory (1953), Long and Ballew (1985) were the first to discuss the taxonomic utility of aetosaur armor ornamentation, and these ornamentation characters are the main dataset used for the alpha-taxonomy and phylogenetic analyses of the clade. The genus *Desmatosuchus* is characterized mainly by the presence of large recurved "horns" in the lateral armor of the posterior cervical region (Case 1920, 1922, Long and Ballew 1985, Parker 2005a).

In 1997, amateur paleontologist and high school teacher Nancy Mikeson discovered bone fragments eroding out of the Upper Triassic Chinle Formation northeast of Many Farms, Arizona (Fig. 1). Mikeson collected a few fragments including a large partial cervical spine diagnostic of *Desmatosuchus* and subsequently contacted the Museum of Northern Arizona (MNA) about her discovery. In the summer of 1999, a team from the MNA led by Dr. David Gillette collected the remainder of the specimen, which consists of an almost complete vertebral column, a complete pelvis, and a large amount of the armor carapace. The specimen (MNA V9300) is the first relatively complete, associated *Desmatosuchus* skeleton from the Chinle Formation, and gives further insight into the detailed morphology of the animal not provided by previous specimens.

Abbreviations—**ANSP,** Academy of Natural Sciences, Philadelphia, Pennsylvania; **BEGC**, Bureau of Economic Geology Collections, Austin, Texas; **BMNH**, The Natural History Museum, London; **EM**, Elgin Museum, Scotland; **GSM**, Geological Survey Museum, London; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **NMMNH,** New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **PEFO,** Petrified Forest National Park, Arizona; **PVL**, Instituto Miguel Lillo, Tucumán, Argentina; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TMM**, Texas Memorial Museum, Austin, Texas; **TTU,** The Museum of Texas Tech University, Lubbock, Texas; **UCMP,** University of California Museum of Paleontology, Berkeley, California; **UMMP,** University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

TAXONOMIC HISTORY

Cope (1892) described a partial carapace (ANSP 14688) from the Tecovas Formation (Dockum Group) of Texas as *Episcoposaurus haplocerus* Cope. Previously, Cope (1875, 1887) had described two other armored forms, *Typothorax coccinarum* Cope and *Episcoposaurus horridus* Cope, from Upper Triassic strata in New Mexico. Cope considered all of these forms to represent parasuchian archosaurs (phytosaurs).

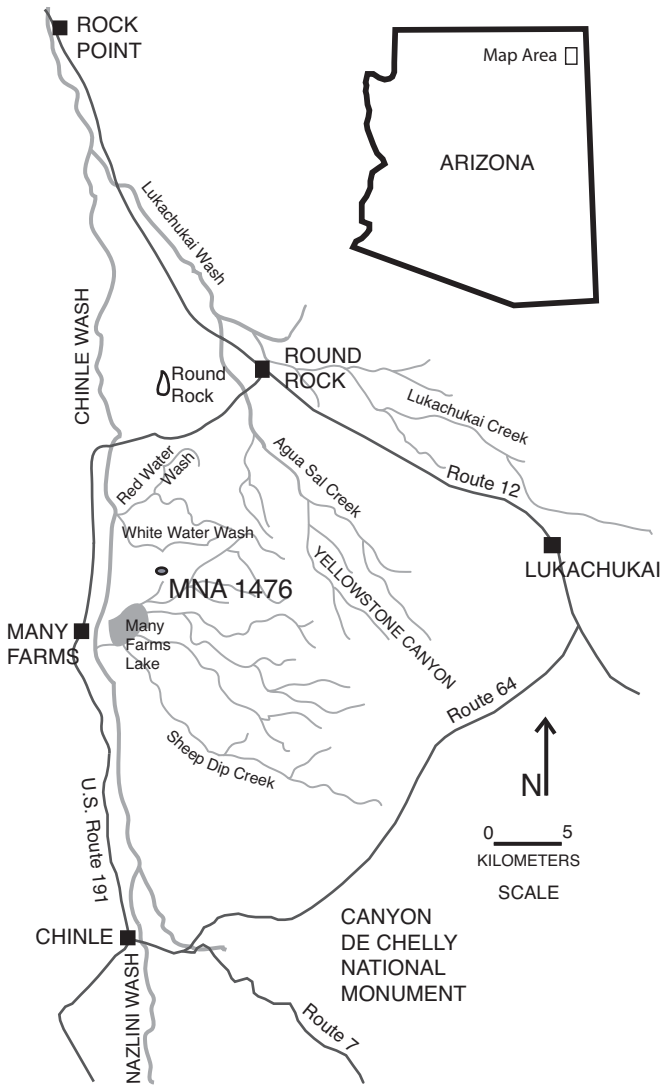


Figure 1. Map showing location of MNA locality 1476.

Case (1920, 1922) described another purported phytosaur, *Desmatosuchus spurensis* Case from the Tecovas Formation of Texas. This material (UMMP 7476) was collected within a few kilometers and at roughly the same stratigraphic horizon as the type specimen of *E. haplocerus*. Gregory (1953) reanalyzed these specimens and concluded that they were not parasuchians, and that *Typothorax coccinarum* and *Episcoposaurus horridus* were synonymous, with *Typothorax* as the senior synonym. Gregory (1953) also determined that *Episcoposaurus haplocerus* and *Desmatosuchus spurensis* were synonymous. Because the genus *Episcoposaurus* was no longer available for the species *haplocerus*, this species was assigned to the next available name, *Desmatosuchus*, and *D. spurensis* was considered a junior synonym of *D. haplocerus*.

Parker (2005a) erected another species of *Desmatosuchus*, *D. smalli* Parker, for material (TTU P-9024) from the Post Quarry of Texas (Cooper Canyon Formation, Dockum Group) that had previously been assigned to *D. haplocerus* (Small 1985, 2002, Long and Murry 1995). Parker (2005a) differentiated *D. smalli* from *D. haplocerus* using characters of the posterior lateral armor as well as several differences of the skull that had previously been discussed in detail by Small (1985, 2002). Zeigler et al. (2002) assigned another species, "*D.*" *chamaensis* Zeigler, Heckert, and Lucas, to *Desmatosuchus* on the basis of armor from the Chinle Formation of north-cental New Mexico. This material was redescribed by Heckert et al. (2003) who reiterated assignment of this taxon to *Desmatosuchus*; however, Parker (2003, 2007) demonstrated that this taxon shares few character states with *Desmatosuchus*, is phylogenetically closer to *Paratypothorax*, and represents a different genus.

GEOLOGICAL SETTING

MNA V9300 was collected from an expansive series of Chinle Formation badlands located approximately 5 kilometers northeast of the town of Many Farms, Arizona (Fig. 1). The site (MNA locality 1496) is in the general vicinity of where Charles Camp of the University of California Museum of Paleontology collected the holotype skeleton of the phytosaur *Leptosuchus gregorii* in 1927 (see map in Camp 1930). The area consists of low hills of variegated siltstone and mudstone capped by a sheet sandstone that Deacon (1990) assigned to the Sonsela Sandstone Bed, which Heckert and Lucas (2002a) and Woody (2003, 2006) recently elevated to member status. At MNA locality 1496, this unit is a trough cross-bedded, medium to coarse-grained sandstone with extrabasinal clasts and petrified wood, a characteristic lithofacies of the Sonsela Member (Woody 2006). Underlying this unit are variegated blue, green, purple, and grey mudstones and siltstones of the Blue Mesa Member. No other units of the Chinle Formation are exposed in the immediate area.

The quarry is in a green-grey mudstone lens of the Blue Mesa Member approximately 17 meters below the base of the Sonsela Member (Fig. 2). The presence of biotite in the matrix suggests a reworked volcaniclastic source for some of the sediment. The mudstone is finely laminated and contains numerous small mud rip-up clasts and is conformably overlain by more than a meter of dark brown pedogenically modified mudstone. There is an erosional contact between the greenish mudstone and an underlying prominent red paleosol. This reddish unit intertongues laterally with a ripple-laminated, fine to medium-grained sandstone. Inclined strata in this unit suggest point bar deposition, whereas ridge and swale topography suggest a scroll bar complex; thus, the quarry likely is in a crevasse splay deposit laterally adjacent to levee and channel facies. The greenish mudstone extends laterally for at least a kilometer. Vertebrate remains are common in this lithofacies and include those of phytosaur, metoposaur, and rauisuchian; however, the only other in-situ bones besides MNA V9300 found in the quarry were two isolated phytosaur teeth and a small reptilian centrum. Several fragments of metoposaur and phytosaur mixed with the surface float appear to be allochthonous as they differ in preservation from the aetosaur remains.

DESCRIPTION OF MNA V9300

Overview

The new specimen, MNA V9300, consists of the partial skeleton of a single large adult. Recovered elements include almost the entire vertebral column, a complete pelvis, and the majority of the dermal armor. The vertebral column is complete from the 3rd presacral through the 12th caudal; however, one or two posterior dorsal vertebrae may be missing and the first six preserved presacrals are fragmentary. The rest of the vertebrae are complete, including neural spines, transverse processes, and articular processes. Many of the vertebrae were in articulation, including the 9th through 14th presacrals and the first six caudals. In addition, numerous caudals from the mid portion of the tail are present.

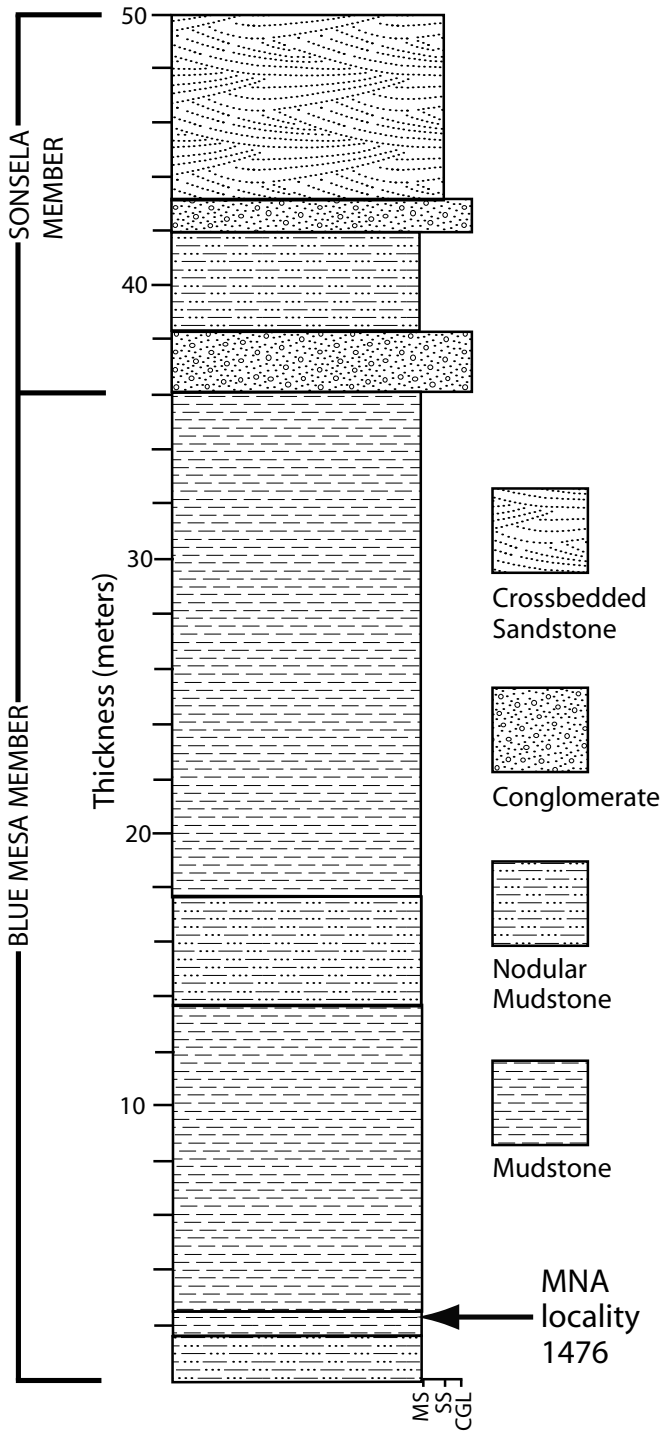


Figure 2. Stratigraphic section at MNA locality 1476 showing level of quarry.

The sacrum is complete and undistorted, possessing both true sacral vertebrae, a fused posterior dorsal vertebra, all four sacral ribs, both ischia, both ilia, and both pubes. All of these elements are solidly fused into a single robust structure.

This specimen includes more than 100 armor plates from the dorsal and lateral regions of the carapace. Almost the entire lateral series from the last cervical through the 12th caudal is present, including the massive recurved cervical spine from the left side. Most of the anterior cervical armor is fragmented or not present; however, most of the recovered plates from the rest of the carapace are complete.

No limb or pectoral elements are present. There are several possible skull fragments from the quarry, but the only identifiable cranial bone collected was the posterior portion of the right mandible. Ribs are represented by several complete dorsal ribs, one cervical rib, and fragments of many others. In addition, numerous chevrons were recovered, some still articulated with their respective vertebrae. It appears that recent weathering of the specimen destroyed the skull and much of the cervical region, vertebrae, ribs, and armor. No limbs or fragments of limbs were recovered, suggesting that transport or winnowing of the carcass occurred prior to burial.

Skull

The skull of *Desmatosuchus spurensis* was described in detail by Case (1920, 1922), Walker (1961), and Small (1985, 2002). The only skull material recovered for MNA V9300 is the posterior portion of the lower right mandible and a dentary fragment, suggesting that the skull was present but lost to erosion prior to discovery. Because the lower jaw of UMMP 7476 is not preserved, and the only other possibly representative mandibular material of *D. spurensis* are isolated elements from the *Placerias* Quarry of uncertain assignment to *Desmatosuchus* (*contra* Long and Murry 1995), this element will be compared with that of TTU P-9024 (*D. smalli*) as described by Small (2002).

This jaw fragment (Fig. 3) contains portions of the four bones that make up the posterior portion of the right mandibular ramus, which is broken just posterior to the external mandibular fenestra. These include the surangular, the posterior portion of the angular, the articular, and the majority of the prearticular. All of these elements are very similar to those figured and described by Small (2002) for TTU P-9024. The mandible is long and shallow in contrast to the short, high mandibles of *Longosuchus* and *Neoaetosauroides* (Parrish 1994, Desojo and Baez 2005). The posterior surangular foramen is present along the upper lateral edge

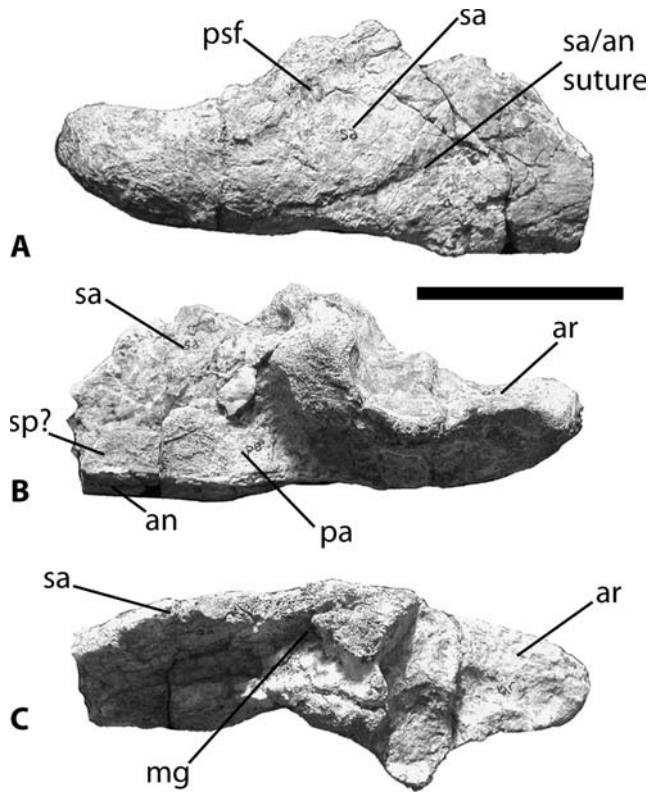


Figure 3. Posterior right mandible of MNA V9300. **A.** Lateral view. **B.** Medial view. **C.** Dorsal view. Abbreviations: **an**, angular; **ar**, articular; **mg**, meckelian groove; **pa**, prearticular; **psf**, posterior surangular foramen; **sa**, surangular; **sp**, splenial. Scale bar = 5 cm.

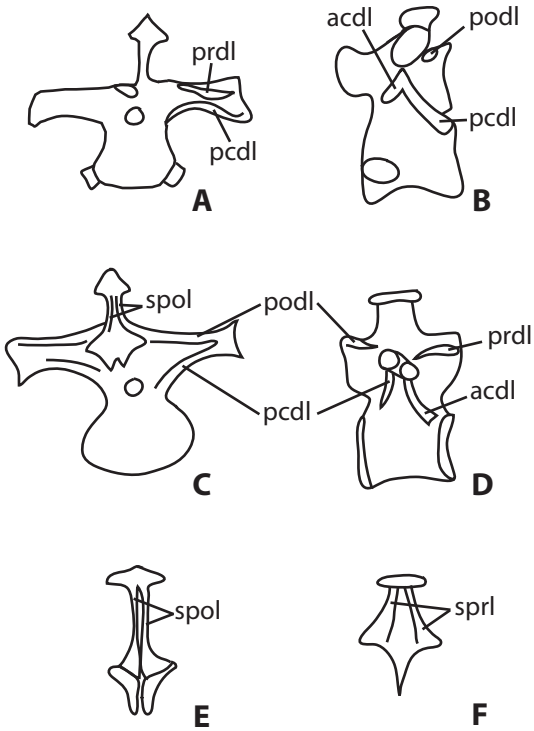


Figure 4. Vertebral laminae in aetosaurs. **A.** Posterior cervical in anterior view. **B.** Posterior cervical in left lateral view. **C.** Posterior cervical in posterior view. **D.** Anterior dorsal in right lateral view. **E.** Neural spine from dorsal region in anterior view. **F.** Neural spine from dorsal region in posterior view. Figures not drawn to scale. Abbreviations: **acdl,** anterior centrodiapophyseal lamina; **pcdl,** posterior centrodiapophyseal lamina; **podl,** postzygodiapophyseal lamina; **prdl,** prezygodiapophyseal lamina; **spol,** spinopostzygopophyseal lamina; **sprl,** spinoprezygopophyseal lamina.

of the surangular (Fig. 3A). The medially projecting articular portion of the glenoid is incomplete but the rest of the articular is preserved (Fig. 3B). The posterior portion of the Meckelian groove is present, formed within the articular and the prearticular (Fig. 3C). The lateral-facing suture between the surangular and the articular is visible (Fig. 3A) in the same position hypothesized by Small (2002), and as described for *Stagonolepis robertsoni* Agassiz and *Longosuchus meadei* Sawin (Walker 1961, Parrish 1994). The medial face of the prearticular below the internal mandibular fenestra is broken, exposing a suture with what is presumably the splenial (Fig. 3C), suggesting that the splenial overlapped the prearticular and that this latter bone formed a rough triangular wedge between the splenial and the articular, similar to the condition found in *Longosuchus* (Parrish 1994).

A dentary fragment containing a broken tooth was collected from float with several bone fragments assignable to phytosaurs and metoposaurs as well as *Desmatosuchus*; hence, its association with MNA V9300 cannot be confirmed. It appears to belong to an aetosaur, but because it contains no new information and its provenance is uncertain, it is not described further.

It is possible to determine an estimated length of the skull from the materials present. The distance from the posterior margin of the articular to the posterior surangular foramen measures 6 cm. The same measurement for the composite skull figured by Small (2002) is 5 cm. These distances are approximately one-eighth the total skull length from the tip of the premaxilla to the posterior process of the squamosal. Thus, if these two measurements scale isometrically, the estimated length for the skull of MNA V9300 would be 54 cm.

Vertebral Laminae

Saurischian dinosaurs possess structurally elaborate vertebrae. Presumably as a weight reducing measure, these vertebrae contain numerous thin bony struts that most likely provide structural support for the vertebral column (Wilson 1999). The arrangement and position of these struts, termed vertebral laminae, are consistent among vertebrae throughout the column and have recently been given standardized anatomical names by Wilson (1999). This same author noted that vertebral laminae are also present in some pseudosuchians, particularly rauisuchians. Desojo et al. (2002) and Nesbitt (2005) recently noted the presence of similar laminae in the Triassic archosauriform *Cuyosuchus huenei* and pseudosuchian *Arizonasaurus*. The presence of these vertebral laminae may

be plesiomorphic for Archosauria.

Some aetosaurs also possess a series of vertebral laminae, which form the T-beam structure first described by Case (1922) for *Desmatosuchus* vertebrae. Cervical vertebrae of *Desmatosuchus* possess at least four forms of vertebral laminae, whereas the dorsal vertebrae possess six, and two laminae are present in the sacral and caudal vertebrae (Fig. 4). Following Wilson (1999), these laminae are defined as follows:

1) acdl (anterior centrodiapophyseal lamina)—originates on the diapophysis and terminates on the anterior margin of the neurocentral suture (Figs. 4B, D).

2) pcdl (posterior centrodiapophyseal lamina)—originates on the diapophysis and terminates on the posterior margin of the neurocentral suture (Figs. 4A–D).

3) podl (postzygodiapophyseal lamina)—originates on the diapophysis and terminates at the postzygapophyses (Figs. 4B–D).

4) prdl (prezygodiapophyseal lamina)—originates on the diapophysis and terminates at the prezygopophyses (Figs. 4A, D).

5) spol (spinopostzygopophyseal lamina)—originates at the postzygopophysis and terminates on the posterior face of the neural spine (Fig. 4E).

6) sprl (spinoprezygopophyseal lamina)—originates at the prezygopophysis and terminates on the anterior face of the neural spine (Fig. 4F).

Cervical Vertebrae

Case (1922) provided a detailed description of the cervical series of *Desmatosuchus* from UMMP 7476. This is fortunate because only one of the seven cervicals preserved in MNA V9300 is complete. The preserved series appears to be from the third to the ninth (last) cervical; the axis and atlas are not present.

The third and fourth cervicals are represented by the right halves of the centra and the lower portion of the neural arch (Figs. 5A, B). Diapophyses are broad and flattened against the lateral face of the centrum, consistent with the anterior cervicals figured in these positions by Case (1922). Parapophyses of all cervicals are round to sub-round in cross-section and are sharply rimmed. With the exception of the ninth cervical, the articular facets of the parapophyses generally possess the same diameter throughout the series even though centra increase in size posteriorly.

The mid-cervical series (vertebrae 5–7) are also represented by partial centra. All three possess ventrolaterally projecting parapophyses. Centra are blocky and robust, with subrectangular articular faces, differing from those of *Stagonolepis robertsoni*, which are more circular (Walker 1961), and those of *Typothorax* (TTU P-9214) and *Neoaetosauroides*, which are ovate (Martz 2002, Desojo 2005). The centra throughout the cervical series are wider than long.

The eighth cervical centrum (Figs. 5C–E) is complete but partially crushed. Most of its neural arch and the entire neural spine are missing but enough is preserved to show that the neurocentral suture is closed, indicating that this was a mature animal (Brochu 1996, Irmis 2007). As for the previous vertebrae, articular faces of the centrum are sub-rectangular with distinct and slightly flaring rims. Parapophyses are ovate in cross-section and project ventrolaterally. The ventral surface is broad and flat, not keeled as in *Stagonolepis* (EM 33W) and *Neoaetosauroides* (PVL 5569). As in other aetosaurs, the neural canal is very large and rounded, in contrast to the slit-like neural canal of aetosaur dorsal vertebrae. The morphology of this vertebra conforms well to that of UMMP 7504 (Fig. 5F), considered to be an eighth cervical by Case (1922:fig. 11E).

The ninth cervical (Fig. 6) is slightly crushed ventrolaterally but complete and articulated with the first five vertebrae of the dorsal series. This vertebra is considered here to represent the last "true" cervical because the parapophyses are still located at the base the centrum. Case (1922) included 11 cervicals in his reconstruction, but this is probably inaccurate because it includes the elements of a second individual in the quarry (see discussions by Case (1922) and Walker (1961). All other aetosaurs, as well as other suchians, possess nine cervical vertebrae (Sawin 1947, Walker 1961). The ninth cervical of

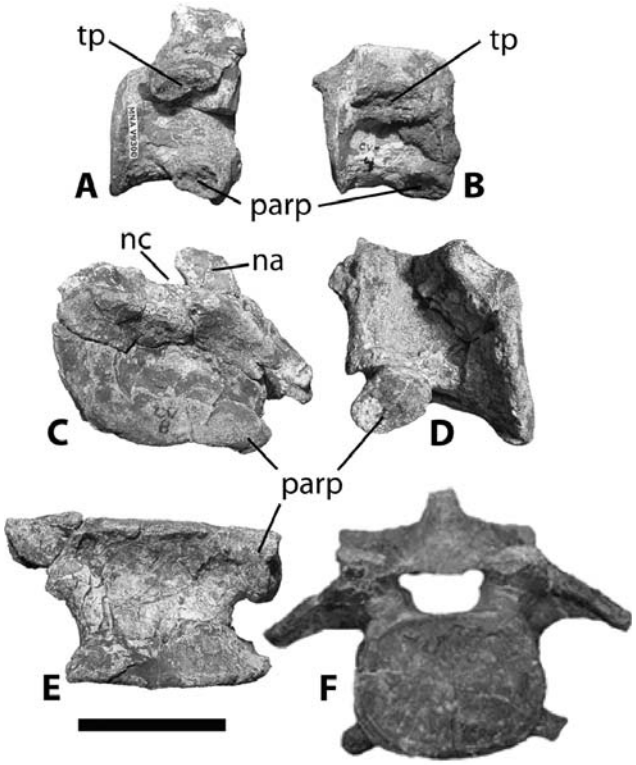


Figure 5. Cervical vertebrae of *Desmatosuchus*. **A.** Third cervical vertebra of MNA V9300 in right lateral view. **B.** Fourth cervical vertebra of MNA V9300 in right lateral view. **C–E.** Eighth cervical vertebra of MNA V9300 in anterior, left lateral and ventral views. **F**. UMMP 7504, eighth cervical vertebra in anterior view. Scale bar = 5 cm. Abbreviations: **na**, neural arch; **nc,** neural canal; **parp**, parapophysis; **tp**, transverse process.

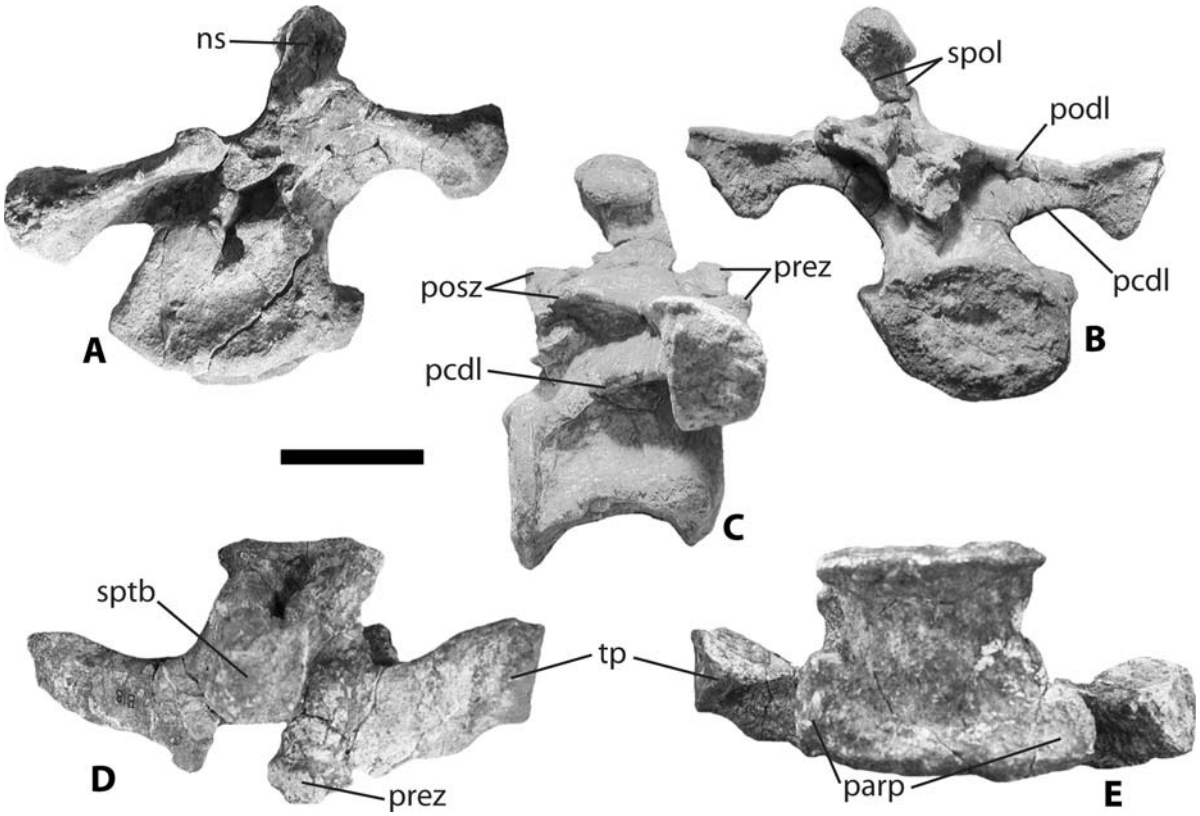


Figure 6. MNA V9300, ninth cervical vertebra. **A.** Anterior view. **B.** Posterior view. **C.** Right lateral view. **D.** Dorsal view. **E.** Ventral view. Scale bar = 5 cm. Abbreviations: **parp**, parapophysis; **pcdl,** posterior centrodiapophyseal lamina; **podl,** postzygodiapophyseal lamina; **posz,** postzygapophysis; **prez**, prezygopophysis; **spol,** spinopostzygopophyseal lamina; **sptb**, neural spine table.

MNA V9300 is identical to ninth vertebra of UMMP 7476 illustrated Case (1922:figs. 10, 11g).

Articular faces of the ninth vertebra are subrectangular with width greater than height. Transverse processes are robust and slightly longer than the width of the centrum. In comparison, the transverse processes of the posterior cervicals of *Typothorax* (TTU P-9214) are almost 1.5 times longer than the width of the centrum (Martz 2002). Transverse processes are directed horizontally and slightly posterolaterally. They are situated forward on the centrum, in the same vertical plane as the parapophyses. Articular faces of the diapophyses are greatly expanded and are robust and almost club-like (Figs. 6A–B). The transverse processes are T-shaped in cross-section (the "T-beam" feature described by Case [1922]), because the posterior centrodiapophyseal laminae are well-developed, which extend obliquely between the diapophysis and the upper rim of the posterior face of the centrum (Figs. 6B–C). The dorsal surface of the process is flattened (Fig. 6D) and expanded anteroposteriorly, consisting of two additional laminae, the prezygopophyseal lamina, and the postzygopophyseal lamina (Fig. 6B). Zygopophyses inclined at approximately 45° suggest that some lateral movement of the neck was possible, but the extreme thickness and fusion of the overlying armor plates in this region would seemingly have prevented such movement.

The neural spine is short both dorsoventrally and anteroposteriorly, unlike the tall neural spines of *Stagonolepis* (EM 30R) and *Neoaetosauroides* (PVL 5669). The apex is slightly expanded and rounded into a spine table so that it appears dome- or helmet-shaped in posterior view (Fig. 6B). Both lateral edges of the spine possess prespinozygopophyseal and postspinozygopophyseal laminae that originate just below the apex, progress ventrally, and are confluent with the zygopophyses (Fig. 6B). The ventral surface is flattened and lacks a keel (Fig. 6E).

Dorsal Vertebrae

Fourteen vertebrae of the dorsal series were recovered with MNA V9300. The first five are in articulation with the last cervical (Fig. 7), and what is presumably the sixteenth dorsal is in articulation with the sacrum. The exact number of dorsal vertebrae for aetosaurs is not clear and may vary among species. Case (1922) figures 17 dorsals for *Desmatosuchus* (UMMP 7476), Sawin (1947) lists 16 or 17 for *Longosuchus*, Walker (1961) lists 16 for *Stagonolepis robertsoni*, and Schoch (2007) lists 14 for *Aetosaurus* (presuming it has nine cervicals). Therefore, possibly none or as many as three vertebrae are missing from the series of MNA V9300; however, based on the number of preserved lateral plates (which have a 1:1 ratio with the vertebrae) in the carapace, it is likely that only

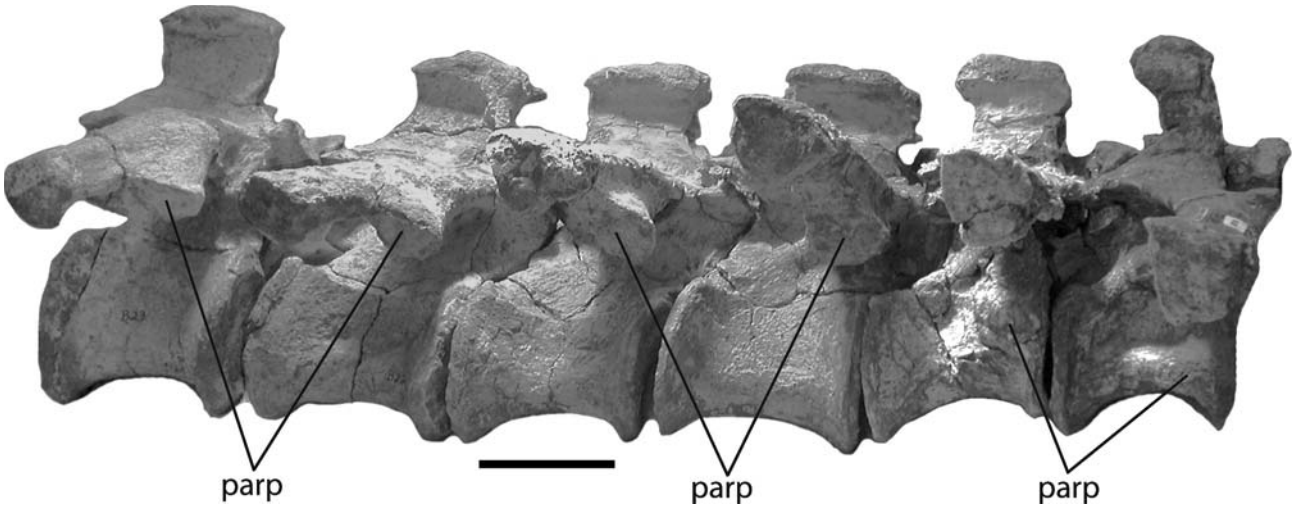


Figure 7. MNA V9300, ninth through fourteenth presacral (ninth cervical and first five dorsals, right to left) vertebrae in right lateral view, showing the transition of the parapophysis. Scale bar = 5 cm. Abbreviation: **parp**, parapophysis.

two dorsal vertebrae are missing because desmatosuchine aetosaurs have a minimum of 16 dorsals (based on the counts given by Sawin, 1947 and Case, 1922) and there are 16 dorsal lateral plates preserved in MNA V9300. Because the anterior portion of the dorsal series was recovered in association, it is the posterior vertebrae that are missing.

The tenth presacral, considered here to represent the first dorsal vertebra (Fig. 8), is transitional in form, possessing parapophyses that are situated at the top of the centrum just below the neurocentral suture (Figs. 8A–C). For the rest of the dorsal series, the parapophysis is located on the transverse process (Fig. 7). This is typical of all aetosaurs and differs from phytosaurs and "rauisuchians" in which the parapophyses of the dorsal series are on the neural arch. For reasons that are unclear, Case (1922:fig. 10a), described an identical vertebra as a twelfth presacral, even though he figures it in the tenth position. Because the fourth through tenth presacrals in UMMP 7476 were found in articulation, the tenth position is most likely correct for that vertebra.

The large parapophyses on the tenth presacral cover almost a quarter of the lateral side of the centrum (Fig. 8C). The anterior articular face of the centrum is ovate with its long axis oriented mediolaterally and consistent with the shape of the posterior cervicals, while the posterior face of the centrum is smaller and round like the rest of the dorsal series (Figs. 8A–B). The centrum is laterally constricted and spool-shaped behind the parapophysis and anteroposteriorly longer than wide, unlike the cervical vertebrae. The ventral surface is flat and unkeeled (Fig. 8D). Transverse processes are robust, mediolaterally short, and situated forward on the neural arch as in the previous vertebra. The three vertebral laminae that make up the T-beam cross-section are still present. The neural spine is short, yet more elongate anteroposteriorly than that of the ninth cervical. Its apex possesses an elongate spinal "table" typical of aetosaurs and most pseudosuchians (Fig. 8E). The spine also possesses the vertical spinozygopophyseal laminae found in the last cervical vertebra.

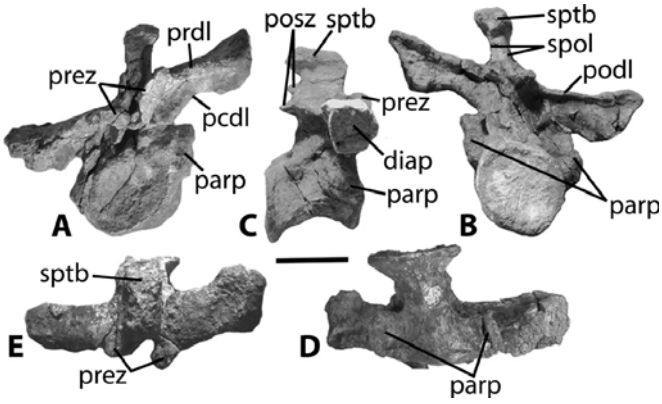
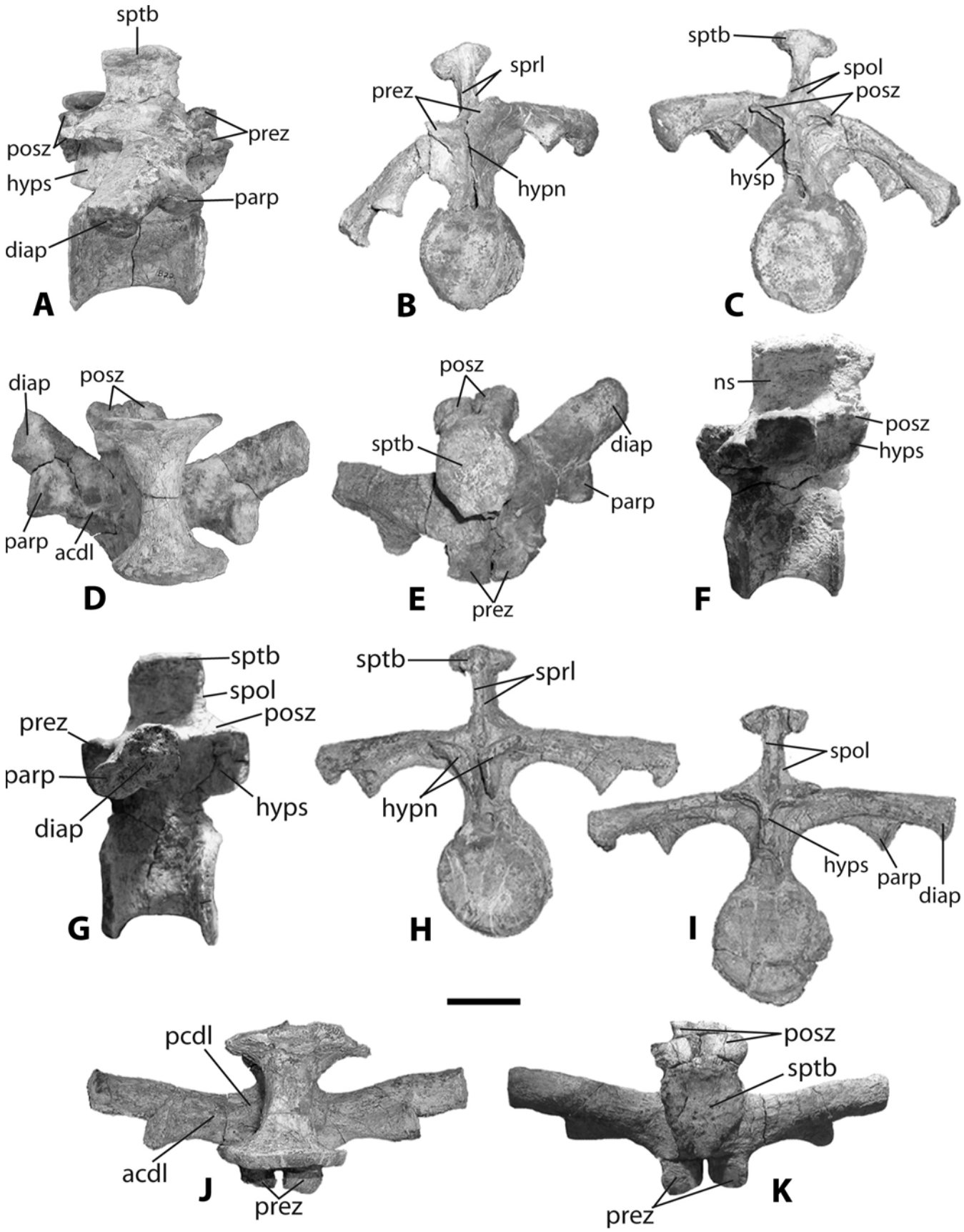


Figure 8. MNA V9300, tenth presacral (first dorsal) vertebra. **A**. Anterior view. **B**. Posterior view. **C**. Right lateral view. **D**. Ventral view. **E**. Dorsal view. Scale bar = 5 cm. Abbreviations: **diap**, diapophysis; **parp**, parapophysis; **pcdl,** posterior centrodiapophyseal lamina; **podl,** postzygodiapophyseal lamina; **prdl,** prezygodiapophyseal lamina; **prez**, prezygopophysis; **spol,** spinopostzygopophyseal lamina; **sptb**, spine table.

The eleventh through fourteenth presacrals (second through fifth dorsals) (Figs. 9A–E) are very similar in form and differ from the remainder of the series. These elements were all found in articulation so their relative position in the vertebral column is certain. A prominent characteristic of these vertebrae is that both rib facets are positioned on the transverse process, with the diapophysis situated on the anterior edge slightly more than halfway along the mediolateral length of the process (Figs. 9B–E). Articular faces are platycoelous and generally round, except for a slight concavity at the apex of the centrum for passage of the neural canal (Fig. 9C). Centra are 1.5 times longer than wide, laterally compressed, and spool-shaped, causing the rims of the articular surfaces to flare. The ventral surface is more ridge-like and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rounded rather than flattened (Figs. 9A, D). The neural arch is tall, equaling the height of the centrum, and more elongate than those of the more anterior vertebrae. Zygopophyses project anteriorly and posteriorly beyond the articular faces of the centra. Prezygopophyses are lunate and distinct from each other, separated by a thin vertical groove or hypantrum. Postzygopophyses coalesce into a Y-shaped ridge with the base of the "Y" forming a well-developed hyposphene (Fig. 9C). Zygopophyses are oriented almost horizontally and the insertion area of the hyposphene for the hypantrum is extremely anteroposteriorly developed, suggesting that lateral movement throughout the dorsal series was restricted.

Transverse processes are situated centrally on the neural arch. They are more elongate than in more anterior vertebrae, yet are still less than twice the width of the centrum. Processes in these four vertebrae are subhorizontal (Fig. 9C) and directed slightly ventrally which could be the original orientation with or without accentuation by diagenetic distortion. Nonetheless, transverse processes are directed posterolaterally as well, especially in the most anterior vertebrae of the series. The addition of the parapophysis onto the transverse process has anteroposteriorly widened this structure. It remains dorsally flattened and ovate in cross section. Parapophyses are reduced and not as robust and club-like as in the previous vertebrae. Rib facets project posterolaterally.

Where the transverse process meets the neural arch, several faint yet discernable laminae are present. These are the anterior and posterior centrodiapophyseal laminae that connect the ventral surface of the diapophysis with the upper rim of the centrum face just above the neurocentral suture. Neural spines are still very short, less than the height of the centrum, and possess lateral pre- and postzygopophyseal laminae. Centra of the eleventh through fourteenth vertebrae are the most anteroposteriorly elongate of the entire column.

The fifteenth presacral (sixth dorsal) vertebra is distinctive within the dorsal series (Fig. 9F). Its neural arch is taller and there is a prominent ventral strut consisting of both centrodiapophyseal laminae that originate from the central portion of the lateral face of the neural arch and curve dorsolaterally to merge with the capitular portion of the transverse process. This structure occurs throughout the rest of the dorsal series and differs from previous vertebrae in that the centrodiapophyseal laminae are joined and no longer distinct.

The neural arch and spine on the fifteenth vertebra are abnormally elongate anteroposteriorly, projecting posteriorly to the farthest extension of the postzygopophyses (Fig. 9F). Curiously, the spine table is of normal proportions and therefore does not cover the entire anteroposterior length of the spine. This is probably unique to this specimen and represents some kind of abnormality, although it is not clearly pathologic. Transverse processes of the fifteenth vertebra are directed horizontally and laterally, lacking the slight posterior curvature found in the previous vertebrae. The diapophysis is located three-quarters of the way along the transverse process laterally, almost reaching the position of the parapophysis; thus, the rib heads in this position and the rest of the mid-dorsal series are shallow. Hyposphenes and hypantra are strongly developed.

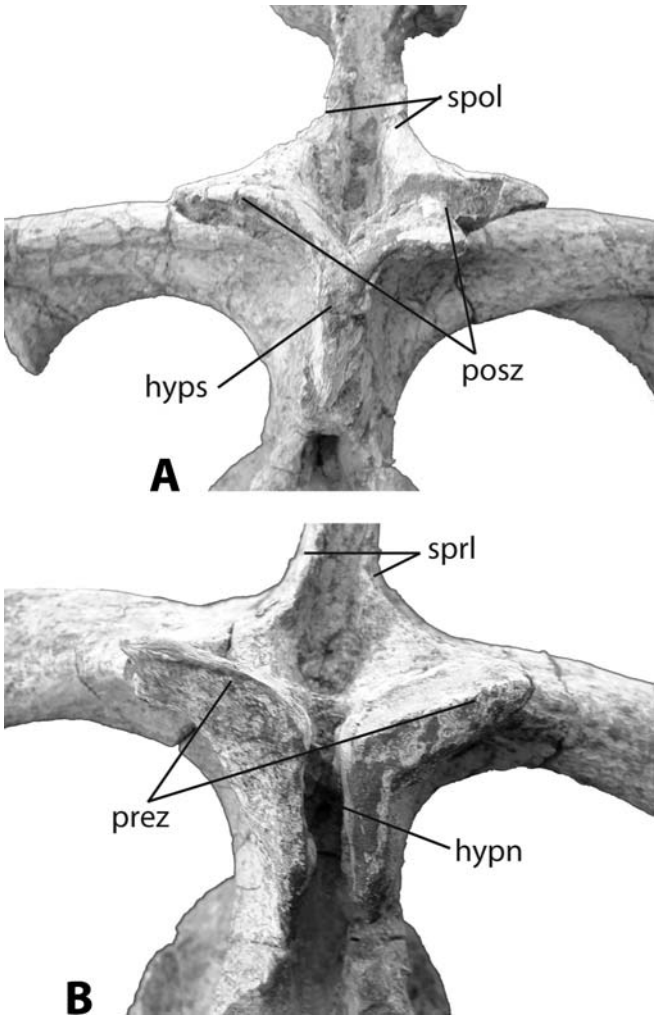

Figure 10. MNA V9300, accessory articulations and spinal laminae on mid-dorsal vertebrae. **A.** Posterior view. **B.** Anterior view. Abbreviations: **hypn**, hypantrum; **hyps,** hyposphene; **posz,** postzygopophysis; **prez**, prezygopophysis; **spol,** spinopostzygopophyseal lamina; **sprl,** spinoprezygopophyseal lamina.

◄ **Figure 9.** MNA V9300, anterior dorsal and mid-dorsal vertebrae. **A.** Fourth dorsal in right lateral view. **B.** Fourth dorsal in anterior view. **C.** Fourth dorsal in posterior view. **D.** Fifth dorsal in ventral view. **E.** Fifth dorsal in dorsal view. **F.** Sixth dorsal vertebra in left lateral view showing posterior extent of neural spine. **G-K.** Seventh dorsal vertebra. **G.** Left lateral view. **H.** Posterior view. **I.** Anterior view. **J.** Ventral view. **K.** Dorsal view. Scale bar = 5 cm. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **diap**, diapophysis; **hypn**, hypantrum; **hyps,** hyposphene; **parp**, parapophysis; **posz,** postzygopophysis; **prez**, prezygopophysis; **spol,** spinopostzygopophyseal lamina; **sprl,** spinoprezygopophyseal lamina; **sptb**, spine table.

Starting with the fifteenth presacral, the transverse processes begin to elongate mediolaterally. The sixteenth through twenty-third presacral (seventh through fourteenth dorsal) vertebrae were not found in association so their exact position can only be estimated. In addition, vertebral counts in other aetosaurs suggest that two vertebrae in this series are missing.

The sixteenth presacral (seventh dorsal) is the best preserved of all of the dorsal vertebrae (Figs. 9G–K). It was recovered in association with most of the other anterior dorsal and posterior cervical vertebrae and armor, and judging by its size, the vertebra was most likely found in the proper position in the column. Articular faces of the centrum are round and the centrum is spool-shaped as in the other dorsals; however, it differs from the previous dorsals in the further mediolateral elongation of the transverse processes, which are shorter anteroposteriorly and not as broad as the processes in the more anterior vertebrae. Vertebral laminae and accessory articular structures are well-developed similar to the previous vertebra, and the zygopophyses are nearly horizontal (Fig. 10).

The following two vertebrae from within the range of the eighth through eleventh dorsals are very similar to the seventh dorsal (Figs. 11A–E). Centrum length decreases gradually beginning with the fourteenth presacral (sixth dorsal), and these vertebrae continue that trend. The centra are generally more massive and dorsoventrally taller than the previous dorsals. This increase in overall robustness and height continues through the rest of the dorsal series. In all other details they are similar to the previous vertebrae (i.e., the accessory processes are still strongly developed, neural spines remain short, and the centrodiapophyseal and the spinozygopophyseal laminae are still present and unchanged).

The twelfth through fifteenth dorsal vertebrae are distinctive in several ways. They are extremely robust and are dorsoventrally the tallest vertebrae in the entire column (Figs. 11F–J). Centrum length is strongly reduced so that the centra are taller than long (Fig. 11G). Centrodiapophyseal laminae are no longer distinguishable, although the spinozygopophyseal laminae are still present (Fig. 11J). On these vertebrae, the diapophyses are no longer distinct on the transverse processes but have presumably merged with the parapophyses (Case 1922). In addition, the ribs and transverse processes are strongly fused so that it is difficult to determine where the articulation point is located. Approximately a third of the way down this combined element, there is a slight swelling that may represent the confluence of the transverse process and a rib, but this is not conclusive (Fig. 11F). For dorsal vertebra 14, the process/rib measures 35 cm in length and extends ventrolaterally from the upper portion of the neural arch, curving sharply downwards approximately two-thirds of the way along its total length. At this point the process also flattens dorsoventrally and widens anteroposteriorly, becoming a flat blade for much of the downward curve (Fig. 11J). The distal end of the process extends ventrally for several centimeters past the ventral margin of the centrum face.

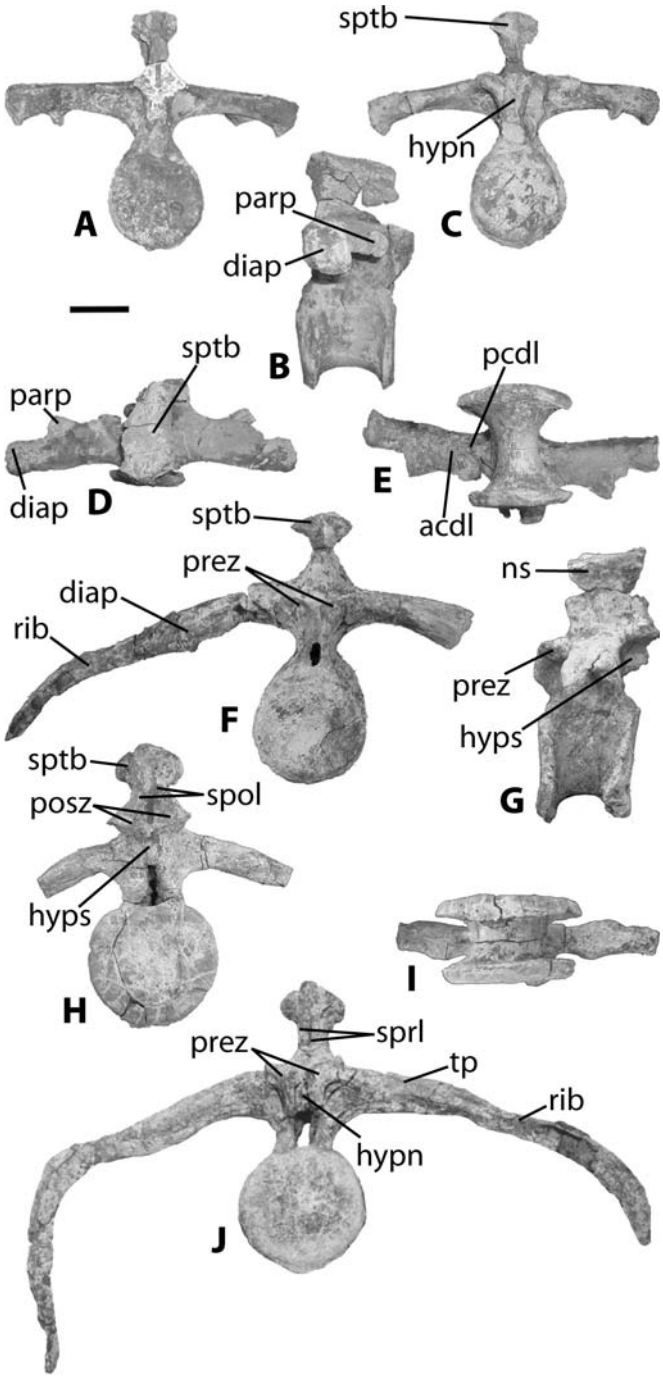

Figure 11. MNA V9300, posterior dorsal vertebrae. **A–E.** Posterior mid-dorsal vertebra (eleventh?). **A.** Posterior view. **B.** Left lateral view. **C.** Anterior view. **D.** Dorsal view. **E.** Ventral view. **F–J.** Posterior dorsal vertebrae. **F.** Twelfth vertebra in dorsal view. **G.** Twelfth vertebra in left lateral view (rib is broken away). **H.** Thirteenth vertebra in posterior view. **I.** Thirteenth vertebra in ventral view. **J.** Fourteenth vertebra in anterior view. Scale bar = 5 cm. Abbreviations: **diap**, diapophysis; **hypn**, hypantrum; **hyps,** hyposphene; **parp**, parapophysis; **posz,** postzygopophysis; **prez**, prezygopophysis; **spol,** spinopostzygopophyseal lamina; **sprl,** spinoprezygopophyseal lamina; **sptb**, spine table.

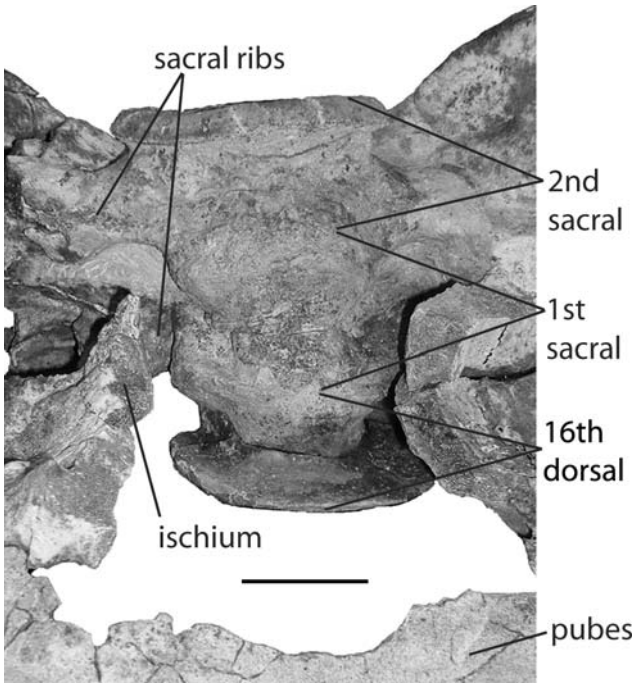

Figure 12. MNA V9300, ventral view of the sacrum with most of the ischia removed to show fusion of the last dorsal and first sacral vertebrae.

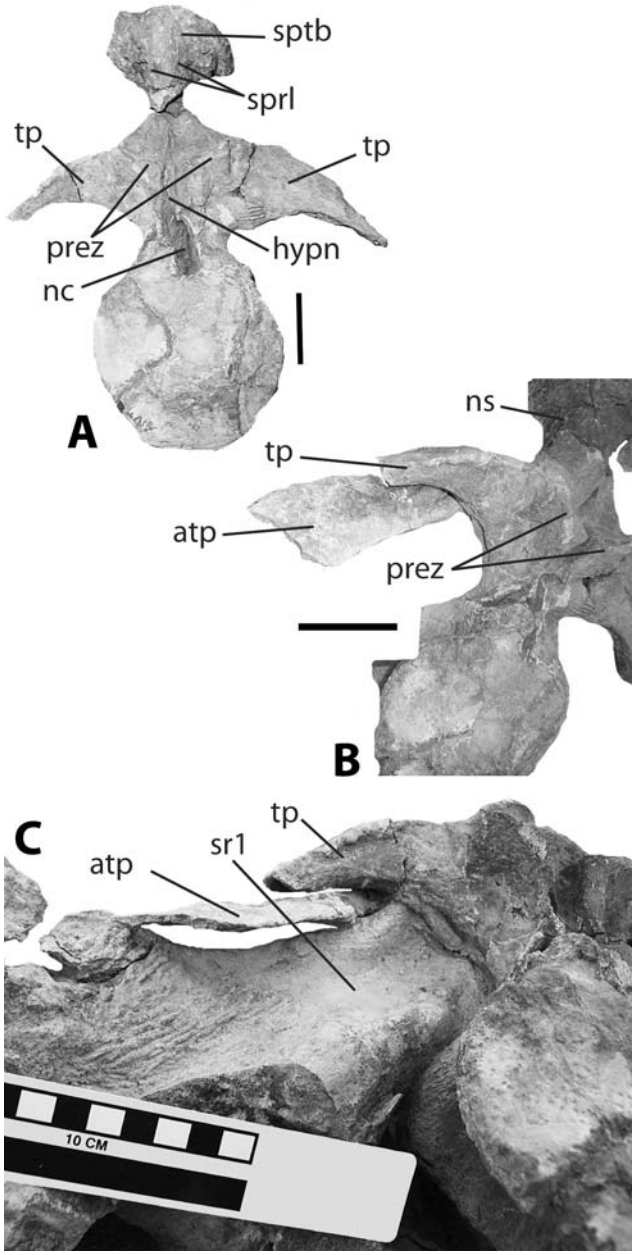

Figure 13. MNA V9300, sixteenth (last) dorsal vertebra. **A.** Anterior view (atp removed), scale bar = 5 cm. **B.** Bifurcate transverse process in anterodorsolateral view. **C.** Bifurcate transverse process in anteroventrolateral view. Abbreviations: **atp**, accessory transverse process; **hypn,** hypantrum; **nc**, neural canal; **ns,** neural spine; **prez,** prezygopophysis; **prez**, prezygopophysis; **sprl,** spinoprezygopophyseal lamina; **sr1,** 1st sacral rib; **sptb**, spine table; **tp**, transverse process.

This fusion of ribs or elongation of the transverse processes is notable because it has never been clearly documented in aetosaurs. Hunt et al. (1993) preliminarily described the ribs of *Typothorax* (NMMNH P-12964) as fused to the transverse processes, and Case (1922:41) states that "there is evidence that even to the last the ribs were articulated with the transverse process and not reduced and co-ossified with them; in this sense there are not true lumbars." Nevertheless, *Desmatosuchus* is often reconstructed with a mediolateral narrowing (waist) just anterior to the pelvis and reduced ribs throughout the posterior region of the dorsal series (e.g., Long and Murry 1995:figs. 85, 86), probably because this region was unknown prior to the discovery of MNA V9300. Given the size of the armor and the fusion of the ribs (or expansion of the transverse processes) in the region, the narrowing of the carapace anterior to the sacrum is minimal, in contrast to *Stagonolepis* (Walker 1961).

The last dorsal vertebra of *Desmatosuchus* is strongly fused to the first sacral vertebra (Fig. 12). This fusion is so complete that the details of the articulation of the zygopophyses, neural arches, and neural spines between these two vertebrae have been obliterated; however, this vertebra is not a true dorsosacral because it does not possess a sacral rib. It is the largest in the entire vertebral series both in dorsoventral height and in total diameter of the centrum (Fig. 13A). The anterior articular face of the centrum possesses a strongly flared outer rim. The centrum is extremely shortened anteroposteriorly, half the length of the width of the centrum face. The posterior face of the centrum is completely fused with the first sacral vertebra, but there is a pronounced swelling along the closed suture where it ends and the sacrum begins (Fig. 12). As for other posterior dorsal vertebrae, the neural arch is slightly taller than the centrum. The neural spine is a little more than half the dorsoventral height of the centrum. The apex of the spine possesses a broad, strongly

developed spine table. Posteriorly, the spine and table fuse with the corresponding elements of the first sacral without an apparent suture.

Prezygopophyses are short anteroposteriorly and broad mediolaterally, with articular faces that are slightly crescentic or concave in anterior view and that face slightly dorsomedially. The hypantrum is wide and well developed for insertion of the hyposphene from the preceding vertebra. The slight obliqueness of the zygopophyses may have allowed for a small amount of lateral movement in this area.

Transverse processes of the last dorsal vertebra are very short and almost horn-like in anterior view (Fig. 13A). They project laterally from the center of the neural arch and are slightly recurved ventrally. A broad dorsoventrally flattened, elongate sheet of bone projects from the neural arch from behind the posterolateral edge of the horn-like transverse process. The laterally extending sheet of bone, termed here the "accessory transverse process", passes ventrally beneath the transverse process, where it appears to slightly overlap the ilium (Figs. 13B–C), but this cannot be verified because the distal end of the accessory process is incomplete. This part of the strange bifurcation seems to be somewhat similar to the sheet of bone described by Walker (1961) for *Stagonolepis* (GSM 90884, BMNH R.4793), although *Stagonolepis* does not appear to possess horn-like transverse processes. A complete pelvis of *Desmatosuchus* (TTU P-9172) from the Tecovas Formation of Texas does not appear to possess this structure, although the accessory process is so thin and delicate that it could have easily been broken off during postmortem transport or collection. It is possible that this sheet of bone represents an incipient sacral rib. A similar structure is also present in the enigmatic probable archosauriform *Doswellia kaltenbachi* Weems (USNM 244214), which also possesses a posteriormost dorsal vertebrae sutured with the first sacral (Weems 1980). Known sacra of *D. smalli* are too poorly preserved to determine if this structure is present in that taxon, and it has not been reported for other aetosaurs except for the condition found in *Stagonolepis robertsoni* (Walker, 1961) mentioned above.

It does not appear that the incorporation of the last dorsal into the pelvis is solely due to ontogeny. TTU P-9172 (*Desmatosuchus* sp.), all known pelves of *Longosuchus* (TMM 31185-40, 31100-236), and *Lucasuchus* (TMM 31100-313) also possess a fused dorsal (Elder 1978, Long and Murry 1995). Known pelves of *Calyptosuchus* (UMMP 7470, UMMP 13950), "*Acompsosaurus*", *Neoaetosauroides* (PVL 5669), and *Typothorax* (NMMNH P-36075, PEFO 33967) possess only two unfused sacrals and lack a fused dorsal (Mehl et al. 1916, Case 1929, Case 1932, Walker 1961, Lucas et al. 2002, Desojo and Báez 2005). Thus, it appears that this character may be taxonomically useful (Parker 2007).

Sacral Vertebrae

Desmatosuchus possesses two sacral vertebrae, *contra* Small's (1985) count of three. As previously discussed, this "third sacral" actually is the last dorsal vertebra and is not considered here to represent a true sacral vertebra because it lacks a distinct sacral rib.

The first sacral vertebra is strongly fused with the last dorsal and the second sacral (Fig. 12); however, a swelling between the sacral centra is equivalent to the outward flaring of the rim of the anterior face of the centrum in the dorsal vertebrae. The ventral surface of the centrum is very broad and flattened, a feature typical of aetosaur sacrals (personal observation). Laterally, at the suture between the two sacrals, there is a thickened process that appears knob-like in ventral view. Dorsally this process connects with the sacral rib, but because of the compactness and suturing of the sacrum, the exact relationship between this process and the rib is difficult to discern, although it appears to act as a buttress for the sacral rib.

The second sacral vertebra is solidly fused anteriorly with the first sacral, and no details of the prezygopophyses are observable. The posterior articular face of the centrum is flared with a strong rim. It is wider than tall and thus ovate in posterior view. The neural arch is reduced in height compared to those of the posterior dorsal vertebrae, and more closely resembles the arches of the caudal vertebrae (Fig. 14). Sacral ribs are strongly attached laterally the base of the centrum and are situated more anteriorly than posteriorly. In addition, mediolaterally shortened, dorsoventrally flattened, broad transverse processes extend laterally from the

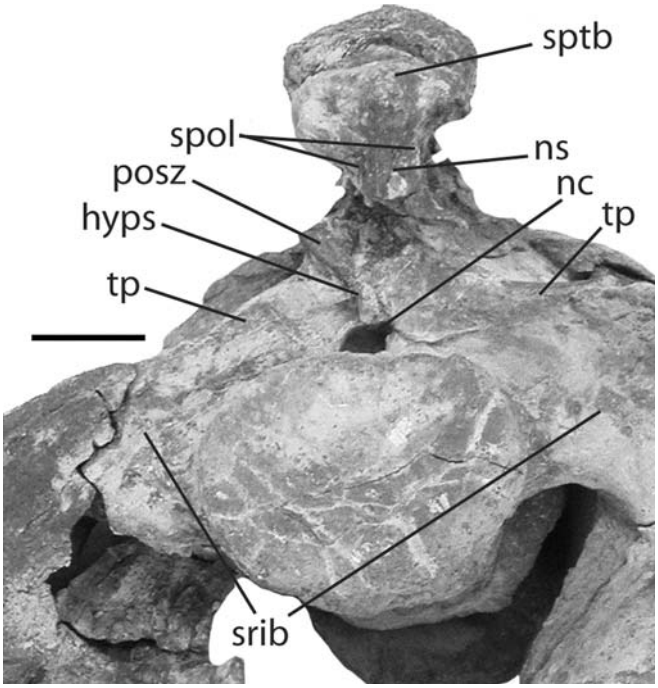

Figure 14. MNA V9300, second sacral vertebra in posterior view. Abbreviations: **atp**, accessory transverse process; **hyps,** hyposphene; **nc**, neural canal; **ns,** neural spine; **posz,** postzygopophysis; **prez**, prezygopophysis; **spol,** spinopostzygopophyseal lamina; **srib,** sacral rib; **sptb**, spine table; **tp**, transverse process.

neural arch. These overlap the posteromediodorsal portion of the associated sacral rib. Postzygopophyses meet at a developed hyposphene and are inclined approximately 50° from horizontal.

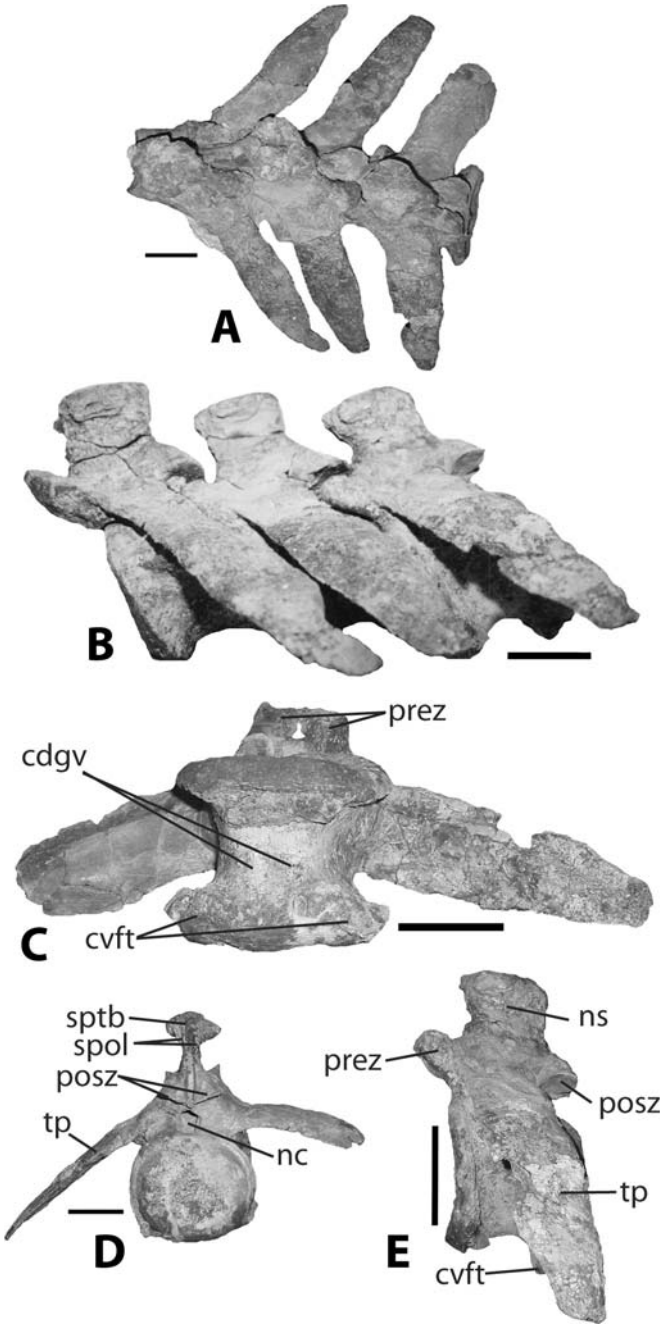

Figure 15. MNA V9300, anterior caudal vertebrae. **A.** First three caudal vertebrae in dorsal view. **B**. First three caudal vertebrae in left lateral view. **C**. Third caudal vertebra, ventral view. **D**. Third caudal vertebra, posterior view. **E**. Third caudal vertebra, left lateral view. Scale bars = 5 cm. Abbreviations: **cdgv**, ventral caudal groove; **cvft**, chevron facet; nc, neural canal; **prez**, prezygopophyses; **posz,** postzygopophysis; **spol,** spinopostzygopophyseal lamina; **sptb**, spine table; **tp**, transverse process.

Neural spines for the last dorsal and two sacral vertebrae are fused together; however, the spine table of the first sacral is much broader mediolaterally than that of the second sacral. Spine tables for the last dorsal and first sacral are fully fused with no apparent suture. Conversely, the spine table on the first sacral is telescoped over that of the second sacral making the suture between the two sacral neural spines apparent. The spine tables also possess longitudinal fluting along their lateral sides that may represent points for the attachment of ligaments. Neural spines of the sacral series possess spinozygopophyseal laminae.

Caudal Vertebrae

Nineteen caudal vertebrae are preserved with MNA V9300. This includes the first through the twelfth caudals; the first six caudals were found in articulation. All of the known caudal vertebrae are well preserved, complete, and are representative of most the caudal vertebral series (Figs. 15–17). Although the total number of caudals in *Desmatosuchus* is unknown, Walker (1961) inferred 43 caudals for *Aetosaurus* based upon the number of caudal plates present, which suggests that less than half the tail of MNA V9300 is preserved; however, only 26 caudals are present in the complete tail of *Neoaetosauroides* (Desojo and Bàez 2005). A short tail is considered to be an autapomorphy of *Neoaetosauroides* (Desojo and Bàez 2005, Desojo 2007), but this is tentative because complete tails are unknown for most aetosaur taxa. The supposedly short (25 or 25 centra) tail of *Longosuchus* (Sawin 1947) is probably because it was not recognized that the anterior portion of the caudal carapace was missing, as was first suggested by Walker (1961).

Pronounced breadth and depth is the most striking feature of the *Desmatosuchus* tail. Transverse processes of the first three caudals are extremely long and directed posterolaterally and slightly ventrally, with the processes of the first caudal measuring 21 cm in length (Figs. 15A–B). Transverse processes are very similar to those of the anterior caudal figured by Walker (1961:fig. 10d) for *Stagonolepis robertsoni.* These processes are dorsoventrally flattened and are slightly recurved and rounded at the distal tips. Lucas et al. (2002) assigned vertebrae of *Typothorax* (NMMNH P-36075) with an identical morphology to the dorsal region, discussing the peculiarity of the ventrally directed transverse processes. Examination of the figures (Lucas et al. 2002:figs. 5a–b) reveal that these vertebrae are caudals rather than dorsals. A similar error made by Heckert and Lucas (2002e:855) accounts for the "remarkably wide transverse processes" in the "dorsal vertebrae" of *Aetosauroides scagliai.* These too are caudal vertebrae, not dorsals, as evidenced by the presence of chevron facets on their ventral surfaces (Parker 2003, Desojo 2005).

Anterior caudal vertebrae are very robust with large articular faces that are subrounded and possess greatly thickened rims (Figs. 15C–D). Posterior articular faces are strongly offset ventrally from the anterior faces (Figs. 15B, E). This is probably not a result of diagenesis because it is also a

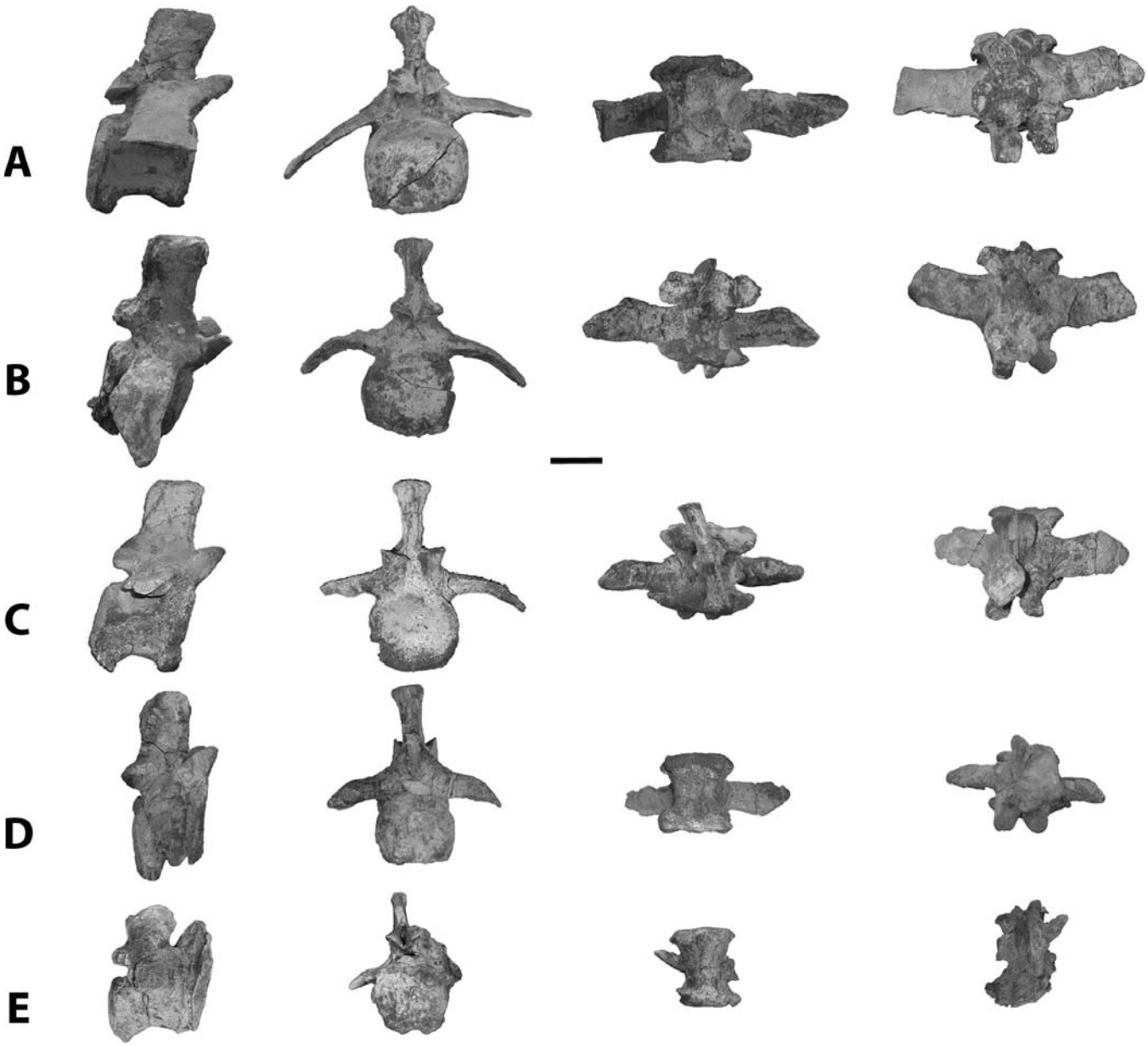

Figure 16. MNA V9300, caudal vertebrae. **A.** Fifth caudal in right lateral, posterior, ventral and dorsal views. **B.** Sixth caudal in right lateral, posterior, ventral and dorsal views. **C.** Seventh caudal in right lateral, anterior, ventral and dorsal views. **D.** Eighth caudal in right lateral, posterior, ventral and dorsal views. **E.** Eleventh caudal in right lateral, posterior, ventral and dorsal views. Scale bar = 5 cm.

feature of the anterior caudals of *Paratypothorax* (PEFO 3004). Centra are blocky and equidimensional. Lateral surfaces of the centra are slightly constricted, yet they do not have the spool-like appearance of the dorsal vertebrae. The ventral surface is broad and possesses a wide shallow groove that extends anteroposteriorly for the length of the centrum (Fig. 15C). Starting with the third vertebra, flattened areas for attachment of chevrons are present slightly lateral to the posterolateral edges of these grooves (Fig. 15C). These platforms face ventrolaterally and slightly posteriorly. Zygopophyses are anteroposteriorly expanded (Fig. 15E), the prezygopophyses are inclined medioventrally and slightly anteroventrally, and the postzygopophysis are inclined ventromedially. Accessory articulations such as hyposphenes and hypantra are not apparent.

Neural arches are short, approximately three-quarters the height of the centrum. The neural canal is round, unlike the slit-like opening in the dorsals, and its cross-section is also larger than that of the neural canal from the dorsal vertebrae. Neural spines are short, and slightly higher than the neural arches. Spine tables are present and similar to those of the dorsal series. Spinozygopophyseal laminae occur on all of the anterior caudal vertebrae (Fig. 15D).

Transverse process lengths rapidly decrease posteriorly

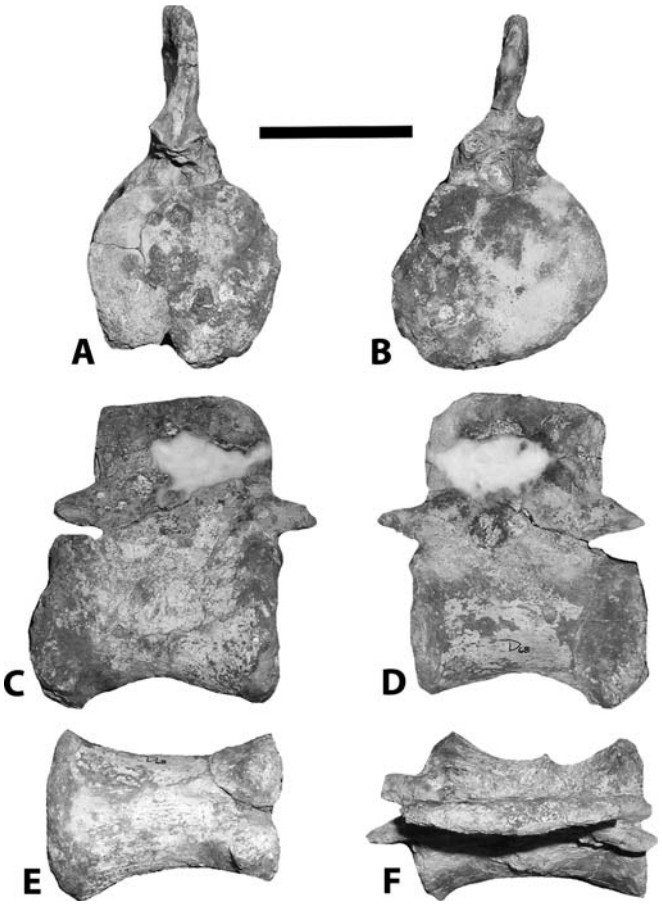

Figure 17. MNA V9300, posterior mid-caudal vertebra. **A.** Posterior view. **B.** Anterior view. **C.** Right lateral view. **D.** Left lateral view. **E.** Ventral view. **F.** Dorsal view. Scale bar = 5 cm.

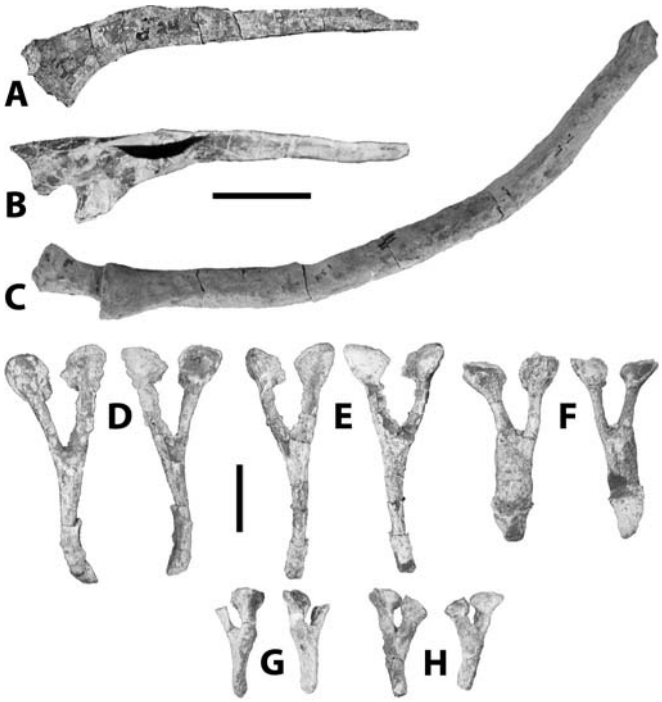

Figure 18. *Desmatosuchus spurensis*, ribs and chevrons. **A.** MNA V9300, ninth cervical rib. **B.** UMMP 7476, ninth cervical rib. **C**. MNA V9300, dorsal rib in posterior view. **D–F.** MNA V9300, anterior "slim"chevrons. **D.** First chevron, anterior and posterior views. **E**. Second chevron, anterior and posterior views. **F**. MNA V9300, mid "fat" chevron in anterior and posterior views. **G–H**. MNA V9300, distal chevrons in anterior and posterior views. Scale bars = 5 cm.

through the caudal series. Compared to the transverse process of the first caudal, that of the seventh caudal is half as long and that of the eleventh caudal is a quarter as long (Figs. 16A–E). By the thirteenth or fourteenth caudal, transverse processes are strongly reduced or absent (Figs. 17A–B). Size of the vertebrae also decreases posteriorly through the series. Centrum lengths increase posteriorly, with the more posterior vertebrae becoming increasingly less blocky to relatively elongate in the more distal vertebrae where the length/width ratio for the centrum is about 2:1 (Figs. 16A–E, 17C–F).

Neural arch heights tend to increase posteriorly to the eleventh caudal and then rapidly decrease. This decrease in neural spine height is accompanied by an anteroposterior lengthening of the spine (Figs. 17C–D). Spine tables disappear after the tenth caudal.

Ribs

A single preserved cervical rib, which is missing much of its proximal end, measures 20 cm in length (Fig. 18A). This rib is nearly identical to those figured and described by Case (1922) for UMMP 7476 (Fig. 18B). It was found associated with the ninth cervical to which it could possibly belong. Fragments likely derived from other cervical ribs were collected as float.

Besides those ribs fused to the posterior dorsal vertebrae, several disarticulated dorsal ribs were recovered with MNA V9300. Dorsal ribs are bifurcated for articulation with both the diapophysis and the parapophysis. Two relatively complete specimens as well as numerous fragments are identifiable. Dorsal ribs are robust and expand anteroposteriorly where they become ovate in cross section. They project laterally and slightly ventrally for most of their length before curving ventrally near their distal end (Fig. 18C). This suggests a broad barrel-shaped carapace unlike the narrow carapace reconstructed by Long and Murry (1995). Ribs flatten distally and are rounded on the distal end. The longest rib segment measures 61 cm and is at least three-quarters complete.

Chevrons

Numerous chevrons are present (Figs. 18D–H), including several that are in articulation with the third through sixth caudal vertebrae. This association, along with the appearance of chevron facets at the base of the third caudal, clearly shows that the chevrons started in this position. Chevrons strongly resemble those described for *Desmatosuchus*, *Stagonolepis*, and *Typothorax* (Case 1922, Walker 1961, Martz 2002). Martz

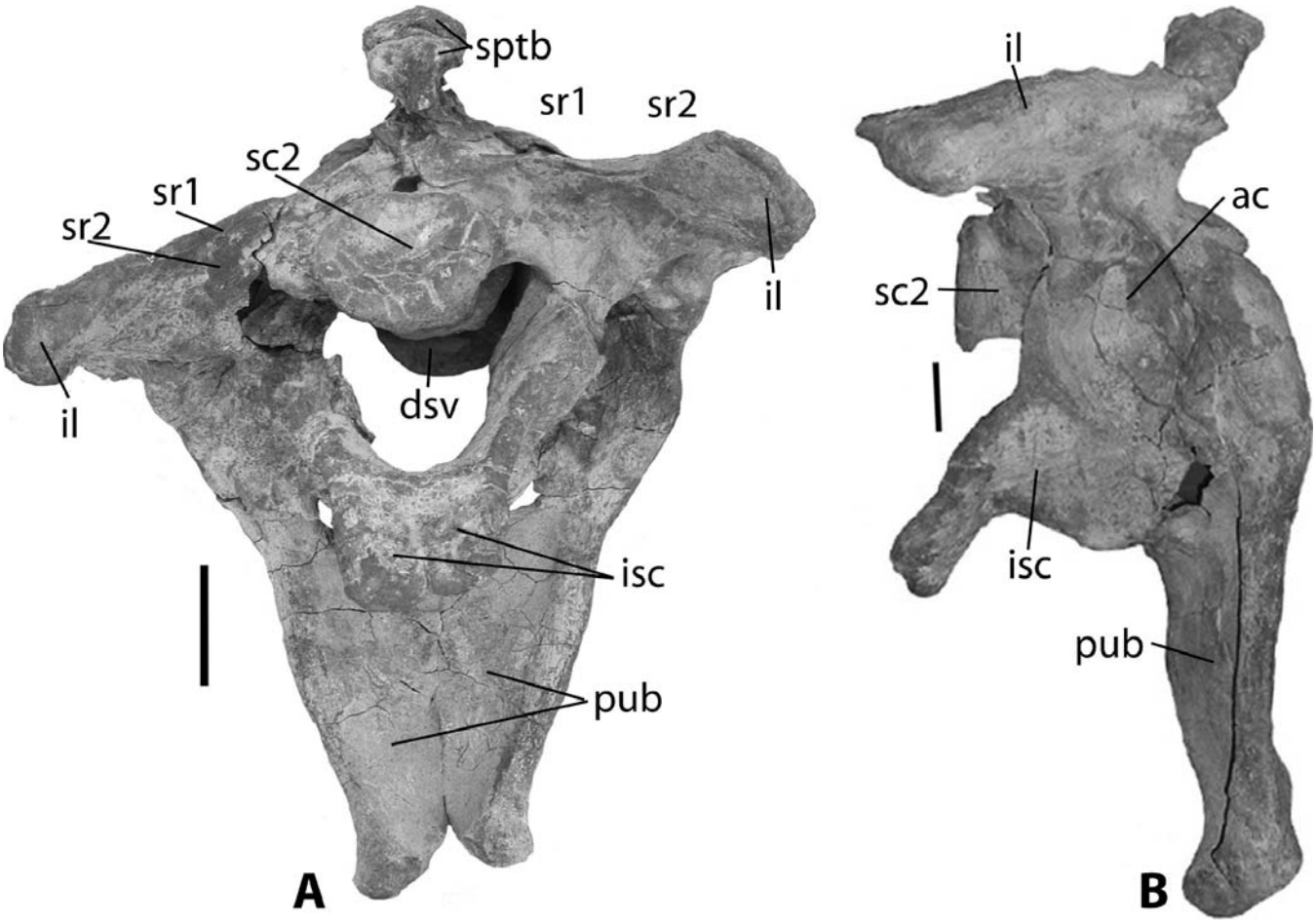

Figure 19. MNA V9300, sacrum. **A**. Posterior view. Scale bar = 10 cm. **B**. Right lateral view. Scale bar = 5 cm. Abbreviations: **ac**, acetabulum; **dsv**, dorsal vertebra; **il**, ilium; **isc**, ischium; **pub**, pubis; **sc2**, second sacral vertebra; **sptb**, spine table; **sr1**, first sacral rib; **sr2**, second sacral rib.

(2002) described two forms of chevrons for *Typothorax*, "slim" and "fat," but was unclear regarding the exact anteroposterior position of each type. MNA V9300 shows that the "slim" type occurs more anteriorly in *Desmatosuchus* and that the chevrons become shorter and fatter as they progress backwards. Anterior chevrons measure over 20 cm in length, indicating that the tail was extremely dorsoventrally deep directly behind the pelvis (Figs. 18D–E).

Pelvis

MNA V9300 possesses a well-preserved sacrum (Fig. 19A) that is extremely large compared to that of most known aetosaur specimens. Both ilia, both ischia, both pubes, a fused posterior dorsal vertebra, two sacral vertebrae, and four sacral ribs are present. Because the pelvis is encased in a thin crust of hematite, gypsum, and calcite, some of the details (including sutures) are obscured, precluding a more complete description of the individual elements. The pelvis is slightly crushed laterally and anterodorsally, folding the right ilium slightly, distorting the acetabulum of the left side, and possibly distorting the right preacetabular blade of the ilium and the distal ischia as well (see discussions below) (Fig. 19B).

The ilium is a more robust element, strongly fused into the pelvis by the sacral ribs. Details of this element are obscured by carbonate crust and overgrowths of bone on the ribs and iliac blade (Figs. 19A–B). The posterior blade is robust and elongate, projecting posteriorly well past the posterior face of the last sacral vertebrae and just past the distal end of the ischial peduncle, as in *Longosuchus* (Long and Murry 1995) but unlike those of *Stagonolepis* and *Typothorax* (Walker 1961, Martz 2002). The postacetabular blade is triangular in lateral view, similar to the isolated right ilium of UMMP 7322 assigned to *Desmatosuchus* by Long and Murry (1995), and differing from that of *Calyptosuchus* (UMMP 7470, UCMP 32422), in which the ilium is subrectangular in lateral view (Case 1922, Long and Murry 1995). The supra-acetabular "neck" of the ilium is constricted more like *Typothorax* (UCMP 34255); both specimens are more constricted than a specimen referred to *Desmatosuchus* (UMMP 7322) by Long and Murry (1995).

The right preacetabular blade of MNA V9300 is oddly distorted, with a strongly upturned mass of bone at the distal

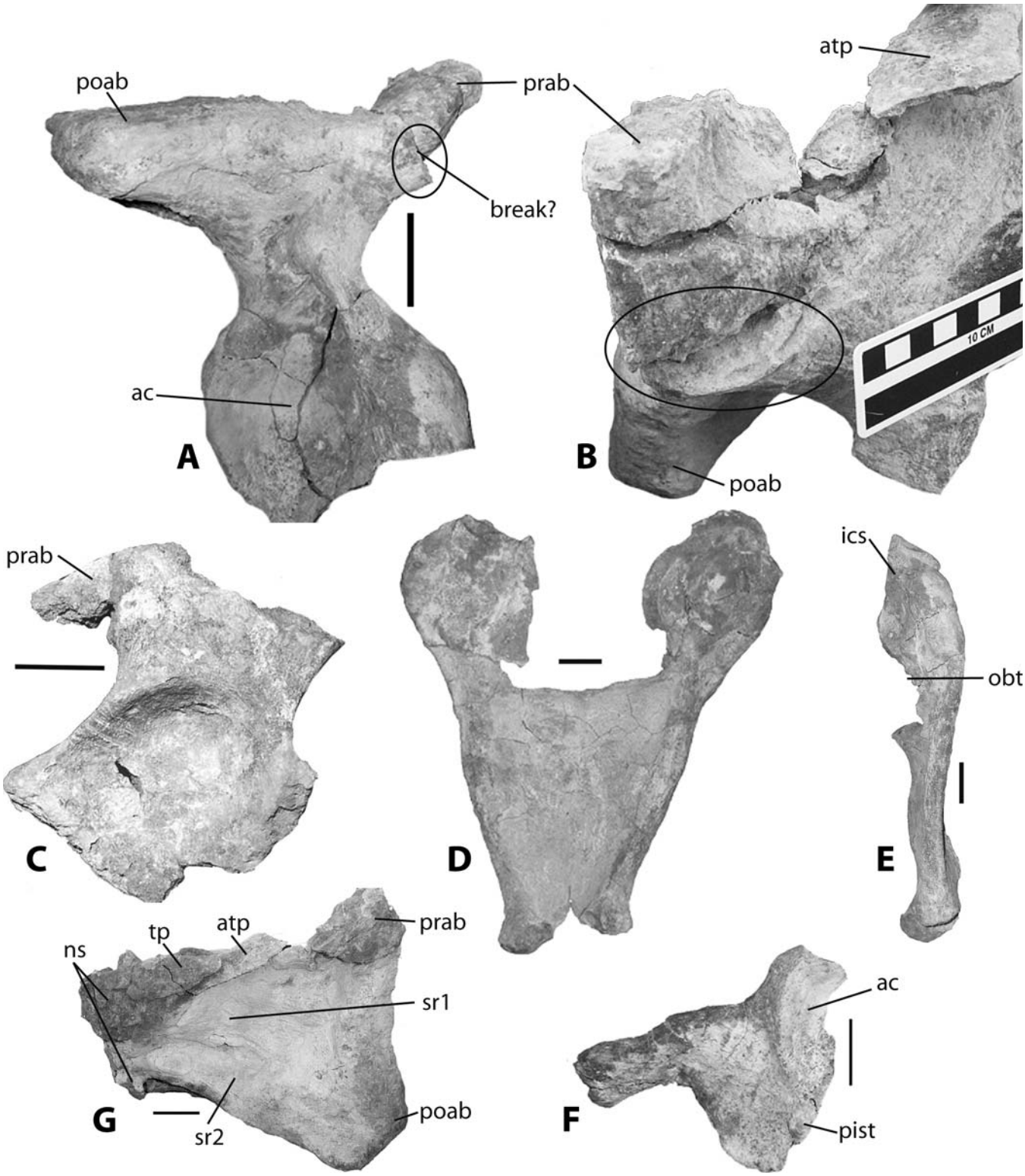

Figure 20. *Desmatosuchus spurensis*, pelvic elements. **A.** MNA V9300, right ilium in lateral view (circled area represent possible pathology), scale bar = 5cm. **B.** MNA V9300, close-up of anterolateral surface of right ilium showing irregular scalloped out area of smooth bone (circled). **C.** UMMP 7476, partial left ilium in lateral view. **D**. MNA V9300, fused pubes in posterior view. **E**. MNA V9300, fused pubes in right lateral view. **F.** MNA V9300, fused ischia in right lateral view. **G**. MNA V9300, sacral ribs of the right side in dorsal view. Scale bars for figs. C–G = 5 cm. Abbreviations: **ac**, acetabulum; **atp**, accessory transverse process; **ics**, iliac contact surface; **ns,** neural spine; **obt**, obturator foramen; **pist**, pubo-ischiatic suture; **poab**, post acetabular blade; **prab**, preacetabular blade; **sr1**, first sacral rib; **sr2**, second sacral rib; **tp**, transverse process.

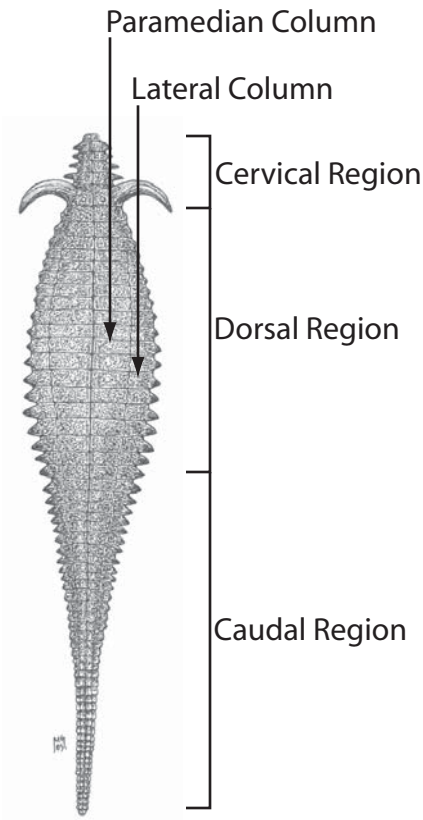

Figure 21. Nomenclature guide for armor positions in aetosaurs.

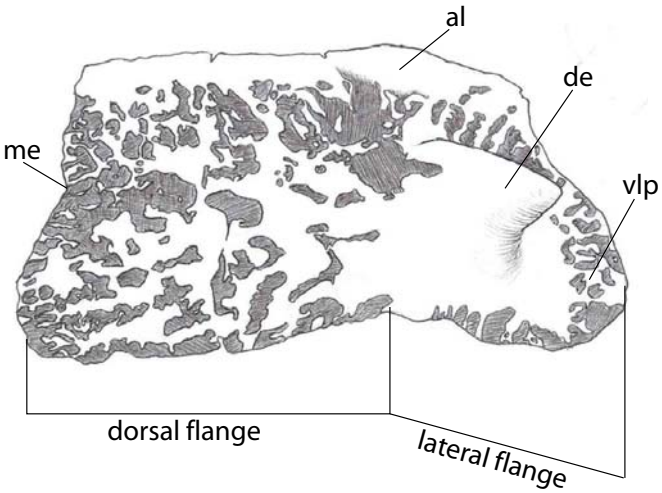

Figure 22. Morphological terminology for aetosaur plates. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **me**, medial edge; **vlp**, ventrolateral process.

end. Beneath this mass is a sharp ridge of bone bordering a scalloped face of smooth bone that resembles an articular surface (Figs. 20A–B). Strangely, this surface is located where the iliac blade should continue on to form the anterior iliac blade. This morphology is unique to the right side of this specimen and may be pathological; however, the left preacetabular blade is broken and incomplete so its exact morphology cannot be ascertained. In all other respects the ilium resembles that of a typical aetosaur, including the partial left ilium from UMMP 7476 (Fig. 20C).

The ilium contributes to the majority of the acetabulum and is laterally oriented oblique to the sagittal plane, as in *Lucasuchus* (TMM 31000-313) and *Neoaetosauroides* (PVL 5669) but unlike aetosaurs such as *Longosuchus* (TMM 31100-236), *Typothorax* (NMMNH P-36075, PEFO 33967), and *Aetosauroides* (PVL 2052), where the acetabulum is oriented ventrally (Long and Murry 1995, Desojo and Bàez 2005).

The pubes are extremely elongate. They are twisted in the typical pseudosuchian fashion (Walker 1961) with the two shafts extending ventrally and terminating with two expanded club-like ends that are probably homologous to the pubic boot of other suchians (Figs. 20D–E). The proximal ends are strongly curved posterodorsally, where they are completely fused to the pubic peduncles of the ilia. Typical of aetosaurs, the pubic apron is deep and broad (Fig. 20D). The regions that should contain the obturator foramina are broken and incomplete, so the morphology of the foramina is indeterminate.

The ischia are tightly fused to the posteroventral face of the ilium and the posterior edge of the proximal pubes (Fig. 19B), and are directed posteroventrally as is typical for aetosaurs. Closer to the distal end, however, the ischia are strongly bent ventrally, giving the anterodorsal edges an angle of almost 90° in lateral view (Fig. 20F), whereas in other aetosaur ischia the distal portion continues straight posteriorly. The bend occurs where the ischia appear to be somewhat broken and telescoped. Again, it is unclear whether this is pathological or post-mortem in origin.

Sacral ribs are large, winglike, and triangular in dorsal view (Fig. 20G) with the expanded lateral edge of the rib overlying the medial edge of the iliac blade. The posterolateral corner of the first sacral rib overlaps the anterodorsal corner of the second rib. Proximal ends are thickened and articulate with the lateral sides of the sacral vertebra.

Dermal Armor

Aetosaurs possess an extensive carapace of dermal osteoderms, which cover the entire back of the animal from behind the parietals of the skull to the tip of the tail, as well as the limbs (Fig. 21). Ventral "belly" armor is also present in many specimens. The armor over the back of the animal is arranged in four antero-posterior "columns," resulting in a carapace that is segmented into quadrangular plates that form transverse bands (or "rows") across the back of the animal (Heckert and Lucas 1999). These four columns include two paramedian columns on either side of the midline of the animal, and each paramedian column is flanked by a column of lateral plates. Thus, each transverse row consists of two paramedian and two lateral plates. These rows can be divided into cervical, dorsal, pelvic, and caudal plates, based upon the type of vertebra the plate is covering (Long and Ballew

1985). In most aetosaurs, such as *Stagonolepis* and *Typothorax* (Walker 1961, Martz 2002), each plate corresponds to the single vertebra that it covers. Although *Desmatosuchus* and *Longosuchus* were thought to have five or possibly six rows of plates covering nine cervical vertebrae (Case 1920, 1922, Elder 1978, Long and Ballew 1985), there is evidence that suggests the plates of the dorsal and caudal regions each cover a single vertebra. For example, the third dorsal paramedian is situated above the third dorsal vertebra. In addition, some aetosaurs have a ventral carapace consisting mainly of equant (square) overlapping plates covering the underbelly (e.g., Walker 1961). Also, in aetosaurs known from articulated remains, the upper appendages are at least partially covered with small round to sub-round scutes that do not articulate in an organized fashion (e.g., Heckert and Lucas 1999).

For many aetosaur taxa, the ornamentation of dermal armor is diagnostic to at least the genus level (Long and Ballew 1985). Aetosaur dermal plates possess suites of characters relating mainly to shape and ornamentation and it is the combination of these characters within individual plates that is diagnostic; rarely are individual characters autapomorphic by themselves (Martz and Small 2006). Long and Ballew (1985) introduced morphological names for many of these characters, and their terminology (Fig. 22) has been adopted by most workers. An additional term, "ventrolateral process of the lateral flange," is introduced here. The plate in Fig. 22 can be described following the terminology of Long and Ballew (1985) as having a random, not radial, pattern of pits and ridges for the dorsal surface ornamentation.

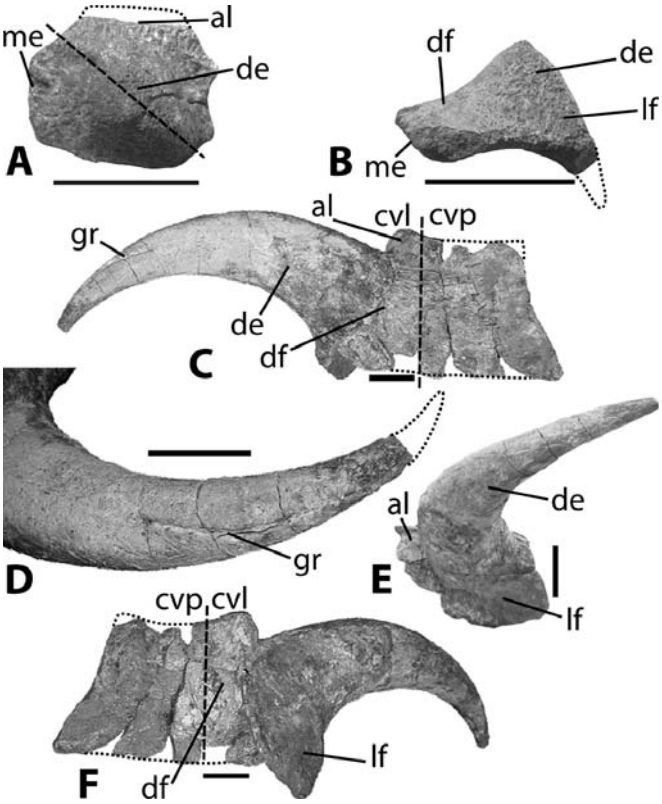

Figure 23. MNA V9300, cervical lateral armor. **A.** First right cervical lateral plate in dorsal view, dashed line shows trend of the dorsal eminence. **B.** First right cervical lateral plate in posterior view. **C.** Fifth left cervical lateral plate with fused paramedian plate in dorsal view. Dashed line shows approximate line of division between two plates. **D.** Distal end of spine of fifth left cervical lateral plate showing distinct groove. **E.** Fifth left cervical lateral plate in left lateral view. **F.** Fifth left cervical lateral plate with fused paramedian plate in ventral view. Dashed line shows approximate line of division between two plates. Dotted lines show missing portions of bone. Scale bars = 5 cm. Abbreviations: **al**, anterior lamina; **cvl**, cervical lateral; **cvp**, cervical paramedian; **de**, dorsal eminence; **df**, dorsal flange; **gr**, groove; **lf**, lateral flange; **me**, medial edge.

Cervical Paramedian Plates

The cervical paramedian plates of *Desmatosuchus* are described and figured in detail by Case (1922) and Long and Ballew (1985), and MNA V9300 does not add anything new to our knowledge of this region because much of the cervical paramedian armor of the specimen was lost to erosion prior to collection. Several plates were pieced back together from fragments recovered as float. These include what is probably the left paramedian plate of the first cervical series, and the left plate from what traditionally would be considered the fifth cervical series (Case 1922). The fifth plate is strongly fused to the associated left lateral plate, which possesses the huge recurved horn, and to the medial portion of the right paramedian plate of the same series. Like those of many other aetosaurs, cervical plates from all series maintain the same overall morphology with an increase in size and thickness posteriorly. Parker (2005a) suggested that *Desmatosuchus* had six rows of paramedian plates rather than the five depicted for UMMP 7476 (Case 1922, Long and Ballew 1985, Long and Murry 1995). The possibility that *Desmatosuchus* had the same number was first proposed by Elder (1978). Because the cervical armor series of MNA V9300 is not well preserved, it does not resolve this problem. *Desmatosuchus spurensis* is considered here to have five rows of plates, even though it is likely that a sixth row was present in the form of two small paramedians that articulated directly with the back of the parietals. This first row of plates would probably have been without laterals; similar to the condition in aetosaurines like *Aetosaurus* (Schoch 2007) and *Neoaetosauroides* (Desojo and Bàez 2005). Six cervical plates are also present in the desmatosuchine *Longosuchus* (Sawin 1947).

Cervical Lateral Plates

Cervical lateral plates are the most diagnostic plates of the *Desmatosuchus* carapace, as they possess the large, recurved horns that characterize the genus. These were described in detail by Case (1922) and Long and Ballew (1985). MNA V9300 preserves only two of these plates. The first element is a right plate from probably the first cervical lateral series just behind the skull (Fig. 23A). Although incomplete, this

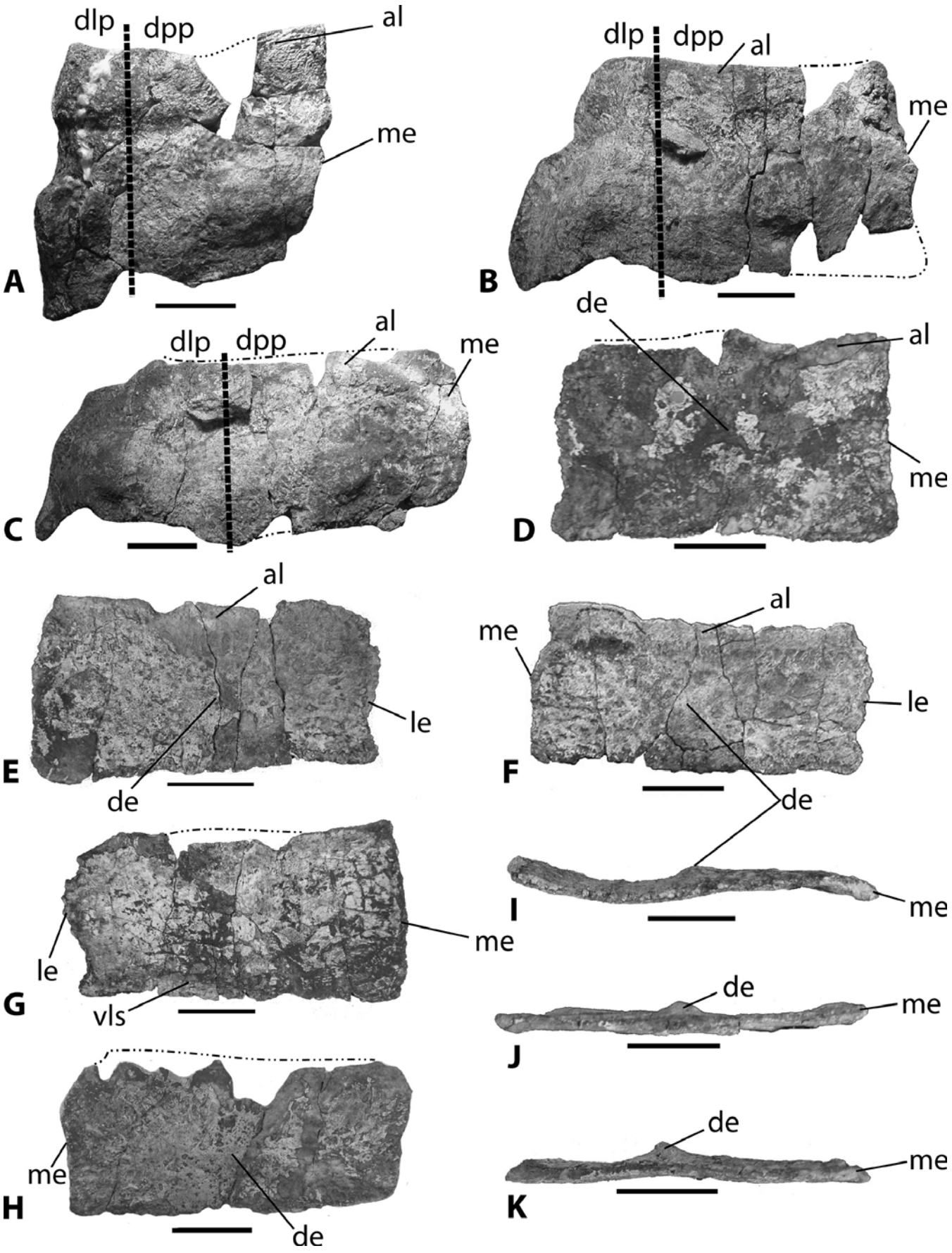
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plate is very thick like all cervical plates of *Desmatosuchus*, and it possesses a short, blunt, pyramidal eminence that is barely above the dorsal flange surface. In posterior view, this plate appears triangular (Fig. 23B) with the dorsal and lateral sides of the eminence meeting at almost 90°. This is similar to the condition of UMMP 7476 and differs from that of *Desmatosuchus smalli*, which possesses a more elongate sharp spine. This also differs from *Longosuchus*, which has a longer posterodorsally projecting spine. The boss on the anterior cervical lateral of MNA V9300 is oriented obliquely. Bosses on plates of the right side have their long axes from the anteromedial edge to the posterolateral edge of the plate (Fig. 23A). This condition is present in both species of *Desmatosuchus* and in *Longosuchus* as well.

The other preserved lateral plate includes the large recurved horn of the fifth (or possibly sixth; see discussion above) series, which is complete and more than 61 cm in length along its anterior edge (Fig. 23C). The plate is similar in overall morphology to the corresponding plate of UMMP 7476, but it is much more robust. It also is considerably more elongate, robust, and recurved than those of TTU P-9024 and ANSP 14688. The anterodorsal edge of the distal end has an elongate groove extending from the apex of the spine medially along nearly one third of the total spine length (Fig. 23D). This groove was probably a channel for blood vessels feeding the constantly growing horn and it is similarly positioned in many of the large spines of *Desmatosuchus*. The characteristic orientation of this groove allows for easy differentiation of the left and right sides of spines that have only their distal end preserved.

The horn differs from those of *Longosuchus* in its strong recurvature, robustness, and lack of faceting, and in its overall proportion to the other lateral plates of the carapace. This spine is at least three times longer than the next largest carapace spine, whereas those of *Longosuchus* are more consistent in length throughout the cervical series. The horn of *Desmatosuchus spurensis* is flattened dorsoventrally, thus its cross-section is subcircular (Case 1922:fig. 17b). The spine is strongly recurved backwards, extending as far as the posterior border of the corresponding paramedian plate. The distal third of the spine is curved slightly upwards and laterally (Fig. 23E).

The dorsal flange is short mediolaterally, extending little more than half the length of the lateral flange. The medial edge of the dorsal flange thickens dorsoventrally and is the thickest plate in the entire carapace; it is strongly fused with the corresponding paramedian plate (Figs. 23C, F). The anterior lamina is also greatly thickened and extends anteriorly approximately 3 cm past the anterior edge of the horn (Fig. 23E). The lateral flange is deflected ventromedially at an approximate angle of 45°, although this flexion is probably due to postmortem crushing given that the flanges of the similar horn of UMMP 7476 are at a right angle to each other. Overall, these plates are extremely alike in both MNA V9300 and UMMP 7476. The corresponding plate in TTU P-9024 (*D. smalli*) lacks a strongly developed dorsal flange and the horn is not as recurved as in UMMP 7476 and MNA V9300. The corresponding element in ANSP 14688, although incomplete, is more similar to TTU P-9024 than UMMP 7476.

With the exception of a weathered fragment of what could be a third or fourth series plate, the other cervical lateral plates of MNA V9300 are not preserved. This element does not resemble the more elongate, gracile spines of *Desmatosuchus smalli* (TTU P-9024), but it is too fragmentary to provide much information.

Dorsal Paramedian Plates (Fig. 24)

MNA V9300 preserves numerous paramedian plates of the dorsal region. Because many of these plates are jumbled and fused diagenetically, it is not possible to place all of them back into their proper order. Nonetheless, the number and preservation of the plates provides new information about their morphology and variation.

Similar to the cervical paramedians, anteriormost dorsal paramedian plates are greatly thickened dorsoventrally; these plates are generally twice the thickness of the mid-dorsal paramedian plates. The width/length ratios of the preserved dorsal paramedians range between 0.7:1 and 1.8:1. In known articulated aetosaur specimens, this ratio increases posteriorly through the mid-dorsal region allowing for hypothetical placement of these plates within the skeleton of MNA V9300. Plates also gradually become dorsoventrally thinner within this same interval. Medial and lateral edges are expanded dorsoventrally in the more anterior plates, possessing complex tongue-and-groove articular surfaces (Long and Ballew 1985). Medial edges are always straight in dorsal view, whereas the lateral edges are strongly sigmoidal throughout the series with the exception of the more posterior dorsal plates, including those of the pelvic region, in which the edge becomes straight. Dorsal eminences are always present, yet barely raised above the plate surface, becoming more pronounced in the more posterior plates, which is typical for aetosaurs. Anterior laminae (Long and Ballew 1985) are thick in the more anterior plates and gradually thin in the more posterior plates. These laminae are generally not as well

◄ **Figure 24.** MNA V9300, paramedian plates of the dorsal series. The first three are fused to lateral plates. **A**. First left series in dorsal view. **B**. Second left series in dorsal view. **C.** Third left series in dorsal view. **D**. Fourth left plate in dorsal view. **E**. Fifth right plate in dorsal view. **F**. Sixth right plate in dorsal view. **G**. Fifth right plate in ventral view. **H**. Left posterior plate in dorsal view. **I**. Mid-paramedian plate in posterior view. **J**. Seventh left plate in posterior view. **K**. Left posterior plate in dorsal view. Scale bars = 5 cm. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **dlp**, dorsal lateral plate; **dpp**, dorsal paramedian plate; **le**, lateral edge; **me**, medial edge; **vls**, ventral longitudinal striations.

defined anteriorly as they are posteriorly. Ornamentation is faint in anterior plates and becomes more deeply incised more posteriorly. In addition, the anteriormost dorsal paramedians are often fused to the adjacent lateral plate.

The first left dorsal paramedian plate (Fig. 24A) is almost complete, missing only small portions of the anterior and posterior margins. This plate is trapezoidal in dorsal view with straight lateral and medial margins and posterolaterally directed anterior and posterior margins. The lateral and medial margins are slightly longer than the maximum plate width. This plate is extremely thickened like the cervical paramedians and could easily be mistaken as such. It is considered a dorsal plate in this study because it is articulated with the first dorsal lateral plate (which can be identified by its lack of a spine). Thus, larger anterior paramedian plates of the carapace can only be accurately assigned to a specific region (cervical or dorsal) when their association with lateral plates is preserved. The dorsal surface possesses a thickened, rugose anterior lamina. Overall plate ornamentation is very faint, like cervical and anterior dorsal plates in other aetosaur taxa (Heckert and Lucas 1999, Parker 2007). The ornamentation consists of a random pattern of pits and ridges consistent with past descriptions of *Desmatosuchus* (e.g., Long and Ballew, 1985). The dorsal eminence is broad and round, yet barely discernable above the rest of the dorsal surface of the plate. The medial edge is extremely thick, flares dorsoventrally, and possesses the complex articular surface diagnostic of this taxon. Laterally, the plate thickens slightly where it is strongly fused to the adjacent lateral plate; thus, characters of the lateral edge are not clearly discernable. The ventral surface is concave transversely and slightly convex anteroposteriorly. The ventral surface is slightly undulating and smooth, except for a series of transverse, raised striations running the entire width of the posterior margin. These striations mark where the posterior portion of the plate overrides the upper anterior surface of the posteriorly adjacent plate. A slight concavity on the ventral surface opposite the dorsal eminence is a common feature in aetosaurs.

The second left dorsal paramedian plate (Fig. 24B) is incomplete, missing much of the posterior margin. This plate is also greatly thickened with an expanded lateral margin that is strongly fused to the adjacent lateral plate. The anterior lamina is thick and not well defined. The dorsal ornamentation and ventral surface characteristics are similar to those of the first plate; however, the area between the anterior lamina and dorsal eminence is slightly depressed, forming a notable band along the entire plate width.

The third left dorsal paramedian plate (Fig. 24C) is very similar to the second plate except that it is thinner and shorter anteroposteriorly, though it is still much thicker than more posterior dorsal plates. The right plate of this series possesses a lateral edge that is not fused to the adjacent lateral plate. This edge is thickened with the complex tongue-and-groove articular surface and is sigmoidal in dorsal view.

The fourth left dorsal paramedian plate (Fig. 24D) is also very similar to the previous plates except that the width/length ratio is greater, the anterior lamina is thinner, and the concavity of the ventral surface is less pronounced, reflecting a lessened flaring and overall thinning of the lateral and medial edges; however, the complex articular surfaces are still apparent. The right paramedian plate of this series is also preserved and is identical to the left plate.

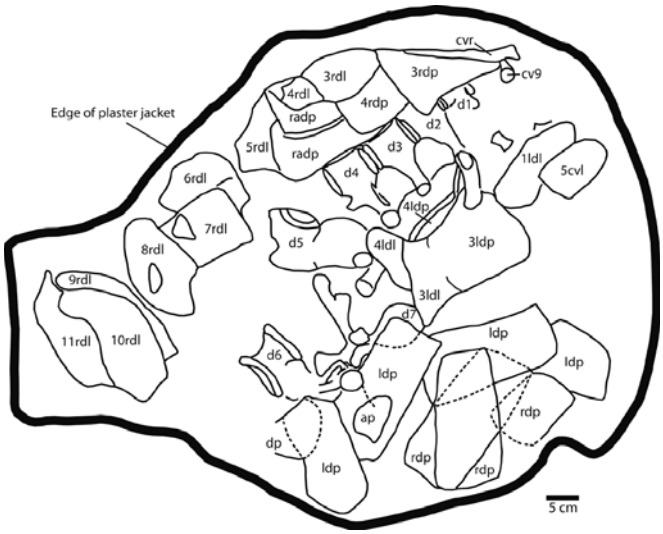

Figure 25. MNA V9300, sketch of in-situ elements as found in a single block (ventral view). Numbers correspond to interpreted positions. Abbreviations: **ap**, appendicular plate; **cv**, cervical vertebra; **cvl**, cervical lateral plate; **cvr**, cervical rib; **d**, dorsal vertebra; **dp**, dorsal paramedian plate; **ldl**, left dorsal lateral; **ldp**, left dorsal paramedian plate; **radp**, right anterior dorsal paramedian; **rdl**, right dorsal lateral; **rdp**, right dorsal paramedian plate.

Plates throughout the rest of this series (numbering approximately 17 on each side, each corresponding with a single vertebra of the dorsal and sacral series) continue to become wider, thinner, and more deeply incised (Figs. 24E–H). Just before the pelvic area, the lateral edges are straight rather than sigmoidal, the ornamentation is more incised, and the dorsal eminences are more pronounced (Figs. 24I–K). Posterior-most dorsal paramedian plates start to develop a slight transverse arching over the pelvic area and abruptly become thicker, although never as thick as the anterior dorsals or cervicals. There is no clear evidence for the rapid narrowing of the series to form the pronounced "waist" suggested by Long and Murry (1995), but the lateral extent of the posteriormost dorsal ribs compared to the pelvic width suggests that the carapace may have narrowed slightly just anterior to the pelvis.

Dorsal Lateral Plates

MNA V9300 preserves an almost complete dorsal lateral series of the right side. Although slightly disarticulated, these plates were found in order and adjacent to the articulated cervico-dorsal vertebral series (Fig. 25). Dorsal lateral plates of the left side are only preserved through the first four or

five rows. The positions and order of the left anterior dorsal series (including the paramedians) and the right dorsal laterals were determined by comparing the fit of the plates with the presumption that the plates become slightly wider and shorter posteriorly. These positions were confirmed by noting the positions of each element as preserved in-situ (Fig. 25).

Except for the first dorsal lateral plate, the dorsal lateral plates are generally rectangular in overall shape with a strong flexion at the center of ossification (i.e., thickest portion of the plate and location of the dorsal eminence), which is closer to the lateral portion of the plate. This flexion separates the plate into distinct dorsal and lateral flanges. In *Desmatosuchus*, the dorsal flange is longer than the lateral flange in the dorsal series. As stated earlier, all previous reconstructions based on Case's (1922) original reconstruction are erroneous because the lateral armor was interpreted in reverse. Dorsal lateral plates can be subdivided into three distinct regions based on morphology.

Anterior Dorsal Lateral Plates: *1st–4th series* (Figs. 24A–C, 26A–I)—The first four plates of the dorsal lateral series can be identified because of their distinct morphology. Most notably, the dorsal eminence is not a spine but rather a large, obliquely oriented, ellipsoidal, low knob. These plates are identical to those figured by Brady (1958:figs. 2,3) (MNA V687), which probably represent the left and right plates of the 2nd series. The peculiar bent outer edge of the left plate, as described by Brady, actually represents the lateral flange of a fused lateral plate and not the flexure of a single paramedian plate (personal observation, Long and Murry 1995). Examination of figure 4 in Brady's description clearly shows the suture on the underside between the associated paramedian and lateral plates. UCMP 126824, as figured in Long and Ballew (1985: fig. 5C), also belongs to this series and is not a mid-dorsal plate as postulated by those authors.

The angle of flexion in these plates is greatly obtuse, presumably to provide space for movement of the forelimb. Lateral margins are gently curved posterolaterally, sometimes forming a tongue-shaped process at the posterolateral extremity (the ventrolateral process). Medial edges are greatly thickened and flared, possessing the complex tongue-and-groove articular surface, although the anteriormost plates are often fused to the adjacent paramedian plate, obscuring this feature. In the plates that are fused, the suture area is particularly thickened with a crescentic suture line with the lateral margin of the paramedian plate being convex in ventral view and the medial margin of the lateral plate being concave in ventral view. The anterior lamina is thick and not well defined, similar to those in the paramedian plates.

The first left dorsal lateral plate (Figs. 24A, 26A–B) is highly distinctive because it is very large, with equant dimensions of the dorsal and lateral flanges, and a strong, acute flexion. The position of this plate can be ascertained by its fusion with what is obviously an anterior dorsal paramedian plate, as well as its taphonomic association with the other plates. If found isolated, its proper position would be ambiguous. It is not clear whether this abnormally strong flexion is diagenetic in nature; however, the angle of this plate is similar to that of the posterior portion of the anteriorly adjacent last cervical lateral plate. In lateral view, the lateral flange is trapezoidal in shape with the anterior and posterior margins being roughly parallel and the posterior margin half the width of the anterior margin. The lateral margin is straight and thin and roughly forms right angles with the two adjoining sides. The upper (dorsal) margin is sloped posteriorly about 60° from the anterior margin. The posterior margin of the dorsal flange is slightly curved anteromedially, joining the posterior edges of the lateral flange and the posterior margin of the associated paramedian plate. This plate is greatly thickened, similar to cervical plates, and solidly fused medially with the adjoining paramedian plate. The anterior lamina is thickened and weakly defined like other plates from the region. Orna-

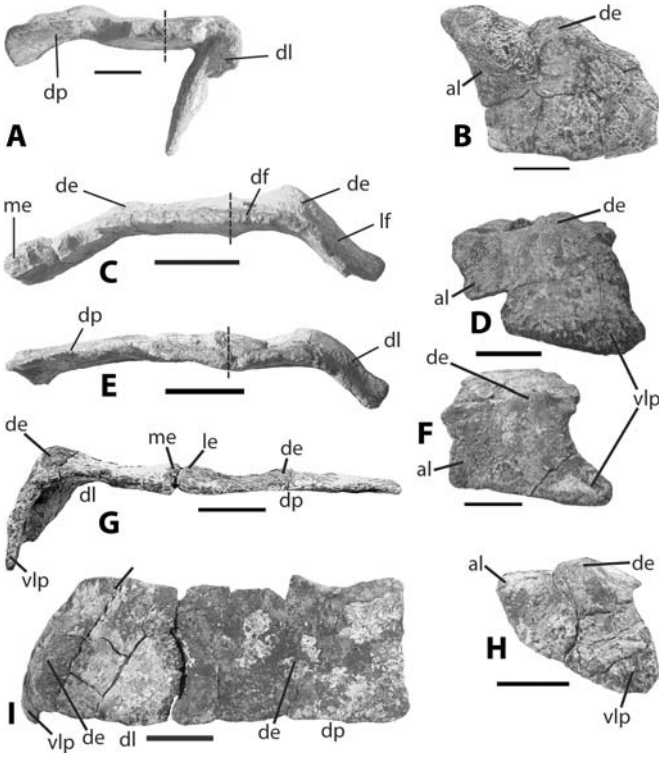

Figure 26. MNA V9300, anterior dorsal armor series. **A**. First left lateral plate with fused paramedian in anterior view. **B**. First left lateral plate in left lateral view. **C**. Second left lateral plate with fused paramedian in anterior view. **D**. Second left lateral plate in left lateral view. **E**. Third left lateral plate with fused paramedian in anterior view. **F**. Third left lateral plate in left lateral view. **G**. Fourth left lateral plate with left paramedian plate of the same series in posterior view. **H**. Fourth left lateral plate in left lateral view. **I**. Fourth left lateral plate with left paramedian plate of the same series in dorsal view. Scale bars = 5 cm. Dashed lines approximate suture between lateral and paramedian plates. Abbreviations: **de**, dorsal eminence; **df**, dorsal flange; **dl**, dorsal lateral; **dp**, dorsal paramedian; **lf**, lateral flange; **me**, medial edge; **vlp**, ventrolateral process.

mentation consists of a shallowly incised pattern of random pits and ridges. On the dorsal surface, there are two distinct anteroposteriorly elongate knobs positioned anteroposteriorly along the ridge of flexion. These knobs are raised and slightly directed dorsolaterally. In the area just ventrolateral to the most anterior knob, the plate appears to be broken with the uppermost portion of the lateral flange appearing to be slightly overlapped by the ventrolateral edge of the knob. This gives the lateral plate an offset "T" shape in anterior view with the lateral flange forming the vertical base and the dorsal flange forming the crossbar (Fig. 26A). This "breakage" does not occur in the posterior portion of the plate nor is it visible in posterior view. It is not clear whether this feature is natural, pathologic, or post-mortem. The ventral surface of this plate is smooth except for a series of thin, raised striations that run transversely along the length of the posterior ventral margin.

The second dorsal lateral series is represented by both plates, although the lateral plate from the right side is incomplete in the area anterior and medial to the dorsal eminence. The left lateral plate of this series (Figs. 24B, 26C–D) is complete; it is dorsoventrally thickened and flexed ventrolaterally at an angle of 45° just lateral to its medial edge. The plate is roughly trapezoidal in lateral view with the anterior and posterior margins sloping posterolaterally. The lateral edge is the thinnest portion of the plate, forming a broad posterolateral curve that terminates in a small posterolateral projection where it meets the posterior edge. The medial edge is strongly fused to the adjacent paramedian plate. A thick anterior lamina on the anterior edge of the plate is separated from the main body of the plate by a slight depression that mediolaterally extends across the entire width of the plate. The ventral surface is smooth. There is a fairly deep depression positioned below the dorsal eminence. Posterior to this depression, there is a strong, thickened ridge forming the posterior border of the plate. The dorsal eminence has the form of a low, broad, oblique, elliptical knob. No spine is apparent.

The third left dorsal lateral plate (Figs. 24C, 26E–F) is very similar to that of the second series except that (1) the plate is shorter anteroposteriorly, (2) the plate is thinner (although it is still thicker than more posterior plates), (3) the posterolateral process is strongly developed and tongue-shaped in dorsolateral view, (4) the depression between the anterior lamina and dorsal eminence is not as deep, and (5) the dorsal eminence is lower and broader. The third plate from the right side is also preserved, although it is missing the entire region lateral to the dorsal eminence. This plate is not fused to its associated paramedian plate and demonstrates that the median edge is thickened with the complex tongue-and-groove articular surface. In addition, the median edge is sigmoidal in both medial and dorsal views.

The fourth left dorsal lateral plate (Figs.26G–I) is also very similar to the previous plates except that (1) it is more shortened anteroposteriorly, (2) the posterolateral process is not developed, (3) the depression between the anterior lamina and dorsal eminence is not present, (4) the dorsal eminence is higher and more elliptical, and (5) the plate is flexed at a steeper angle (this may be diagenetic). The fourth plate from the right side is also present but incomplete. Although the plates of this series are not fused to their associated paramedians, they have the thickened, complex, articular surfaces, as well as medial edges that are sigmoidal in dorsal and medial views (Fig. 26I).

Anterior Mid-dorsal Lateral Plates: 5th–8th series (Figs. 27A–D)—The next four plates of the dorsolateral series can also be grouped according to shared characteristics that make them transitional in form between the more anterior dorsal lateral plates and the rest of the series. The plates from the right side of this series were found semi-articulated. These plates are noticeably thinner dorsoventrally than those of the anterior dorsal and cervical series. Anterior laminae are thin, delicate, and distinct. Posterolateral processes of the lateral flange are well-developed. Dorsal eminences become higher and become progressively sharper until they finally take the form of short conical spines. The dorsal flange is at least twice as long as the lateral flange in this series, and the dorsal eminences are situated more posteriorly on the plate, close to the posterior margin but not in contact with it. Lateral edges are strongly sigmoidal, and the posterior margin of the plate is much longer than the anterior margin. Because the lateral flanges are slightly concave in posterior view, the posterolateral process of this flange is nearly horizontal. This is strikingly different than the condition on the posterior mid-dorsal and posterior dorsal plates. Only the plates of the right side from this series are preserved.

The fifth right dorsal lateral plate is complete (Fig. 27A) and even thinner dorsoventrally than the previous plates. The angle of flexion between the dorsal and lateral flanges is less than 40°, giving the plate and almost horizontal appearance in anterior and posterior views. This is very different from the rest of the plates in the series. The medial edge is sigmoidal in both medial and lateral views and slightly thickened with the tongue-and-groove articular surface. The anterolateral process of the lateral flange is strongly developed, making this flange almost triangular in lateral view. The anterior portion of the lateral flange possesses a deep, crescentic embayment that disrupts the anterior lamina. The plate does not appear to be broken and it is unclear if this feature is pathological because the corresponding plate of the right side is not preserved. The dorsal eminence is strongly developed, forming a broad, oblique, semi-circular knob raised well above the surface of the plate and making up a large portion of the lateral flange. On the ventral surface there is a deep concavity that corresponds with this eminence; however, the strongly developed posterior ridge on the anterior dorsal lateral plates is not present. The ventral surface is smooth except for the usual thin, transverse strip of raised striations on the posterior margin.

The sixth right dorsal lateral plate (Fig. 27B) is broken

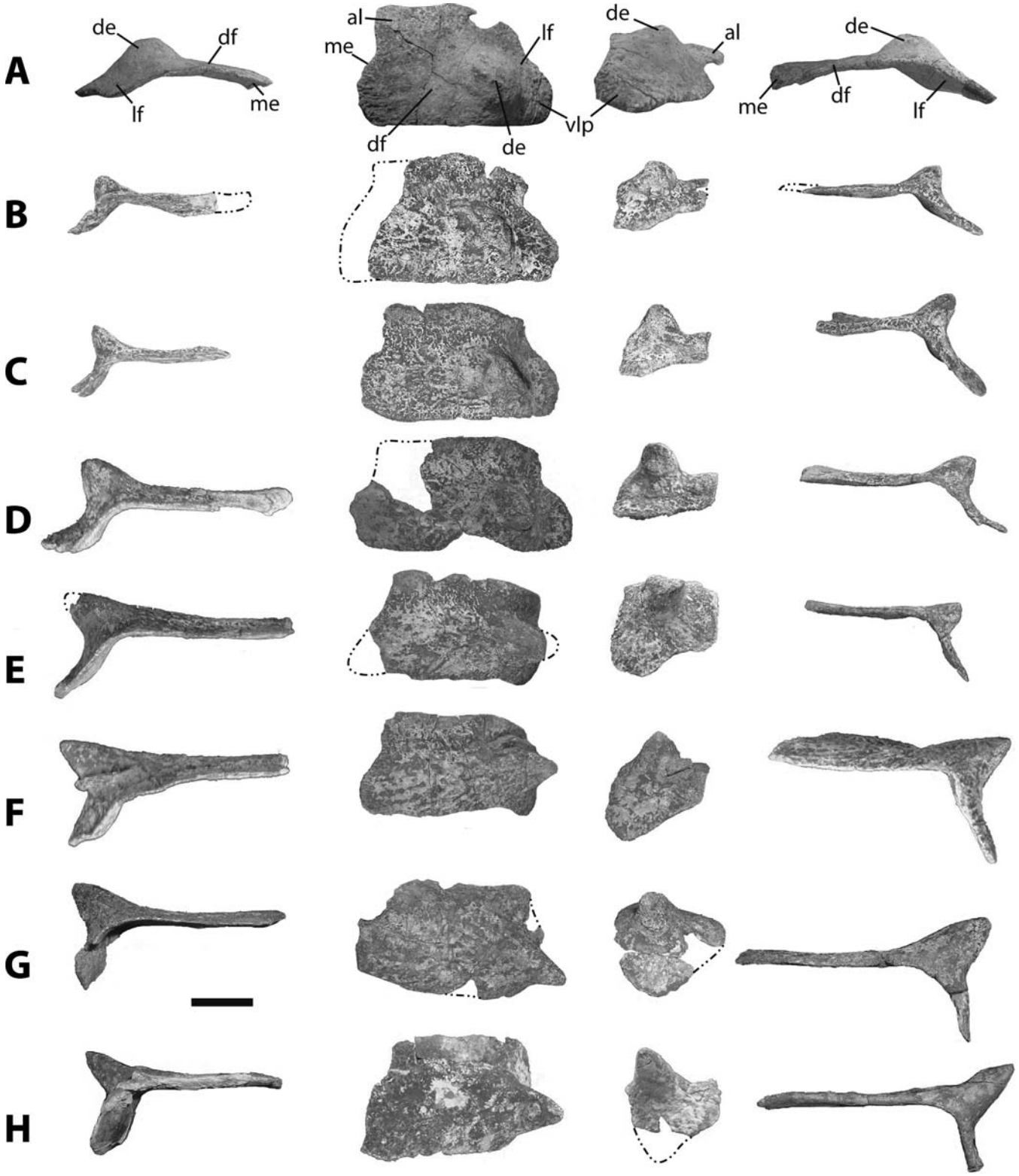

Figure 27. MNA V9300, anterior and mid-dorsal paramedian plates in anterior, dorsal, lateral, and posterior views. **A**. Fifth right dorsal lateral plate. **B**. Sixth right dorsal lateral plate. **C**. Seventh right dorsal lateral plate. **D**. Eighth right dorsal lateral plate. **E**. Ninth right dorsal lateral plate. **F**. Tenth right dorsal lateral plate. **G**. Eleventh right dorsal lateral plate. **H**. Fifteenth right dorsal lateral plate. Scale bar = 5 cm. Dashed lines show missing portions of elements. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **df**, dorsal flange; **lf**, lateral flange; **me**, medial edge; **vlp**, ventrolateral process.

and missing its medial portion. The preserved element is very similar to that of the fifth series except that the dorsal eminence is strongly oriented obliquely and raised to form a low ridge that is slightly acute at the apex. The ridge is higher and sharper on the seventh left dorsal lateral plate (Fig. 27C).

By the eighth series (Fig. 27D), the anteroposterior length of dorsal lateral plates is decreasing. The medial edges are much thinner dorsoventrally but still sigmoidal in dorsal view possessing the tongue-and-groove articular surface. The anterior laminae are extremely thin and delicate; the anterior edge is sharp. In the eighth plate, the dorsal eminence is taller than in the previous plates and thickened mediolaterally, appearing more like a conical spike than a ridge.

Posterior Mid-dorsal Lateral Plates: 9th–15th series (Figs. 27E–H)—The first three plates of this series are the last lateral plates to be found in association with the rest of the right lateral series. From the twelfth dorsal lateral through the anterior caudals, the relative positions have been estimated by fit. It appears as though all of these series are preserved in the specimen.

The posterior mid-dorsal lateral series includes four plates that are distinct from the others in the series. These plates are characterized by dorsal eminences that are robust, spine-like, and strongly directed dorsolaterally; however, the spines are directed more laterally than dorsally contrary to previous reconstructions (Case 1922, Long and Murry 1995), and are at a much lower angle with the lateral flange than with the dorsal flange. The 50° to 80° angle of plate flexion between the two flanges is more acute than that of the more previous plates These plates are shorter anteroposteriorly and wider transversely than the anterior mid-dorsal plates. The median edge is still strongly sigmoidal, and the general trend of dorsoventral thinning of the plates continues. Anterior laminae are extremely thin and delicate. The ventral surface is smooth except for the striations on the posterior margin and there is a deep embayment beneath the dorsal eminence. Just lateral to this embayment on the ventral surface, a slight dorsoventral swelling makes this area the thickest part of the plate.

The ninth right dorsal lateral plate (Fig. 27E) was diagenetically fused to the underside of the tenth plate of the same series. Separation during preparation has destroyed the apex of the dorsal eminence of the ninth plate, which was identical to that of the tenth (Fig. 27F). Both of these plates correspond to the general description of the series as given above except that the angle of flexion between the flanges become more acute.

The tenth left dorsal lateral plate is incomplete, missing most of the lateral flange. It is identical to the corresponding plate of the right side, including the increased angle of flexion.

The eleventh right dorsal lateral plate is the last of the preserved associated series of the right side (Fig. 27G). The distal portion of the lateral flange of this plate is missing. The angle of flexion of this plate is slightly higher than the proceeding one. This plate is also wider transversely than the previous ones, beginning a widening trend that proceeds posteriorly through the plates of the pelvic area.

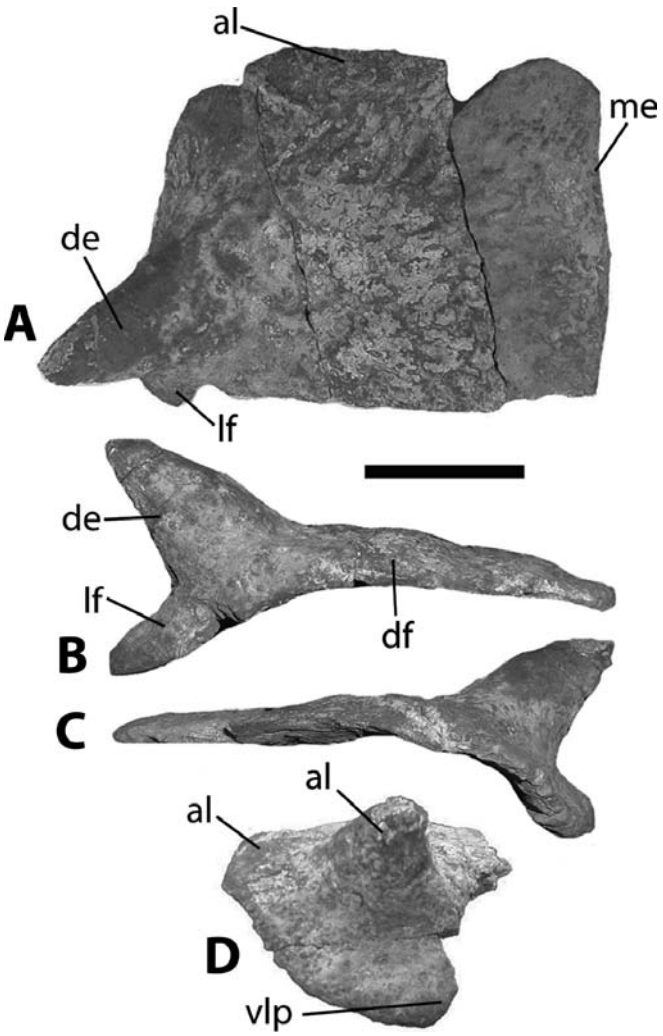

Figure 28. MNA V9300, posterior dorsal or pelvic lateral plate. **A**. Dorsal view. **B**. Posterior view. **C**. Anterior view. **D**. Lateral view. Scale bar = 5 cm. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **df**, dorsal flange; **lf**, lateral flange; **me**, medial edge; **vlp**, ventrolateral process.

The twelfth through seventeenth dorsal lateral plates were found scattered in the quarry, making precise assignment difficult. What are presumably the fourteenth and fifteenth (Fig. 27H) right dorsal lateral plates are similar to the plates from the eleventh through thirteenth series, except that the medial edge is becoming less sigmoidal dorsal view. These plates are still thin dorsoventrally and are the thinnest plates of the entire dorsal series.

Posterior Dorsal Lateral (Pelvic) Plates: 16th–17th series (Figs. 28A–D)—The two plates of this series possess several distinctive features, including a straight medial edge, extreme development of the dorsal eminence of the seventeenth plate, and the reduced size of the lateral flange. In addition, the lateral edge is weakly sigmoidal and only one-quarter the length of the dorsal flange. This is in contrast to the previ-

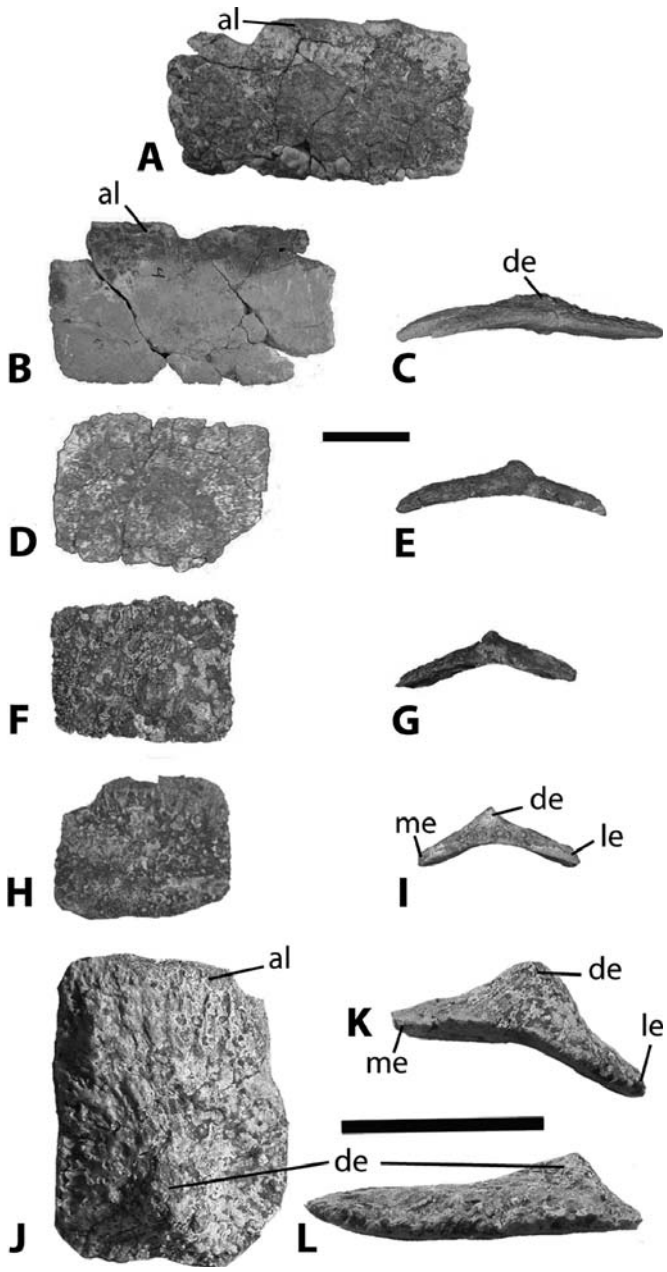

Figure 29. MNA V9300, caudal paramedian plates. **A**. Left anterior plate in dorsal view. **B**. Left anterior plate in dorsal view. **C**. Left anterior plate in posterior view. **D**. Right anterior mid-caudal plate in dorsal view. **E**. Right anterior mid-caudal plate in posterior view. **F**. Right mid-caudal plate in dorsal view. **G**. Right mid-caudal plate in posterior view. **H**. Right posterior mid-caudal plate in dorsal view. **I**. Right posterior mid-caudal plate in posterior view. **J**. Right distal caudal plate in dorsal view. **K**. Right distal caudal plate in posterior view. **L**. Right distal caudal plate in medial view. Scale bars = 5 cm. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **le**, lateral edge; **me**, medial edge.

ous plates in which the lateral flange is half the length of the dorsal flange.

The spine on what is presumably the sixteenth plate is blunt and worn. The plate is diagenetically fused to a partial paramedian plate and an isolated appendicular scute. At >80 mm, the spine on the seventeenth plate is the highest in the dorsal series.

Caudal Paramedian Plates (Figs. 29A–L)

The anteriormost caudal paramedian plates (Figs. 29A–C) are distinctive from the posterior dorsal paramedian plates because the plate is dorsoventrally thickened, the width/length ratio is reduced (between 1.8 and 1.5 to 1), and the plate is slightly arched transversely. Both the medial and lateral edges of these plates are straight and the anteromedial edges lack the anterior projection found in *Typothorax* (UCMP 158670) and *Calyptosuchus* (UCMP 126801). Dorsal eminences are low, rounded, conical knobs slightly medial and posterior to the center of the plate. The ornamentation of random (not radiate) grooves and ridges is apparent but shallower than that of the dorsal series. The anterior lamina is thin, but not delicate like those of the dorsal series. Ventral surfaces are smooth except for the transverse band of raised striations on the posterior margin. These plates rapidly decrease in width posteriorly as the tail tapers. Within the same interval, the transverse arching becomes more pronounced.

The mid-caudal paramedian plates possess width/length ratios in the range of approximately 1:1 to 1.5:1. These plates are very similar to the anterior plates in all aspects except for their reduced size and more pronounced arching (Figs. 29D–I). Most striking is the increased development of the dorsal eminence, which becomes higher and more conical (Fig. 29I).

Distal caudal paramedian plates possess width/length ratios less than 1:1. As a result, they are longer than wide, with straight median edges and slightly rounded lateral edges (Fig. 29J). Dorsal eminences are pronounced and the plate is slightly flexed along this center of ossification (Fig. 29K–L). The anterior lamina is not well developed and barely discernable on these plates. The extreme distal paramedian plates of the *Desmatosuchus* tail are not preserved but it is assumed that they would have been similar to those of *Aetosaurus* and *Typothorax* (Walker 1961, Martz 2002) as opposed to the conjectural reconstruction of *Longosuchus meadei* by Sawin (1947).

Caudal Lateral Plates (Figs. 30A–I, 31A–G)

MNA V9300 preserves much of the caudal lateral armor from both sides of the carapace. The right side is complete through the first twelve rows, and ten of these rows are present for the left side. In addition, the ninth through thirteenth plates of the left side are preserved in articulation. Much of the distal lateral armor is present, although assigning it to a specific position is difficult. It is important to note that the caudal lateral plates described here are equivalent to plates called "dorsolateral plates" by Jepsen (1948). Several aetosaurs, including *Aetosaurus*, "*Stegomus*", and *Stagonolepis* possess at least eight plates per tail segment, including two dorsal paramedians, two dorsolaterals, two ventrolaterals, and

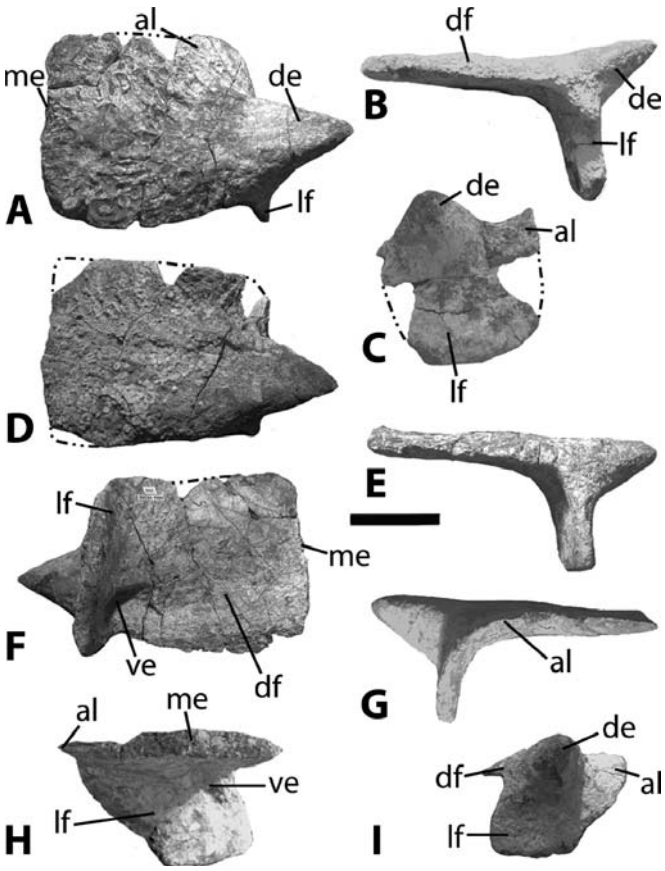

Figure 30. MNA V9300, anterior caudal lateral plates. **A**. Second plate of right side in dorsal view. **B**. Second plate of right side in posterior view. **C**. Second plate of right side in lateral view. **D**. Third plate of right side in dorsal view. **E**. Third plate of right side in posterior view. **F**. Second plate of right side in ventromedial view. **G**. Third plate of right side in anterior view. **H**. Third plate of right side in medial view. **I**. Third plate of right side in lateral view. Scale bar = 5 cm. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **df**, dorsal flange; **lf**, lateral flange; **me**, medial edge; **ve**, ventral emargination.

two ventral paramedians (Jepsen 1948, Walker 1961, Schoch 2007). No ventral caudal armor was recovered for MNA V9300 or UMMP 7476; thus, it is uncertain if *Desmatosuchus* possessed ventrolateral and ventral paramedian armor.

Case (1922:figs. 18, b, c; pl. 6, d, f) accurately described and figured lateral plates of the caudal region, noting that their spines were longer than those in the dorsal series. Unfortunately, Case reconstructed these plates backwards, as he had done with the dorsal series. Caudal laterals of UMMP 7476 and MNA V9300 are identical in lacking the elongate spines with the ventrally recurved tips found in *Desmatosuchus smalli* (TTU P-9024). Long and Ballew (1985:fig. 6, a–d) also described and figured what they interpreted as lateral plates of the caudal region, but their figures are insufficient for certain assignment of these plates to a caudal lateral position. Long and Ballew (1985) described the caudal laterals as possessing eminences that "occur as blunt knobs, circular or polygonal in cross-section, which decrease in size posteriorly." Although the eminences decrease in size posteriorly, they consist of well-developed conical spines rather than "blunt knobs." The first caudal plate figured by Long and Ballew (1985:fig. 6a) is an anterior dorsal lateral plate with a lateral flange that has been crushed flat.

The anterior caudal lateral plates (Figs. 30A–I) are very similar to the posterior dorsal lateral plates except that the dorsal flanges are shorter mediolaterally, the plates are thickened dorsoventrally, and the spines are more strongly developed. In dorsal view (Fig. 30A), the median edge is straight rather than sigmoidal, which matches well with the straight lateral edge of the associated paramedians. The spine is broad at the base and strongly triangular in dorsal view. The dorsal surface of the spine is flattened. The plate is strongly thickened dorsoventrally, especially the lateral flange (Fig. 30B), and one of these plates has the distal end of the lateral flange swollen mediolaterally. The distal edge of the lateral flange is relatively straight, not strongly sigmoidal as in the dorsal lateral plates. The lateral flange remains reduced in comparison with the dorsal flange, similar to the dorsal lateral plates of the pelvic region, and there is no ventrolateral process of the plate (Fig. 30C). The ventral surface is smooth except for the typical transverse band of striations along the posterior margin. There is a slight emargination on the ventral surface beneath the spine, and just anterior to this the ventral surface is swollen and thickened (Fig. 30F). The medial edge is thickened with the complex tongue-and-groove articular surface (Fig. 30H).

The fourth through sixth caudal lateral plates of the right side (Figs. 31A–C) were found in association with their respective vertebrae. Dorsal flanges are two-thirds the length of the lateral flange and are beginning to shorten mediolaterally. Spines remain strongly developed but are slightly reduced in length compared to more anterior plates. In all other ways these three plates resemble slightly smaller versions of the first three caudal plates, except that they are thinner dorsoventrally. By the ninth caudal lateral plate (Fig. 31F), the dorsal and lateral flanges are of almost equal size and the spine is shorter. Behind the thirteenth series, the spines become greatly reduced, appearing as low conical knobs. Flanges remain equal in size throughout the rest of the series. Long and Ballew (1985) state that the anterior caudal lateral plates are moderately arched and become progressively flatter posteriorly, but this is not the case. All anterior caudal laterals are strongly flexed throughout the entire series, although this flexion is reduced slightly in the more posterior plates.

Ventral and Appendicular Armor

Ventral and appendicular armor is known from several aetosaurs, including *Aetosaurus* (Walker 1961, Schoch 2007), *Stagonolepis* (Walker 1961), *Aetosauroides* (Casimiquela 1961), *Coahomasuchus* (Heckert and Lucas 1999), *Typothorax* (Martz 2002) and *Neoaetosauroides* (Desojo and Bàez 2005). Ventral armor of aetosaurs from the belly region usu-

ally consists of numerous rows of small, hexagonal or square plates with reduced ornamentation, and has mainly been described for *Stagonolepis* (Walker 1961) and *Coahomasuchus* (Heckert and Lucas 1999). Martz (2002) described ventral armor from the tail region of *Typothorax* and also ascribed numerous odd plates as ventral armor. Ventral armor has never been described for *Desmatosuchus* and none was recovered with MNA V9300.

Several small, rounded, ornate scutes recovered with MNA V9300 are consistent with the appendicular armor present in the holotypes of *Calyptosuchus wellesi* Long and Ballew and *Coahomasuchus kahleorum* Heckert and Lucas (Case 1932, Long and Murry 1995, Heckert and Lucas 1999). Although not numerous, they represent the first possible appendicular armor discovered for *Desmatosuchus*.

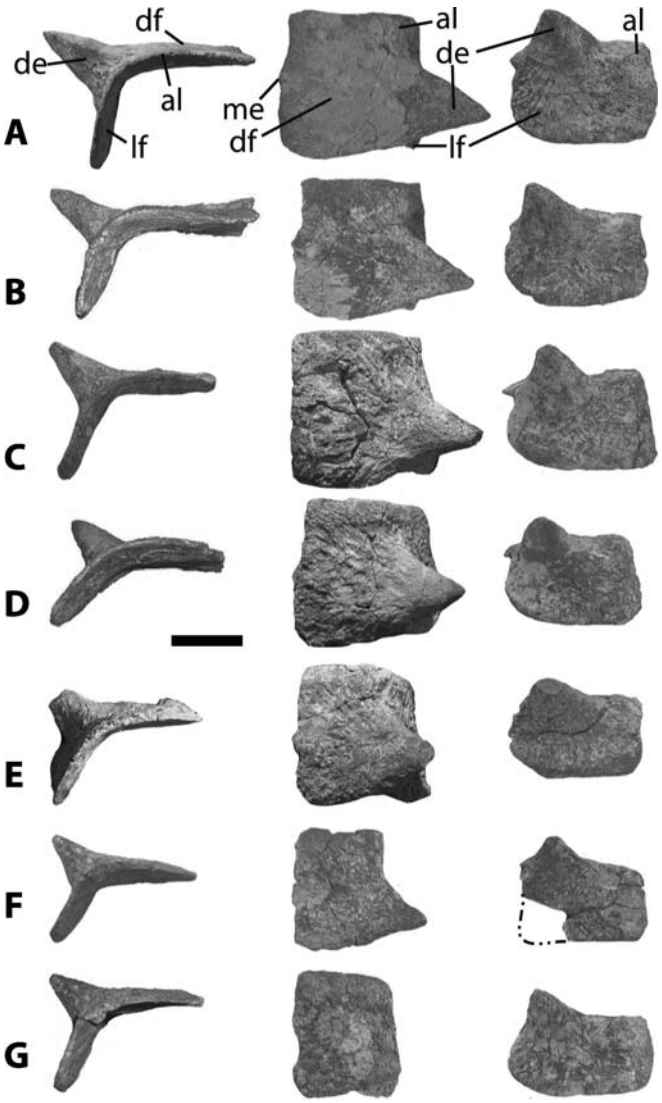

Figure 31. MNA V9300, caudal lateral plates of the right side in anterior, dorsal, and lateral views. **A**. Fourth plate. **B**. Fifth plate. **C**. Sixth plate. **D**. Seventh plate. **E**. Eighth plate. **F**. Ninth plate. **G**. Tenth plate. Scale bar = 5 cm. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **df**, dorsal flange; **lf**, lateral flange; **me**, medial edge.

Reconstructions

As stated previously, when Case (1922) created the first reconstruction of *Desmatosuchus*, he did so incorrectly by orienting the lateral armor backwards because he confused the lateral flange and the medial flange. Figures 32A–B shows the proper articulation of several laterals and dorsals from the paramedian region. Figure 32C shows the incorrectly joined lateral and paramedian plates in UMMP 7476 as reconstructed by Case. Although reconstructed as a series of the left side, the lateral plate is from the right side. Reorienting the lateral plates to their proper side results in a reconstructed animal that is wider than previously depicted (Case 1922:pls. 8–9, fig. 20; Long and Ballew 1985:fig. 18; Long and Murry 1995:figs. 85–86). Figure 33 provides a hypothetical armor reconstruction in dorsal view based upon MNA V9300. The carapace is wider than in previous reconstructions though there is possibly a very slight 'waisting' anterior to the pelvis. Figure 34 shows this new reconstruction of the skeleton in dorsal and lateral views with and without the armor carapace.

Measurement of the elements of the vertebral column combined with the estimated skull length give a total esti-

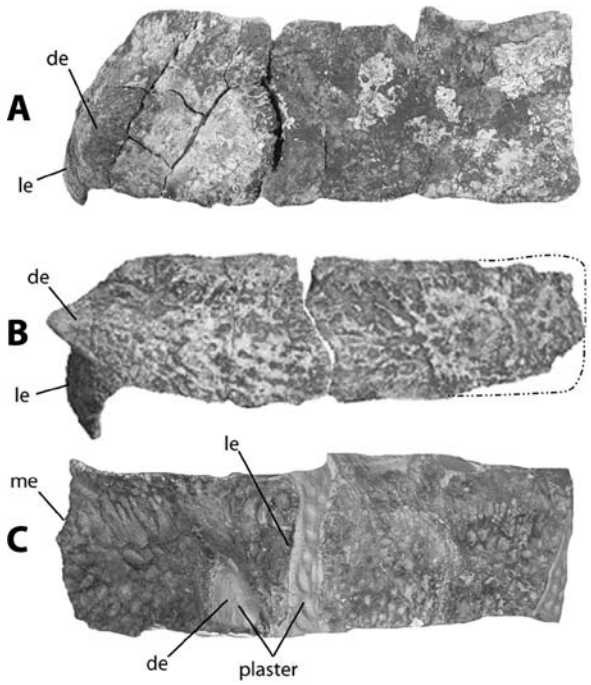

Figure 32. Proper articulation of the paramedian and lateral armor of *Desmatosuchus spurensis*. **A**. Left anterior dorsal series of MNA V9300 in dorsal view. **B.** Right mid-dorsal series (reversed) of MNA V9300 in dorsal view showing correct orientation of plates. **C.** Left mid-dorsal paramedian with right lateral of UMMP 7476 showing incorrect orientation of plates. Note plaster fill between plates and medially oriented spine. Abbreviations: **de**, dorsal eminence; **le**, lateral edge; **me**, medial edge.

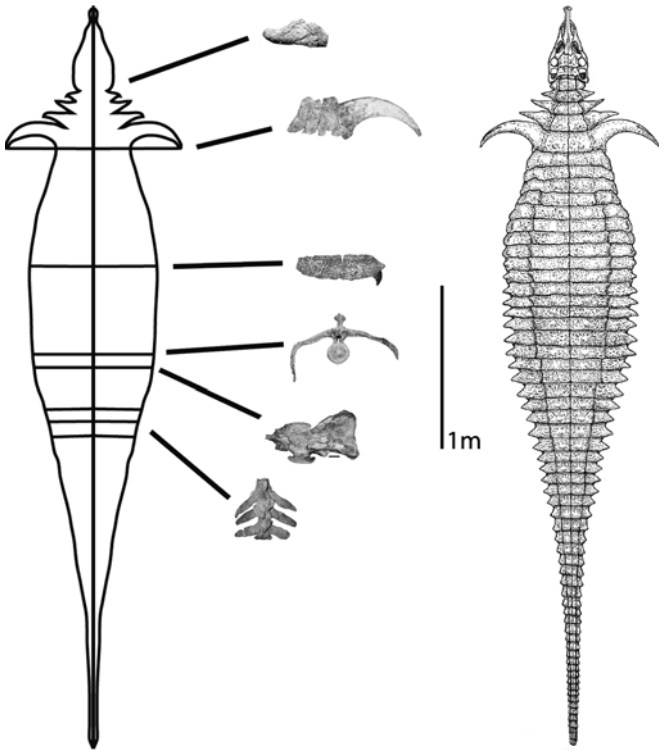

Figure 33. Reconstruction of *Desmatosuchus spurensis* based upon new material from MNA V9300. The body outline was created from measurements of body regions represented by inserted elements.

mated length for MNA V9300 of approximately 5 meters from the tip of the snout to the tip of the tail, although the exact length of the tail is unknown. However, the body length from the skull to the last presacral vertebra includes estimates of 1 cm for each intervertebral disk and gives a hypothetical length of 2.3 meters for that body segment. The pelvis has a length of 0.2 meter, leaving an estimated tail length of 2.5 meters. Reconstructions of *Typothorax* by Martz (2002) based on material from Texas and New Mexico, and of *Stagonolepis* by Walker (1961), based on the type specimens of *Aetosaurus*, suggest that the tail length is approximately equivalent to the combined length of the skull and the presacral vertebral column. This is also supported by Hunt et. al. (1993) who state that the tail of NMMNH P-12964 (*Typothorax*) is half the total length of the animal. Thus, the estimates of tail length and total length for MNA V9300 are justified.

Discussion

Previous descriptions of *Desmatosuchus spurensis* by Case (1920, 1921, 1922, 1929), Long and Ballew (1985), and Long and Murry (1995) have covered most aspects of its morphology. As a result, most workers are satisfied with our overall knowledge of this taxon, including the armor reconstruction by Case (1922). However, the present study of MNA V9300 reveals that Case erred in his reconstruction of the lateral armor by interpreting the dorsal flange of the angular lateral plate, which should articulate with the adjacent paramedian plate, as being the lateral (outside) flange, and referring to the distal end of the lateral flange as the articular surface. As a result, Case positioned the lateral plates backwards and on the wrong side of the body. Therefore, what he identified as right lateral plates are actually left lateral plates and vice-versa. Not recognizing the error, subsequent workers (e.g., Long and Ballew 1985, Long and Murry 1995) also interpreted a carapace that is too narrow in dorsal view. The semi-articulated state and completeness of the elements of MNA V9300 reveal, for the first time, the almost precise arrangement of the lateral armor as well as detailed information regarding variations in armor morphology throughout the carapace. This new information clarifies errors made in past studies. For example, Long and Ballew (1985:48) describe the lateral armor as becoming "progressively smaller and blunter" behind the shoulders, but the reverse is correct. Thus, regional assignments for plates given by those authors are incorrect. The "anterior dorsal scutes" are actually middle to posterior dorsal plates and the "posterior dorsal scutes" are actually anterior plates. The "first caudal scute" described and figured in this same paper (Long and Ballew 1985:fig. 6a), is an anterior dorsal lateral with a diagenetically flattened lateral flange.

The vertebral column is well preserved in both MNA V9300 and UMMP 7476; much of the one in MNA V9300 is articulated and shows minimal damage and distortion. Almost all of the vertebrae from the ninth cervical through the twelfth caudal possess neural arches and spines, transverse processes, and all articular processes (zygapophyses) and accessory structures (hyposphenes/hypantra), allowing a detailed description of the vertebral morphology in this region.

Neither limb nor pectoral girdle elements are preserved in MNA V9300 and UMMP 7476. Whereas the girdle and limb material described by Small (1985) actually belongs to *D. smalli*, these elements are unknown for *D. spurensis*. Although Long and Murry (1995) assigned much isolated aetosaur non-armor material from the *Placerias* Quarry to *D. haplocerus*, at least three aetosaur taxa are now recognized from this quarry; thus most of their assignments cannot be confirmed.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope 1869 *sensu* Gauthier 1986
PSEUDOSUCHIA Zittel 1887–1890 *sensu* Gauthier 1986
AETOSAURIA Marsh 1884 *sensu* Parker 2007
DESMATOSUCHINAE Huene 1942 *sensu* Heckert and Lucas 2000
DESMATOSUCHUS Case 1920

Type Species—*Desmatosuchus spurensis* Case 1920.

Referred Species—*Desmatosuchus smalli* Parker 2005a.

Revised Diagnosis—*Desmatosuchus* can be differentiated from all other aetosaurs by the presence of well-developed, recurved spines on the cervical lateral plates, especially in the

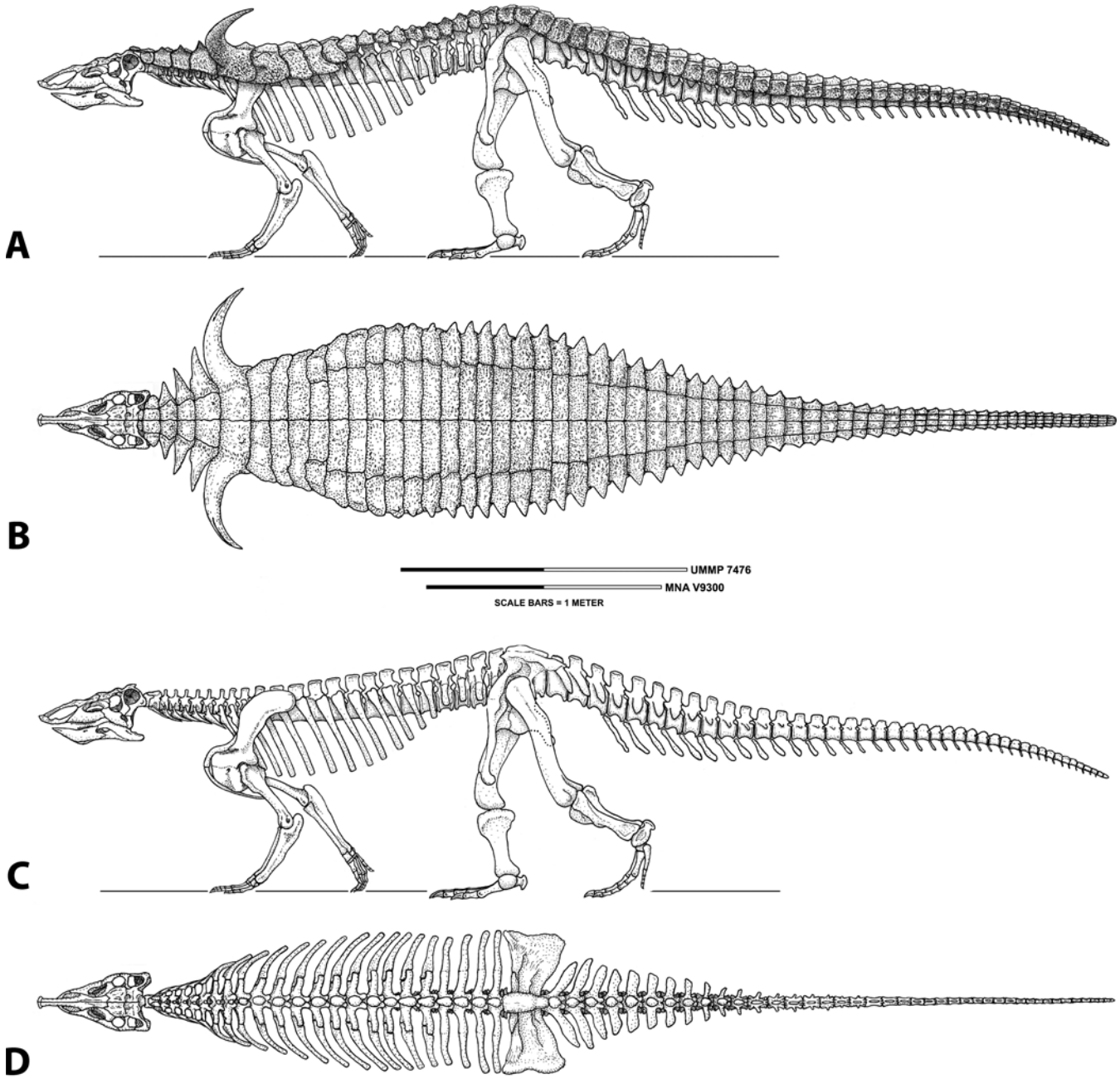

Figure 34. Skeletal reconstructions of *Desmatosuchus spurensis* based on elements from MNA V9300, TTU P-9024, and UMMP 7476. **A**. Left lateral view. **B**. Dorsal view. **C**. Left lateral view, armor removed. **D**. Dorsal view, armor removed.

5th lateral series where the plates are especially large (autapomorphy), paramedian and lateral plates possess thin anterior laminae rather than thickened, raised bars (autapomorphy), and the humerus has an epicondylar foramen instead of a groove (condition unknown for some aetosaurs). Differs from all other aetosaurs except *Typothorax* in possessing an edentulous premaxilla and a paramedian plate ornamentation of pits, grooves, and ridges in a random pattern. Differs from all other aetosaurs except *Longosuchus* in possessing cervical paramedian plates that are longer than wide and extremely thickened dorsoventrally, a dorsal flange of the dorsal and anterior caudal lateral plates that is larger than the lateral flange, and dorsal lateral spines that are more elongate in the more posterior plates with the best developed spines in the pelvic and anterior caudal regions. Differs from all aetosaurs except *Longosuchus* and *Lucasuchus* in that the posterior-most dorsal vertebra is completely fused to first sacral vertebra and that anteriormost dorsal lateral plates that possess large knobs instead of spines. *Desmatosuchus* can also be diagnosed by the unique combination of the following characters: (1) neural spines that are shorter than the height of the corresponding centrum, (2) cervical centra that are wider than tall and lack

ventral keels, (3) the presence of well-developed hyposphenes and hypantra in the dorsal vertebrae, (4) dorsal eminences of the paramedian plates are centered, and (5) an acetabulum that is oriented at an oblique angle to the sagittal plane.

Distribution—Upper Triassic, southwestern United States.

Desmatosuchus spurensis Case 1920

1920 *Desmatosuchus spurensis*: Case, p. 524, figs. 1–4.
1922 *Desmatosuchus spurensis*: Case, p. 26, figs. 7–20, pl. 5–10.
1922 Phytosaur: Case, p. 70, fig. 27B, pl. 13a.
1929 *Desmatosuchus spurensis*: Case, p. 50, fig. 21.
1932 Phytosaur: Case, p. 72, pl. 4 (figs. 2,3).
1942 *Desmatosuchus spurensis*: Huene, p. 233, fig. 50.
1953 *Desmatosuchus haplocerus*: Gregory, p. 1, figs. 1–14.
1954 *Desmatosuchus spurensis*: Brady, p. 19, figs. 1,2.
1958 *Desmatosuchus*: Brady, p. 61, figs. 1–4.
1961 *Desmatosuchus*: Walker, p. 179, fig. 24d.
1976 *Desmatosuchus*: Krebs, p. 78, fig. 26a.
1978 *Desmatosuchus*: Bonaparte, p. 300, fig. 136d.
1979 *Desmatosuchus spurensis*: Hopson, p. 80, figs. 9a, b.
1985 *Desmatosuchus haplocerus*: Long and Ballew, p. 45, figs. 1–7, pl. 1.
1986 *Desmatosuchus haplocerus*: Murry, p. 122, fig. 9.12a
1989 *Desmatosuchus haplocerus*: Long et al., p. 69, figs. 2b–c.
1993 *Desmatosuchus haploceros* [sic]: Parrish, p. 298, fig. 6b.
1995 *Desmatosuchus haplocerus*: Long and Murry, p. 89, figs. 85–98.
2000 *Desmatosuchus haplocerus*: Heckert and Lucas, p. 1559, figs. 6a–c.
2002b *Desmatosuchus*: Heckert and Lucas, p. 205, fig. 4.
2003 *Desmatosuchus haplocerus*: Parker, p.49, figs. 8, 10–15, 16a, 17–35, 37–56, 57c–g.
2005a *Desmatosuchus haplocerus*: Parker, p. 333, figs. 2c–d, 3e–f, 5c–d, 6a–b.
2005 *Desmatosuchus haplocerus*: Parker and Irmis, p. 49, figs. 4b–e.
2005 *Desmatosuchus haplocerus*: Irmis, p. 76, fig. 6a–b.
2007 *Desmatosuchus haplocerus*: Parker, p. 1, figs. 3c, 9d.

Holotype—UMMP 7476, skull and much of the dorsal carapace and vertebral column.

Referred specimen—MNA V9300.

Type Locality—East bank of Blanco River, about a half mile east of the old mail road from Spur to Crosbyton, Crosby County, Texas (from Case 1922). Tecovas Formation, Dockum Group (late Carnian).

Revised Diagnosis—Differs from *Desmatosuchus smalli* by having (1) spines on anterior cervical lateral armor that are very short and not highly developed, (2) spines on posterior dorsal laterals that are short and without ventrally recurved tips, (3) a transversely oriented sulcus or groove on the parietals between the supratemporal openings (autapomorphy), (4) a deep median pharyngeal recess of the basipterygoid, (5) almost no gap apparent between the basal tuber and basipterygoid process, (6) an elongate pit present in the dorsal region of the supraoccipital (7) exoccipitals that meet at the midline in the foramen magnum, (8) a maxillary tooth count of 12-13.

Desmatosuchus smalli Parker 2005a

1985 *Desmatosuchus haplocerus*: Small, p. 1, figs. 3–11.
1985 *Desmatosuchus haplocerus*: Long and Ballew, p. 45, figs. 7a–b.
1986 *Desmatosuchus haplocerus*: Murry, p. 122.
1986 *Desmatosuchus*: Chatterjee, p. 145.
1989 *Desmatosuchus haplocerus*: Small, p. 301, fig. 1b, pls. 5a–f, i.
1995 *Desmatosuchus haplocerus*: Long and Murry, p. 89, fig. 86a.
2002 *Desmatosuchus haplocerus*: Small, p. 97, figs. 1–9.
2005a *Desmatosuchus smalli*: Parker, p. 333, figs. 2a-b, 3a–d, 4a–b, 5a–b, 6c–d.

Holotype—TTU P-9024, almost complete skull and right mandible, partial pelvis, femora, nearly complete cervical armor, and numerous plates from rest of carapace (Parker 2005a).

Type Locality—Post (Miller) Quarry, nine miles southeast of Post, Garza County, Texas, USA (Small 1989). Cooper Canyon Formation, Dockum Group; Norian (Chatterjee 1986).

Diagnosis—*D. smalli* differs from *D. spurensis* in having (1) parietals that lack a shallow concavity or sulcus running transversely between the supratemporal fenestrae, (2) an extremely to moderately shallow medial pharyngeal recess of the basipterygoid, (3) a sizeable gap between the basal tubera and the basipterygoid process, (4) exoccipitals that do not meet at the midline of the foramen magnum, (5) a maxillary tooth count of 10–12 compared to 12–13 in *D. spurensis*, (6) spines of the posterior dorsal lateral armor that are slightly recurved, (7) anterior cervical lateral armor and posterior dorsal lateral armor possess elongate gracile spines that are much more developed than those in *D. spurensis*. The average length of the posterior dorsal lateral spines in similar size specimens is 68 mm for *D. smalli* as opposed to 42 mm for *D. spurensis* (Parker 2005a).

Desmatosuchus haplocerus (Cope 1892)

1892 *Episcoposaurus haplocerus*: Cope, p. 129.
1950 *Episcoposaurus haplocerus*: Wilson, p. 113, figs. 2–3 [*non* p. 113, fig. 1 (= Phytosauridae indet.)].
1953 *Desmatosuchus haplocerus*: Gregory, p. 1, figs. 1–14.
1995 *Episcoposaurus haplocerus*: Spamer and Daeschler, p. 430, fig. 21a–b, d–e [*non* fig. 21c (= Phytosauridae indet.)].
2002 *Desmatosuchus haplocerus*: Heckert and Lucas, p.

193, figs. 1, 2, 3a–d [*non* p. 194, figs. 3e, f (= Phytosauridae indet.)].

Lectotype—ANSP 14688, partial skeleton.

Topotypes—TMM 40041-3 (originally TMM 18569-1), two partial cervical lateral plates (Wilson 1950); TMM 40041-5, cervical osteoderm fragments.

Type Locality—Windmill pasture, 5 km north of Dickens, Dickens County, Texas. Tecovas Formation, Dockum Group; late Carnian (Gregory 1953).

Revised Diagnosis—This material cannot be differentially diagnosed from *D. spurensis* and *D. smalli* without ambiguity (see discussion below).

Discussion—Reanalysis of the lectotype of *Desmatosuchus haplocerus* (ANSP 14688) reveals that this specimen consists mainly of dorsal and lateral armor from the cervical and dorsal regions. The fragmentary nature of the material makes it impossible to differentiate it from the types of *Desmatosuchus spurensis* (UMMP 7476) and *Desmatosuchus smalli* (TTU P-9024). Several characters present in ANSP 14688, such as the strongly dorsally projected 5th cervical horn and the "honeycomb" ornamentation of the dorsal paramedian armor suggest affinities with *D. smalli* (personal observation); however, because no cranial material or complete dorsal lateral plates are present in ANSP 14688, it cannot be compared to the diagnostic features of TTU P-9024. Likewise, although the material has superficial similarities to UMMP 7476, these features are present in all species of *Desmatosuchus* (e.g., enlarged recurved horns on cervical lateral plates, paramedian plates with depressed anterior laminae and thickened tongue-and-groove articular surfaces). The large cervical horn in ANSP 14688 is more dorsally projected and not as recurved as in UMMP 7476. A possibly diagnostic feature of *D. haplocerus*, exhibited by ANSP 14688, is the well-developed, laterally projecting spine on the anterior dorsal lateral plates that is not present in *D. smalli* or *D. spurensis*. However, the assignment of these plates to the anterior dorsal series is ambiguous given the fragmentary nature of the material. If these are actually posterior dorsal or caudal lateral plates, they would not be substantially different from those of *D. spurensis* and *D. smalli*. Thus, *Episcoposaurus haplocerus* is a nomen dubium and the species name should be restricted to ANSP 14688. Consequently, *Desmatosuchus spurensis* Case is reestablished as the type species of *Desmatosuchus*.

DISCUSSION

Distribution of *Desmatosuchus* material

Desmatosuchus spurensis is known solely from the lower portion of the Chinle Formation in Arizona and western New Mexico, and the lower portion of the Dockum Group in Texas and eastern New Mexico. *Desmatosuchus smalli* has been reported from the upper Dockum Group of Texas and the upper Chinle Formation in Arizona. Occurrences of *Desmatosuchus* have also been reported from the Newark Supergroup in North Carolina (Heckert and Lucas 1999, 2000) and the Zarzaitine Series of Algeria (Jalil et al. 1995, Jalil 1999, Heckert and Lucas 2000). The Newark specimens have been reassigned to the aetosaur *Lucasuchus* (Long and Murry 1995, personal observation), and the African specimens most likely represent a new taxon that is not assignable to *Desmatosuchus* (Small 2002). Burmeister (2000) tentatively assigned fragmentary osteoderms from the Isalo II beds of Madagascar to Stagonolepididae indet., but Lucas et al. (2003) referred the same material to *D. haplocerus*. Burmeister et al. (2006) described and figured this material again, assigning it to Crocodylotarsi indet, discussing potential similarities with aetosaurs. Based on personal observation, these osteoderms are not referable to *Desmatosuchus*, and they almost certainly are not aetosaurian. The interdigitating lateral suture (Burmeister et al. 2006:fig. 11.1) is inconsistent with those of aetosaurs and the anterior bar and pitted ornamentation is also found in Jurassic mesoeucrocodylians (e.g., Pierce and Benton 2006).

Both the type specimen of *D. haplocerus* (ANSP 14688) and the type specimen of *D. spurensis* (UMMP 7476) are from the Tecovas Formation of Texas (Case 1920, Cope 1892). This material is the basis for the fundamental morphological descriptions of *Desmatosuchus* (Case 1920, 1921, 1922, Gregory 1953). Other occurrences of *D. spurensis* in the Tecovas have been documented by Murry (1989), Long and Murry (1995), and Parker (2003). *Desmatosuchus spurensis* is also present in the Los Esteros Member of the Santa Rosa Formation in New Mexico (Hunt and Lucas 1988, personal observation). The Post Quarry specimens (mainly TTU P-9024) from the Cooper Canyon Formation (Dockum Group) are all referable to *Desmatosuchus smalli* (Parker 2005a), although much of this material has been used in the past to supplement descriptions of *D. spurensis* (Small 1985, 1989, 2002). Likewise, much of the material from the Otis Chalk quarries (TMM collections) that is catalogued as *Desmatosuchus*, some of which is referenced by Desojo and Báez (2005), actually belongs to *Lucasuchus* or *Longosuchus* (Long and Murry 1995, personal observation).

Whereas *Desmatosuchus spurensis* appears to be very common in Texas, it is relatively rare in Arizona (Long and Murry 1995). Long and Ballew (1985) documented six occurrences of *D. spurensis* (their *D. haplocerus*) from Petrified Forest National Park, but reexamination of these specimens has determined that none are actually assignable to *Desmatosuchus*. Recent collecting in the park has turned up only three very fragmentary specimens (Parker and Irmis 2005) that represent *Desmatosuchus* sp. Brady (1954, 1958) described two other partial specimens from the Chinle Formation of eastern Arizona near Lupton and St. Michaels. These specimens are not unambiguously referable to a species, but the preserved 5th cervical horn more closely resembles that of *D. spurensis* because it is more strongly recurved and not directed dorsally.

By far the largest accumulation of *Desmatosuchus* material from Arizona is from the *Placerias* quarry near St. Johns, where over 600 elements represent more than 14 individuals

(Jacobs and Murry 1980). Yet, the majority of the bones from this quarry are not unambiguously associated (Camp and Welles 1956, Fiorillo et al. 2000), and discussion by Murry and Long (1989) suggest that robustness of elements was the criterion used to assign non-armor elements from this quarry to either *Calyptosuchus* (gracile) or *Desmatosuchus* (robust), rather than discrete character states. The recent recognition of a paratypothoracisin aetosaur taxon from the quarry (Parker 2005b) casts doubt on many of these assignments; therefore, previous referral of non-armor elements from the quarry to specific aetosaur taxa should be viewed with caution. Furthermore, many elements assigned to any one particular taxon (e.g., isolated braincases assigned to *Desmatosuchus*) display much morphological variation suggesting that they do not all belong to the same taxon. As a result, unless unambiguous apomorphies are present, non-armor elements assigned to *Desmatosuchus* from the *Placerias* and Downs quarries by Long and Murry (1995) are not unambiguously assignable to *Desmatosuchus*. Unfortunately, this has already caused possible confusion in recent descriptions of *Desmatosuchus* material (e.g., Heckert et al. 2003, Desojo and Báez 2005). Dorsal lateral armor elements in the quarry are not referable to *D. smalli* (TTU P-9024) because they lack the elongate spines with ventrally downturned apices. They are identical to the lateral plates of MNA V9300 and UMMP 7476, and therefore are referable to *Desmatosuchus spurensis*. This assignment is also true for the paramedian armor from the quarry that is assignable to *Desmatosuchus*.

Further comments on *Desmatosuchus* (*Episcoposaurus*) *haplocerus*

Heckert and Lucas (2002b) established a lectotype for *Desmatosuchus haplocerus* because Cope (1892) did not specifically designate ANSP 14688 as the holotype. These authors also stress that although Gregory (1953) redescribed and figured this material, he too did not select any primary types; however, throughout his paper Gregory specifically refers to ANSP 14688 as the type specimen of *Desmatosuchus haplocerus*. Because there is no evidence that ANSP 14688 belongs to more than a single aetosaur specimen, according to section 74.5 of the International Code of Zoological Nomenclature (ICZN) Gregory's (1953:15) reference is considered a fixation of a lectotype because his referral to a single specimen (ANSP 14688) as "the type" is unambiguous. Furthermore, two specimens within this material that pertain to phytosaurs (dorsal centrum, ilium) were explicitly removed by Gregory in this same description and therefore these elements do not conflict with this designation. Thus, according to ICZN section 74.2, the lectotype designated by Heckert and Lucas (2002b) is rejected.

Heckert and Lucas (2002b:194, figs. 3e–f) explicitly assign a non-aetosaurian element (phytosaur ilium) to the type materials (as a paralectotype). According to Gregory (1953) and field tags associated with the specimen, this ilium was collected by Cope from the same locality as the type material a year after the original collection was made. This element was not mentioned in Cope's (1892) original description and was excluded from the type materials by Gregory (1953). Without explanation, after clearly assigning this specimen to *D. haplocerus* as a paralectotype, Heckert and Lucas (2002b:200, 203) later note in the same publication that they agree with Gregory's removal of the specimen; hence, their true intent regarding this ilium is unclear. Nonetheless, the ilium does not belong to an aetosaur, was not part of the original collection, and is not one of the original syntypes; therefore, it is not included in the lectotype of *D. haplocerus* following Gregory (1953).

Spamer and Daeschler (1995:fig. 21c) also figure this ilium as a type specimen of *D. haplocerus* and refer to elements catalogued as ANSP 14688 as representing syntypes. These authors were probably unaware of Gregory's paper, a conclusion also reached by Heckert and Lucas (2002b), as they included this material among "taxa for which no illustrations of their types have ever been published," and did not cite Gregory (1953). As a result, Spamer and Daeschler (1995) misinterpreted the status of the type materials; thus, their assignment of the ilium to *D. haplocerus* should be disregarded.

In summary, the lectotype of *Desmatosuchus haplocerus* consists mainly of the cervical armor of a single individual (ANSP 14688). The removal of the ilium and dorsal vertebra by Gregory (1953) during his fixation of ANSP 14688 as the lectotype should stand. The single sacral vertebra and caudal vertebra, although fragmentary, do not differ significantly from those of aetosaurs and most likely belong to the specimen. As concluded above, *D. haplocerus* is now considered a nomen dubium.

Comments on the topotype material of *Desmatosuchus* (*Episcoposaurus*) *haplocerus*

Field tags with ANSP 14688 indicate that the type material of *E. haplocerus* was collected by W.F. Cummins on June 20, 1891. Wilson (1950) reported several figured specimens

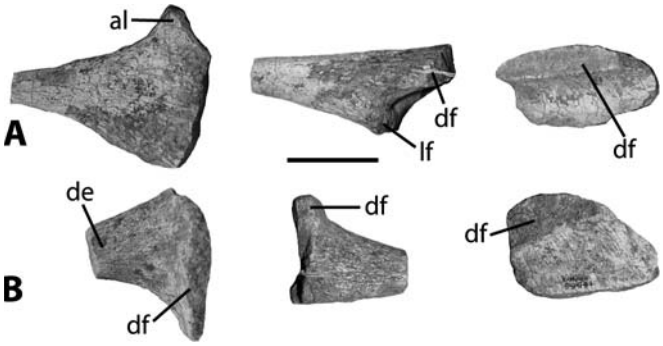

Figure 35. TMM 40041-3, topotype lateral cervical plates of *Desmatosuchus haplocerus*. **A**. Posterior left lateral plate in dorsal, anterior, and medial views. **B**. Medial right lateral plate in ventrolateral, posterior, and medial view. Scale bar = 5 cm. Abbreviations: **al**, anterior lamina; **de**, dorsal eminence; **df**, dorsal flange; **lf**, lateral flange.

(TTM 40041-3, originally BEGC 18569) labeled "*Episcoposaurus haploceros* [sic] Cope, remainder of the bones from typical and original locality. 5/25/92." Thus, this material and the previously mentioned phytosaur ilium apparently were collected when Cope returned to the area with Cummins in 1892. As the original association of this material is unknown, Wilson (1950) designated the TMM specimens as topotypes. Although the field tag for TMM 40041-3 predates the original 1892 publication by Cope (Spamer and Daeschler 1995), Cope does not mention these specimens; therefore, it is not clear if they were available to him when he wrote the original description and they should be considered only as topotypes (Wilson 1950). Reexamination of TMM 40041-3 (dorsal vertebra, two lateral plates) suggests that the dorsal vertebra (Wilson 1950:fig. 1) most likely are from a phytosaur, not an aetosaur. The two lateral plates are aetosaurian and the presence of well-developed spines allows for an assignment to at least the Desmatosuchinae. The first plate (Fig. 35A, Wilson 1950:figs. 2, 3) preserves most of the spine as well as much of the dorsal and lateral flanges. The dorsal flange is thickened and the spine is slightly recurved posteriorly, suggesting that this is a cervical lateral plate of the left side of *Desmatosuchus*. The lateral flange is short for a cervical series vertebra but appears to be eroded. Although the second spine (Fig. 35B), which was not figured by Wilson (1950), is on a fragmentary lateral plate, much of the base of the spine and the thickened dorsal flange are preserved. This represents a right cervical lateral plate of *Desmatosuchus*.

TMM 40041-5 (originally BEGC 18631) is labeled as representing "fragments found with *Episcoposaurus* bones (18569)" and consists of 39 fragments of aetosaur plates including portions of cervical and anterior dorsal plates. This specimen has not been mentioned by previous authors but is considered here to represent a topotype of *D. haplocerus* . Although the fragments from TMM 40041-5 and the two armor plates of TMM 40041-3 are morphologically consistent with *Desmatosuchus*, they lack species-specific features.

Comments on the *Desmatosuchus spurensis* skull

Case (1922) provided a complete yet partly erroneous description of the skull of *D. spurensis*. Walker (1961) later commented on this skull and rectified its description. The most recent description of the "*D. haplocerus*" skull (Small 2002) is a composite based on material of both *D. spurensis* and *D. smalli* (see discussion below).

The holotype skull of *D. spurensis* is only missing the anterior portions of the nasals, the premaxillae, much of the palate, both quadratojugals and both quadrates. In posterior view, the posterior projection of the squamosal looks deceptively like a quadrate, which puzzled Case (1922) and was later clarified by Walker (1961). Case (1921, 1922).presents a detailed description of the well-preserved braincase and endocast of UMMP 7476

Small (2002) incorporated UMMP 7476 and several other specimens (i.e., TTU P-9023, TTU P-9024, TTU P-9025, TTU P-9420, and UCMP 27408) in his description of the skull of "*D. haplocerus*;" however, UMMP 7476 represents *D. spurensis*, whereas TTU P-9023, TTU P-9024, and TTU P-9025 represent *D. smalli* (Parker 2005a). TTU P-9420 is distinct and probably not referable to *Desmatosuchus* (J. Martz personal commun. 2004). Because UCMP 27408 has characters in common with UMMP 7476, such as a well-developed parietal sulcus, it is ascribed to *D. spurensis*.

The skull of *D. spurensis* differs from that of *D. smalli* by having a broad sulcus in the posterior portion of the parietals. The two also differ in the development of the medial pharyngeal recess, the degree of separation between the basal tuber and the basipterygoid process, and the number of maxillary teeth. (Small 1985, 2002, Parker 2005a).

Small's (2002) reconstruction of the *Desmatosuchus* skull does not show a prefrontal, and he mentions that he could not find any sign of this element. The absence of a prefrontal would be an autapomorphy because the element is present in skull material of other aetosaurs, including *Aetosaurus*, *Stagonolepis*, *Neoaetosauroides*, and *Longosuchus* (Walker 1961, Parrish 1994, Desojo and Bàez 2007, Schoch 2007).

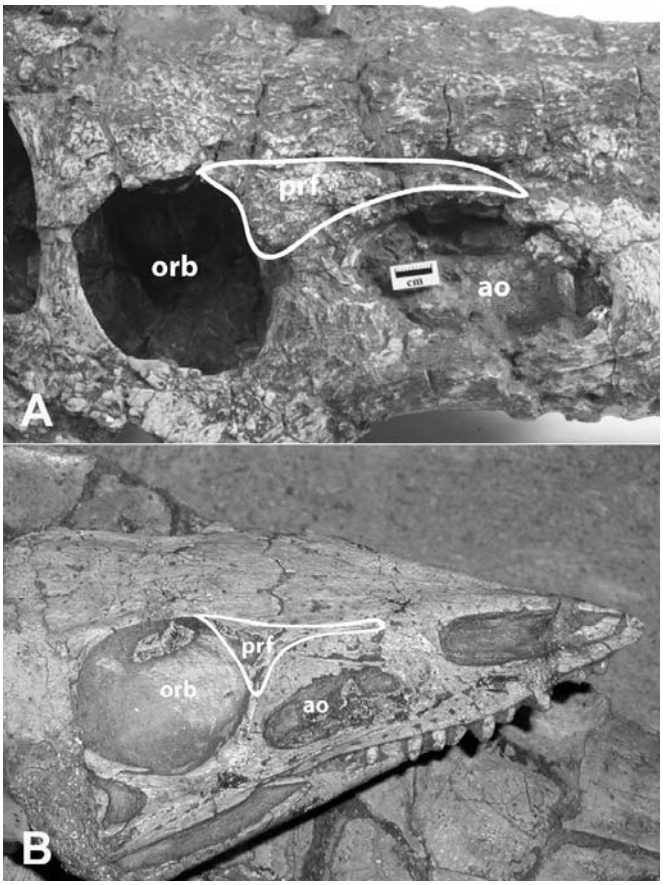

Figure 36. Aetosaur skulls in left lateral view showing the position of the prefrontal. **A**. TTU P-9024, *Desmatosuchus smalli*; **B**. SMNS 5770 (Specimen XVI), *Aetosaurus ferratus*. Abbreviations: **ao**, antorbital fenestra; **prf**, prefrontal; **orb**, orbit.

Case (1922) also was not able to find clear sutures for the prefrontal in UMMP 7476; however, he noted that short traces of the sutures were evidence of the element's presence (see Case 1922:fig. 7a). Examination of casts of TTU P-9024 and UMMP 7476 show a clear suture that extends from the dorsal margin of the antorbital fenestra posteriorly to the anterior dorsal margin of the orbit. This suture is in the same position as the prefrontal-frontal suture in *Aetosaurus* (Fig. 36, Schoch 2007) and in the reconstructions of *Longosuchus*, *Neoaetosauroides*, and *D. spurensis* (Case 1922, Parrish 1994, Desojo and Bàez 2007). Thus, a prefrontal must be present in *Desmatosuchus*.

Descriptions of the premaxilla, palatal complex, quadratojugal, quadrate, and mandible by Small (2002) apply solely to *D. smalli*, as these elements are presently unknown for *D. spurensis*.

Comments on the taxonomic status of *Acaenasuchus geoffreyi*

Heckert and Lucas (1999, 2000, 2002c) consider the holotype (Fig. 37A) and referred material of *Acaenasuchus geoffreyi* Long and Murry as a juvenile *Desmatosuchus*. In support of this synonymy, Heckert and Lucas (2002b) list the following characters as shared by *Acaenasuchus* and *Desmatosuchus*; (1) presence of a depressed anterior lamina instead of a raised anterior bar; (2) random pitting on the dorsal paramedian and lateral plates; (3) incipient tongue-and-groove articular surfaces on the dorsal paramedian plates; (4) low width/length ratio of the paramedian plates; and (5) the presence of spike-like eminences on the lateral plates, some of which are recurved. Furthermore, they consider ontogenetic morphological transformations in *Desmatosuchus* to be represented by its deeper pitting and the tri-radiate division of the dorsal eminence of the paramedian plate.

It is possible that *Acaenasuchus* does not represent an aetosaur because the pseudosuchian *Revueltosaurus callenderi* possesses rectangular paramedian plates (Parker et al. 2005) very similar to those of aetosaurs. Indeed, paramedian plates of *Revueltosaurus* from near St. Johns, Arizona, were previously considered to belong to juveniles of the aetosaur *Calyptosuchus* (Heckert and Lucas 2002d, see Irmis et al. 2007). However, only aetosaurs and crocodyliforms possess lateral plates; therefore, if all of the *Acaenasuchus* material belongs to the same taxon, it is most likely an aetosaur.

The synapomorphies of *Desmatosuchus* and *Acaenasuchus* listed by Heckert and Lucas (2002b) are inaccurate for several reasons: (1) many of the illustrations in Long and Murry (1995) and Heckert and Lucas (2002b) show a distinct raised anterior bar instead of a depressed lamina (Figs. 37A–F, Murry and Long 1989, Irmis 2005, Parker 2005); (2) the much more radial pattern of ornamentation is uncharacteristic of *Desmatosuchus* (Figs. 37A, C, Parker 2005); (3) the "incipient tongue-and-groove articular surfaces" are similar to the distinct transverse grooves on the medial and lateral plate surfaces of many other aetosaurs;

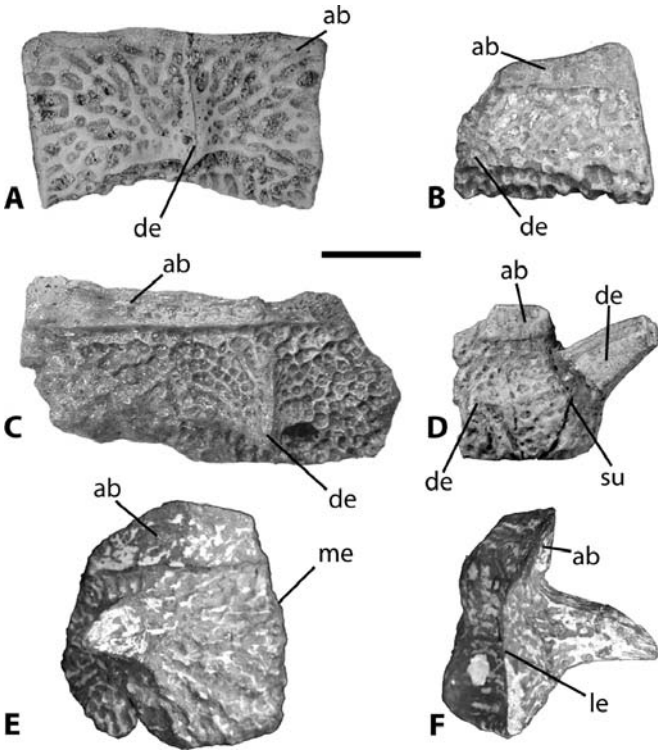

Figure 37. *Acaenasuchus geoffreyi* osteoderms. **A**. UCMP 7308/139576, holotype right dorsal paramedian plate in dorsal view; **B**. UCMP 7308/139584, referred ?right partial dorsal paramedian plate in dorsal view; **C**. MNA V3714, referred left dorsal paramedian plate in dorsal view; **D**. UCMP 7308/139583, referred fused right dorsal and lateral plates in dorsal view; **E**. UCMP, referred left lateral plate in dorsal view; **F**. UCMP 7308/139577, referred left lateral plate in ventrolateral view. Scale bar = 1 cm. Abbreviations: **ab**, anterior bar; **de**, dorsal eminence; **le**, lateral edge; **me**, medial edge; **su**, suture.

(4) all desmatosuchine and most aetosaurine aetosaurs have low width/length ratios; and (5) spine-like eminences on the lateral plates are a desmatosuchine synapomorphy, not an autapomorphy of *Desmatosuchus* (Parker 2007). Heckert and Lucas (2002b) state that the lateral plates with recurved spines of *Acaenasuchus* are homologous to the cervical laterals of *Desmatosuchus*; however, the *Acaenasuchus* plates have dorsal flanges that are longer than the ventral flanges (Fig. 37E). This is a character of *Desmatosuchus* dorsal lateral plates, not of cervical lateral plates; in addition, the dorsal lateral plates of *D. spurensis* lack recurved spine-like dorsal eminences. One pair of conjoined plates, UCMP 139583 (Fig. 37D), may represent a partial cervical paramedian and adjacent cervical lateral. Characters supporting this include a narrow paramedian plate (determined by the position of the dorsal eminence) and a short dorsal flange of the lateral plate. If this specimen is from the cervical region, it would verify the claim by Long and Murry (1995) that *Acaenasuchus* cervical plates were wider than long (*contra* Murry and Long 1989).

Other characters that distinguish *Acaenasuchus* from *Desmatosuchus* include (1) a dorsal eminence of the paramedian plates that forms an elongate keel stretching from just below the anterior bar to the posterior plate margin (Fig. 37A–C), (2) a dorsal eminence of the paramedian plates that is situated more laterally in some plates (Fig. 37C), and (3) a beveled posterior edge that is demarcated by a pronounced transverse ridge that separates it from the rest of the plate (Figs. 37A–C, Murry and Long 1989, Long and Murry 1995, Irmis 2005).

Regarding the juvenile status of *Acaenasuchus*, histological studies suggest that the plates of *Acaenasuchus* are not from a young juvenile (R. Irmis personal comm. 2006), though this does not necessarily mean they are fully grown. Deeper pitting may prove to be a juvenile character in future studies, but more incised ornamentation also occurs in the more posterior portions of the adult carapace (Heckert and Lucas 1999, Parker 2007). Furthermore, changes in aetosaur armor morphology through ontogeny are poorly understood. Although several aetosaur specimens (e.g., the *Aetosauroides* holotype) show signs of "immaturity" (i.e., open neurocentral sutures in the dorsal series), the only unambiguous young juvenile aetosaur material known is from *Typothorax*, and in that taxon there are no observable differences in plate ornamentation and morphology between adult and juvenile animals (Hunt 2001, Parker and Irmis 2005, also see discussion by Martz and Small 2006). Heckert and Lucas (2002b) also considered the division of the dorsal eminence into three flanges as a juvenile character; however, the posterior two flanges are actually the ridge that demarcates the posterior beveling of the plate, similar to what is seen in large, presumably mature specimens of *Paratypothorax* (UMMP 8858) and *Tecovasuchus* (TTU P-545).

Regardless of whether or not *Acaenasuchus* is a juvenile aetosaur, it appears unlikely that the morphological characters listed by Heckert and Lucas (2002b) are sufficient to refer *Acaenasuchus* to *Desmatosuchus* with conviction. Although the case for synonymy is supported by the shared stratigraphic range of *Acaenasuchus* to *Desmatosuchus*, the current data and our poor understanding of aetosaur ontogeny preclude its certainty.

CONCLUSIONS

The new skeleton of *Desmatosuchus spurensis* (MNA V9300) from the Chinle Formation of Arizona provides for a detailed analysis of the vertebral column and armor that augments previous descriptions of this taxon. In addition, the preservation of complete and partially articulated lateral armor in MNA V9300 reveals that previous reconstructions of *Desmatosuchus* erred in placement of the lateral osteoderms. The carapace is wider than previously thought and most likely is not strongly waisted. This material indicates that some aetosaurs were approximately five meters in length. Reanalysis of the holotype skull of *D. spurensis* confirms that a prefrontal is present (*contra* Small 2002).

Acaenasuchus geoffreyi does not appear to represent a juvenile form of *Desmatosuchus*. *D. haplocerus* is nondiagnostic below the genus level and is therefore a nomen dubium. Accordingly, the genus *Desmatosuchus* currently consists of only two valid species, *D. spurensis* and *D. smalli*.

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LITERATURE CITED

Bonaparte, J.F. 1978. El Mesozoico de America del Sur y sus tetrapodos. *Opera Lilloana* 26:1–596.

Brady, L.F. 1954. *Desmatosuchus* in northern Arizona. *Plateau* 27:19–21.

Brady, L.F. 1958. New occurrence of *Desmatosuchus* in northern Arizona. *Plateau* 30:61–63.

Brochu, C.A. 1996. Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil

archosaurs. *Journal of Vertebrate Paleontology* 16:49–62.

Burmeister, K.C. 2000. Paleogeographic and biostratigraphic implications of new early Mesozoic terrestrial vertebrate fossils from the Poamay site, central Morondava basin, Madagascar. M.S. thesis. University of California, Santa Barbara, CA.

Burmeister, K.C., J.J. Flynn, J.M. Parrish, and A.R. Wyss. 2006. Paleogeographic and biostratigraphic implications of new early Mesozoic vertebrates from Poamay, central Morondava Basin, Madagascar. *New Mexico Museum of Natural History & Science Bulletin* 37:457–475.

Camp, C.L. 1930. A study of the phytosaurs with description of new material from western North America. *Memoirs of the University of California* 10:1–174.

Camp, C.L., and S.P. Welles. 1956. Triassic dicynodont reptiles I. The North American genus *Placerias. Memoirs of the University of California* 10:244–348.

Case, E.C. 1920. Preliminary description of a new suborder of phytosaurian reptiles with a description of a new species of *Phytosaurus. Journal of Geology* 28:524–535.

Case, E.C. 1921. On an endocranial cast from a reptile, *Desmatosuchus spurensis*, from the Upper Triassic of western Texas. *Journal of Comparative Neurology* 22:122–147.

Case, E.C. 1922. New reptiles and stegocephalians from the Upper Triassic of western Texas. *Carnegie Institution Publication* 321:1–84.

Case, E.C. 1929. Description of the skull of a new form of phytosaur with notes on the characters of described North American phytosaurs. *Memoirs of the University of Michigan Museums, Museum of Paleontology* 2:1–56.

Case, E.C. 1932. A perfectly preserved segment of the armor of a phytosaur, with associated vertebrae. *Contributions from the Museum of Paleontology, University of Michigan* 4:57–80.

Casimiquela, R.M. 1961. Dos nuevos estagonolepoideos Argentinos (de Ischigualsto, San Juan). *Revista Asociacion Geológia de Argentina* 16:143–203.

Chatterjee, S. 1986. The late Triassic Dockum vertebrates: their stratigraphic and paleobiogeographical significance. Pp. 139–150 *in* K. Padian (ed.). The Beginning of the Age of Dinosaurs: Faunal Change Across the Triassic-Jurassic Boundary. Cambridge University Press, Cambridge.

Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. *Transactions of the American Philosophical Society, new series* 14:1–252.

Cope, E.D. 1875. Report on the geology of that part of northwestern New Mexico examined during the field-season of 1874: *Annual Report upon the geographical explorations west of the 100th meridian [Wheeler Survey], Appendix LL, Annual Report Chief of Engineers for 1875*:981–1017.

Cope, E.D. 1887. A contribution to the history of the Vertebrata of the Trias of North America. *Proceedings of the American Philosophical Society* 24:209–228.

Cope, E.D. 1892. A contribution to the vertebrate paleontology of Texas. *Proceedings of the American Philosophical Society* 30:123–131.

Deacon, M.W. 1990. Depositional analysis of the Sonsela Sandstone Bed, Chinle Formation, northeast Arizona and northwest New Mexico. M.S. thesis. Northern Arizona University, Flagstaff, AZ.

Desojo, J.B. 2005. Los aetosaurios (Amniota, Diapsida) de America Del Sur: sus relations y aportes a la biogeografia y biostratigrafia del Triasico continental. Ph.D. diss. Universidad de Buenos Aires, Buenos Aires, Argentina.

Desojo, J.B., A.B. Arcucci, and C.A. Marsicano. 2002. Reassessment of *Cuyosuchus huenei*, a Middle-Late Triassic archosauriform from the Cuyo Basin, west-central Argentina. *New Mexico Museum of Natural History & Science Bulletin* 21:143–148.

Desojo, J.B., and A.M. Báez. 2005. El esqueleto postcraneano de *Neoaetosauroides* (Archosauria: Aetosauria) del Triásico Superior del centro-oeste de Argentina. *Ameghiniana* 42:115–126.

Desojo, J.B., and A.M. Báez. 2007. Cranial morphology of the Late Triassic South American archosaur *Neoaetosauroides engaeus*: evidence for aetosaurian diversity. *Palaeontology* 50:267–276.

Elder, R.L. 1978. Paleontology and paleoecology of the Dockum Group, upper Triassic, Howard County, Texas. M.S. thesis. University of Texas, Austin, TX.

Fiorillo, A.R., K. Padian, and C. Musikasinthorn. 2000. Taphonomy and depositional setting of the *Placerias* Quarry (Chinle Formation: Late Triassic, Arizona). *Palaios* 15:373–386.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8:1–55.

Gregory, J.T. 1953. *Typothorax* and *Desmatosuchus. Postilla* 16:1–27.

Heckert, A.B., and S.G. Lucas. 1999. A new aetosaur from the Upper Triassic of Texas and the phylogeny of aetosaurs. *Journal of Vertebrate Paleontology* 19:50–68.

Heckert, A.B., and S.G. Lucas. 2000. Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria:Crurotarsi). *Zentralblatt für Geologie und Paläontologie* 1998:1539–1587.

Heckert, A.B., and S.G. Lucas. 2002a. Revised Upper Triassic stratigraphy of the Petrified Forest National Park, Arizona, USA. *New Mexico Museum of Natural History & Science Bulletin* 21:1–36.

Heckert, A.B., and S.G. Lucas. 2002b. Historical taxonomy of the Late Triassic aetosaurs *Typothorax* and *Desmatosuchus* (Archosauria: Crurotarsi), including a lectotype designation for *Desmatosuchus haplocerus. New Mexico Museum of Natural History & Science Bulletin* 21:193–203.

Heckert, A.B., and S.G. Lucas. 2002c. *Acaenasuchus geoffreyi* (Archosauria:Aetosauria) from the Upper Triassic Chinle Group: juvenile of *Desmatosuchus haplocerus. New Mexico Museum of Natural History & Science Bulletin* 21:205–214.

Heckert, A.B., and S.G. Lucas. 2002d. Osteoderms of juveniles of *Stagonolepis* (Archosauria: Aetosauria) from the lower Chinle Group, east-central Arizona. *New Mexico Museum of Natural History & Science Bulletin* 21:235–239.

Heckert, A.B., and S.G. Lucas. 2002e. South American occurrences of the Adamanian (Late Triassic: latest Carnian) index taxon *Stagonolepis* (Archosauria: Aetosauria) and their biochronological significance. *Journal of Paleontology* 76:852–863.

Heckert, A.B., K.E. Zeigler, and S.G. Lucas. 2003. Aetosaurs (Archosauria: Stagonolepididae) from the Upper Triassic (Revueltian) Snyder Quarry, New Mexico. *New Mexico Museum of Natural History & Science Bulletin* 24:115–126.

Hopson, J.A. 1979. Paleoneurology. Pp. 39–146 *in* C. Gans, R. G. Northcutt, and P. Ulinski (eds.). Biology of the Reptilia, Volume 9: Neurology A. Academic Press, New York.

Huene, F.von. 1942. Die fossilen Reptilien des südamerikanischen Gonwanalandes. Ergebnisse dur Sauriergrabung in Südbrasilien 1928/1929. C.H. Beck, München, pp. 161–332.

Hunt, A.P. 2001. The vertebrate fauna, biostratigraphy, and biochronology of the type Revueltian land-vertebrate faunachron, Bull Canyon Formation (Upper Triassic), east-central New Mexico. *New Mexico Geological Society Guidebook* 52:123–152.

Hunt, A.P., and S.G. Lucas. 1988. Late Triassic fauna from the Los Esteros Member of the Santa Rosa Formation, Santa Fe County, New Mexico and its biochronological implications. *New Mexico Journal of Science* 28:107–116.

Hunt, A.P., S.G. Lucas, and P.K. Reser. 1993. A complete skeleton of the stagonolepidid *Typothorax coccinarum* from the Upper Triassic Bull Canyon Formation of east-central New Mexico, U.S.A. *New Mexico Museum of Natural History & Science Bulletin* 3:209–212.

Irmis, R.B. 2005. The vertebrate fauna of the Upper Triassic Chinle Formation in northern Arizona. *Mesa Southwest Museum Bulletin* 9:63–88.

Irmis, R.B. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology* 27:350–361.

Irmis, R.B., W.G. Parker, S.J. Nesbitt, and J. Liu. 2007. Early ornithischian dinosaurs: the Triassic record. *Historical Biology* 19:3–22.

Jacobs, L.L., and P.A. Murry. 1980. The vertebrate community of the Triassic Chinle Formation near St. Johns, Arizona. Pp. 55–73 *in* L.L. Jacobs (ed.). Aspects of Vertebrate History. Museum of Northern Arizona Press, Flagstaff.

Jalil, N.E. 1999. Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. *Journal of African Earth Sciences* 29:219–226.

Jalil, N., S.G. Lucas, and A.P. Hunt. 1995. Late Triassic aetosaurs and phytosaur from Algeria. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1995:173–181.

Jepsen, G.L. 1948. A Triassic armored reptile from New Jersey. *State of New Jersey Department of Conservation Miscellaneous Geologic Paper*, 20 pp.

Krebs, B. 1976. Pseudosuchia. Pp. 40–98 *in* O. Kuhn (ed.). Handbuch der Paläoherpetologie, Volume 13. Gustav Fischer Verlag, Stuttgart.

Long, R.A., and K.L. Ballew. 1985. Aetosaur dermal armor from the Late Triassic of southwestern North America, with special reference to material from the Chinle Formation of Petrified Forest National Park. *Museum of Northern Arizona Bulletin* 47:45–68.

Long, R.A., and P.A. Murry. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *New Mexico Museum of Natural History & Science Bulletin* 4:1–254.

Long, R.A., S.G. Lucas, A.P. Hunt, and R.T. McCrea. 1989. Charles Camp: collecting Late Triassic vertebrates in the American Southwest during the 1920s and 1930s. Pp. 65–71 *in* S.G. Lucas and A.P. Hunt (eds.). Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.

Lucas, S.G., A.B. Heckert, and A.P. Hunt. 2002. A new species of the aetosaur *Typothorax* (Archosauria: Stagonolepididae) from the Upper Triassic of east-central New Mexico. *New Mexico Museum of Natural Science & History Bulletin* 21:221–233.

Lucas, S.G., K.E. Zeigler, A.B. Heckert, and A.P. Hunt. 2003. Upper Triassic stratigraphy and biostratigraphy, Chama Basin, north-central New Mexico. *New Mexico Museum of Natural History & Science Bulletin* 24:15–39.

Marsh, O.C. 1884. The classification and affinities of dinosaurian reptiles. *Nature* 31:68–69.

Martz, J.W. 2002. The morphology and ontogeny of *Typothorax coccinarum* (Archosauria, Stagonolepididae) from the Upper Triassic of the American Southwest. M.S. thesis. Texas Tech University, Lubbock, TX.

Martz, J.W., and B.J. Small. 2006. *Tecovasuchus chatterjeei*, a new aetosaur (Archosauria: Stagonolepididae) from the Tecovas Formation (Carnian, Upper Triassic) of Texas. *Journal of Vertebrate Paleontology* 26:308–320.

Mehl, M.G., W.C. Toepelman, and G.M. Schwartz. 1916. New or little known reptiles from the Trias of Arizona and New Mexico with notes on the fossil bearing horizons near Wingate, New Mexico. *Bulletin of the University of Oklahoma New Series* 103:1–45.

Murry, P.A. 1986. Vertebrate paleontology of the Dockum Group, western Texas and eastern New Mexico. Pp. 109–137 *in* K. Padian (ed.). The Beginning of the Age of Dinosaurs: Faunal Change Across the Triassic-Jurassic Boundary. Cambridge University Press, Cambridge.

Murry, P.A. 1989. Geology and paleontology of the Dockum Formation (Upper Triassic), west Texas and eastern New Mexico. Pp. 102–144 *in* S.G. Lucas and A.P. Hunt (eds.). Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.

Murry, P.A., and R.A. Long, 1989. Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the southwestern upper Triassic. Pp. 29–64 *in* S.G. Lucas and A.P. Hunt (eds.). Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.

Nesbitt, S.J. 2005. Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti. Historical Biology* 17:19–47.

Parker, W.G. 2003. Description of a new specimen of *Desmatosuchus haplocerus* from the Late Triassic of Northern Arizona. M.S. thesis. Northern Arizona University, Flagstaff, AZ.

Parker, W.G. 2005a. A new species of the Late Triassic aetosaur *Desmatosuchus* (Archosauria:Pseudosuchia). *Comptes Rendus Palevol* 4:327–340.

Parker, W.G. 2005b. Faunal review of the Upper Triassic Chinle Formation of Arizona. *Mesa Southwest Museum Bulletin* 11:34–54.

Parker, W.G. 2007. Reassessment of the aetosaur "*Desmatosuchus*" *chamaensis* with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia). *Journal of Systematic Palaeontology* 5:41–68.

Parker, W.G., and R.B. Irmis. 2005. Advances in Late Triassic vertebrate paleontology based on new material from Petrified Forest National Park, Arizona. *In* A.B. Heckert and S.G. Lucas (eds.). Vertebrate Paleontology in Arizona. *New Mexico Museum of Natural History & Science Bulletin* 29:45–58.

Parker, W.G., R.B. Irmis, S.J. Nesbitt, J.W. Martz, and L.S. Browne. 2005. The pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs. *Proceedings of the Royal Society London B* 272:963–969.

Parrish, J.M. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology* 13:287–308.

Parrish, J.M. 1994. Cranial osteology of *Longosuchus meadei* and the phylogeny and distribution of the Aetosauria. *Journal of Vertebrate Paleontology* 14:196–209. Pierce, S.E., and M.J. Benton. 2006. *Pelagosaurus typus* Bronn, 1841 (Mesoeucrocodylia: Thalattosuchia) from the upper Lias (Toarcian, Lower Jurassic) of Somerset, England. *Journal of Vertebrate Paleontology* 26:621–635.

Sawin, H.J. 1947. The pseudosuchian reptile *Typothorax meadei*. *Journal of Paleontology* 21:201–238.

Schoch, R.R. 2007. Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 246:1–35.

Small, B.J. 1985. The Triassic thecodontian reptile *Desmatosuchus*: osteology and relationships. M.S. thesis. Texas Tech University, Lubbock, TX.

Small, B.J. 1989. Aetosaurs from the Upper Triassic Dockum Formation, Post Quarry, west Texas. Pp. 301–308 *in* S.G. Lucas and A.P. Hunt (eds.). Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.

Small, B.J. 2002. Cranial anatomy of *Desmatosuchus haplocerus* (Reptilia: Archosauria: Stagonolepididae). *Zoological Journal of the Linnean Society* 136:97–111.

Spamer, E.E., and E.B. Daeschler. 1995. Previously unfigured type specimens of fossil fish, reptiles, and mammals in the Academy of Natural Sciences of Philadelphia. *Proceedings of the Academy of Natural Sciences, Philadelphia* 146:429–458.

Sues, H.-D. 1992. A remarkable new armored archosaur from the Upper Triassic of Virginia. *Journal of Vertebrate Paleontology* 12:142–149.

Walker, A.D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society London, Series B* 248:103–204.

Weems, R.E. 1980. An unusual newly discovered archosaur from the Upper Triassic of Virginia, U.S.A. *Transactions of the American Philosophical Society* 70:1–53.

Wilson, J.A. 1950. Cope's types of fossil reptiles in the collection of the Bureau of Economic Geology, the University of Texas. *Journal of Paleontology* 24:113–115.

Wilson, J.A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* 19:639–653.

Woody, D.T. 2003. Revised geological assessment of the Sonsela Member, Chinle Formation, Petrified Forest National Park, Arizona. M.S. thesis. Northern Arizona University, Flagstaff, AZ.

Woody, D.T. 2006. Revised stratigraphy of the lower Chinle Formation (Upper Triassic) of Petrified Forest National Park, Arizona. *Museum of Northern Arizona Bulletin* 62:17–45.

Zeigler, K.E., A.B. Heckert, and S.G. Lucas. 2002. A new species of *Desmatosuchus* (Archosauria: Aetosauria) from the Upper Triassic of the Chama Basin, north-central New Mexico. *New Mexico Museum of Natural History & Science Bulletin* 21:215–219.

Zittel, K.A. 1887–90. Handbuch der Palaeontologie. 1. Abteilung: Palaeozoologie, 3. München & Leipzig.