

ACAENASUCHUS GEOFFREYI (ARCHOSAURIA:AETOSAURIA) FROM THE UPPER TRIASSIC CHINLE GROUP: JUVENILE OF *DESMATOSUCHUS HAPLOCERUS*

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Abstract—Aetosaur scutes assigned to *Acaenasuchus geoffreyi* Long and Murry, 1995, are juvenile scutes of *Desmatosuchus haplocerus* (Cope, 1892), so *A. geoffreyi* is a junior subjective synonym of *D. haplocerus*. Scutes previously assigned to *Acaenasuchus* lack anterior bars and a strong radial pattern of elongate pits and ridges, but do possess an anterior lamina and a raised boss emanating from the mid-dorsal surface of the scute. *Desmatosuchus* is the only aetosaur with this combination of features, and the replacement of the anterior bar with a lamina is an autapomorphy of *Desmatosuchus*. Other characters used by previous workers to distinguish *Acaenasuchus* from *Desmatosuchus* include deeply incised pitting on the dorsal scutes and the division of the raised boss posteriorly into two lateral flanges in *Acaenasuchus*. We interpret the deeply incised pitting as an artifact of ontogenetic variation. The more exaggerated pits and thin grooves on the scutes of “*Acaenasuchus*” represent a juvenile stage of development, an ontogenetic feature we have observed on other aetosaurs, notably *Aetosaurus*. The divided boss is the most unique characteristic of “*Acaenasuchus*,” but even this feature could also represent immature development. Further, of the four localities (the Blue Hills, the *Placerias* quarry and the Downs’ quarry—all near St. John’s, AZ, and another locality near Winslow, AZ) that have produced scutes assigned to *Acaenasuchus*, two (the *Placerias* and Downs’ quarries) also produce abundant adult specimens of *Desmatosuchus*, and all four localities are in strata of equivalent (latest Carnian) age. Thus, in all critical details of morphology, except size, scutes assigned to *Acaenasuchus* appear to represent scutes of *Desmatosuchus*. The apparent rarity and limited geographic and stratigraphic range of *Acaenasuchus* relative to *Desmatosuchus* are artifacts of preservational and collecting biases.

Keywords: Aetosaur, juvenile, taxonomy, Upper Triassic, *Desmatosuchus*, *Acaenasuchus*

INTRODUCTION

Aetosaurs were armored, quadrupedal, primarily herbivorous archosaurs known from Upper Triassic strata on five modern continents. Perhaps the most striking feature of aetosaurs was their carapace, composed of two columns each of dorsal (paramedian) and lateral scutes. Morphological features of the paramedian and lateral scutes vary widely among aetosaurs, so that the type specimens of several genera are isolated scutes. Recently, we (Heckert and Lucas, 2000) revised the taxonomy of the Aetosauria, and considered *Acaenasuchus geoffreyi* Long and Murry, 1995 to be based on the juvenile morphology of *Desmatosuchus haplocerus* (Cope, 1892).

Here, we identify and describe all repositied specimens of *Acaenasuchus* and compare them to *Desmatosuchus* to justify the synonymy of the two genera. In doing so, we will recount the history of specimens of *Acaenasuchus*, evaluate their morphology, and compare them to known aetosaurs. This study includes more than twice as many scutes as originally studied by Long and Murry (1995) and we provide detailed measurements of many scutes (Tables 1-2—see Appendix). We utilize the terminology for aetosaur armor we used in our revision of the Aetosauria (Heckert and Lucas, 2000). Namely, we identify four columns of scutes, two lateral and two dorsal, extending from the cervical region to the tail. Dorsal scutes (the two central columns) are termed paramedians (following Long and Ballew, 1985).

Abbreviations used in this paper are: ANSP = Academy of Natural Sciences, Philadelphia; MNA = Museum of Northern Arizona, Flagstaff; UCMP = University of California Museum of Paleontology, Berkeley; UMMP = University of Michigan Museum of Paleontology, Ann Arbor.

HISTORY

Charles Camp of the UCMP collected numerous small tetrapods, including specimens of “*Acaenasuchus*” from what he (1930) termed “meal pots” localities in the Blue Hills north and east of St. Johns, Arizona (Fig. 1). Later collecting parties associated with the MNA obtained additional material of “*Acaenasuchus*” from the *Placerias* and Downs’ quarries south of St. Johns. Long and Ballew (1985, p. 61) briefly discussed the small aetosaur scutes that form part of this collection, and identified them as probable juvenile specimens of *Desmatosuchus haplocerus*. Murry and Long (1989, p. 33) referred to these scutes as “*Acaenasuchus geoffreyi*” without identifying a holotype or providing a diagnosis, render-

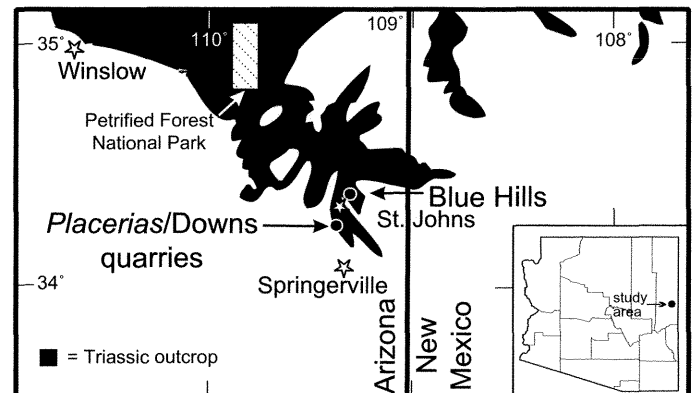


FIGURE 1. Index map of Triassic strata in east-central Arizona (after Stewart et al., 1972) indicating localities yielding fossils of “*Acaenasuchus*.”

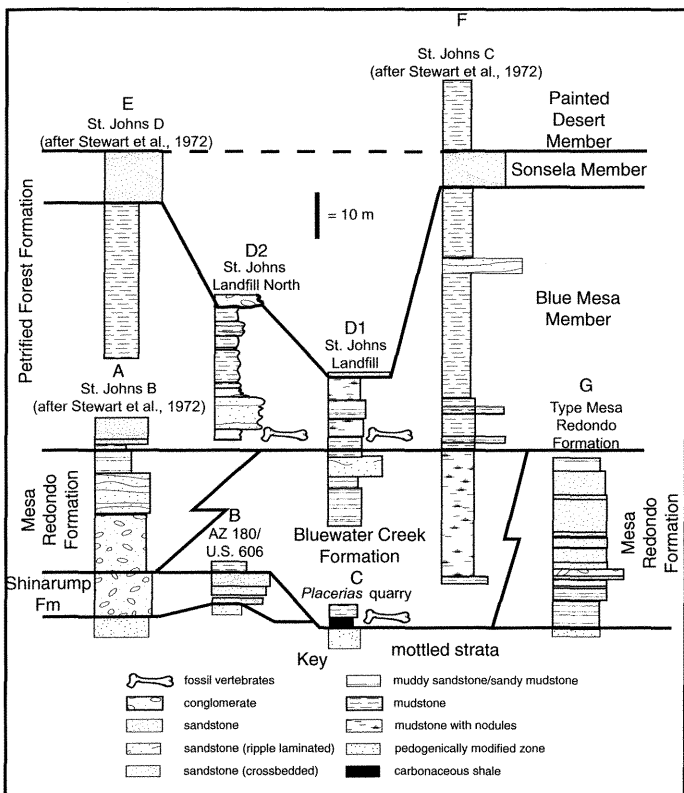


FIGURE 2. Correlated measured sections of the lower Chinle Group near St. Johns, Arizona (after Heckert and Lucas, 2001). Bones show the stratigraphic position of *Acaenasuchus* and *Desmatosuchus* localities.

ing the binomen a *nomen nudum*. Long and Murry (1995) formally named and diagnosed the aetosaur *Acaenasuchus geoffreyi*, designating UCMP 139576 (from UCMP locality 7308 in the Blue Hills) as the holotype and referring numerous catalogued and uncatalogued scutes from this and other localities to this taxon (Long and Murry, 1995, figs. 117, 118). Notably, all of these specimens were collected from a narrow stratigraphic interval (Fig. 2). We have borrowed and restudied the hypodigm of *Acaenasuchus*, all of which are now catalogued (Table 1). Many of these scutes are illustrated here in our Figure 3. As part of this study, one of us (ABH) examined Camp's collections at UCMP and identified approximately 50 additional specimens of *Acaenasuchus*, more than doubling the sample described by Long and Murry (1995). Additional specimens were reported, but not illustrated or described in detail, from "Dinosaur Ridge" in the Blue Mesa Member in the Petrified Forest National Park (PEFO) (Hunt et al., 1996; Hunt, 1998, Hunt and Wright, 1999). We have not studied this collection, which is on loan from PEFO to Hunt at this time.

SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1758

ARCHOSAURIA Cope, 1869

CROCODYLOTARSI Benton and Clark, 1988

AETOSAURIA Nicholson and Lydekker, 1889

STAGONOLEPIDIDAE Lydekker, 1887

Specimens assigned to *Acaenasuchus* clearly pertain to aetosaurs (Long and Murry, 1995). The definitive traits of the Aetosauria, and thus the Stagonolepididae, evident on the holotype dorsal paramedian scute of *Acaenasuchus* (Fig. 3A-E) are that it is wider than long, sculptured, and lacks either anteriorly or posteriorly projecting lappets. These characteristics, when taken

together, are a synapomorphy of the Aetosauria (Parrish, 1994; Long and Murry, 1995; Heckert and Lucas, 1999, 2000). All paramedian scutes referred to *Acaenasuchus* share this synapomorphy. All lateral scutes assigned to *Acaenasuchus* show evidence of articulating with the paramedian scutes, and the presence of such lateral scutes is also a synapomorphy of the Aetosauria (Parrish, 1994; Long and Murry, 1995; Heckert and Lucas, 1999, 2000).

DESMATOSUCHINAE Huene, 1942

Huene (1942) erected the subfamily Desmatosuchinae for the aetosaurs *Desmatosuchus*, *Acompsosaurus* (= *Stagonolepis*) and *?Hoplitosuchus*. Heckert and Lucas (2000) recently re-defined the Desmatosuchinae as all aetosaurs more closely related to *Desmatosuchus* than the last common ancestor of *Stagonolepis* and *Desmatosuchus*, utilizing the phylogeny of Heckert and Lucas (1999). The presence of spikes or horned processes on the lateral scutes unites all desmatosuchines except *Neoetosauroides*, and excludes other aetosaurs with the possible exception of *Stagonolepis wellsi*, which is purported to have spikes on its cervical lateral scutes (Long and Murry, 1995). Although the holotype specimen of *Acaenasuchus* is a paramedian scute, the presence of these spikes on the syntype lateral scutes assigned to *Acaenasuchus* indicates that these scutes pertain to a derived desmatosuchine.

Unnamed Clade: *Typothorax* + *Desmatosuchus*

Heckert and Lucas (1999, 2000) united *Typothorax* and *Desmatosuchus* by the following four synapomorphies: posterior premaxillary teeth absent, random to faintly radial pitting (lacking elongate radial grooves and ridges) on cervical paramedian scutes, random to faintly radial pitting on dorsal paramedian scutes, random to faintly radial pitting on lateral scutes. The presence of random to faintly radial pitting unites these taxa with the poorly known aetosaur *Redondasuchus* (Heckert et al., 1996), which is represented by material too incomplete to incorporate into a cladistic phylogenetic hypothesis at this time. All scutes assigned to *Acaenasuchus* (Fig. 3) lack elongate radial grooves and ridges, and have a sculptured ornamentation that consists of a random to faintly radial pattern of pits, indicating that they clearly pertain to the clade of *Typothorax* + *Desmatosuchus*.

DESMATOSUCHUS HAPLOCERUS (Cope, 1892)

(Figs. 3-4; Tables 1-2)

Synonym: *Acaenasuchus geoffreyi* Long and Murry 1995, p. 1, figs. 117-118. A complete synonymy of *Desmatosuchus* appears in Heckert and Lucas (2000; see also Zeigler et al., 2002; Heckert and Lucas, 2002a).

Syntypes: ANSP 14688, "A dorsal and probably two caudal vertebrae; a scapula of the right side, a few fragments of ribs, and about thirty dermal bones" (Cope 1892, p. 129). See Heckert and Lucas (2002a) for a discussion of the type material of *Desmatosuchus haplocerus*.

Type locality: Dickens County, Texas.

Type horizon: Tecovas Formation, Chinle Group. The Tecovas Formation is of well-established Adamanian (latest Carnian) age (Lucas and Hunt, 1993; Lucas, 1997, 1998).

Revised diagnosis: Aetosaur genus readily diagnosed from all other aetosaurs by the presence of anterior laminae on the paramedian and lateral scutes (Fig. 4), dorso-ventrally thickened cervical paramedian scutes that are longer than wide, and cervical lateral scutes that bear large, posteriorly recurved spikes (Fig. 4); distinguished from all aetosaurs except *Typothorax* and *Redondasuchus* by the absence of elongate grooves and ridges on paramedian and lateral scutes.

Discussion: Gregory (1953) demonstrated that the holotype of *D. spurensis* Case (1920) is congeneric with the type material of

Episcoposaurus haplocerus Cope, 1892 and that the type species of *Episcoposaurus*, *E. horridus* Cope, 1887, is a junior synonym of *Typpothorax coccinarum* Cope, 1875, or else indeterminate. Thus, the type species of *Desmatosuchus* is *D. haplocerus* (see also Heckert and Lucas, 2000; Zeigler et al., 2002; Heckert and Lucas, 2002a).

Desmatosuchus is one of the best known Chinle aetosaurs, and is easily recognized by the giant recurved lateral spikes developed on anterior lateral scutes (Cope, 1892; Case, 1922) and the lack of anterior bars on the paramedian and lateral scutes (Long and Ballew, 1985). These features, as well as the random pitting on dorsal paramedian scutes, are present in the holotype and referred specimens of *Acaenasuchus*, supporting our assignment of *Acaenasuchus* to *Desmatosuchus*. The most complete osteology of *Desmatosuchus* was presented by Case (1922), and more recent descriptions of *Desmatosuchus* include Gregory (1953), Long and Ballew (1985), Small (1985, 1989), Long and Murry (1995), and Zeigler et al. (2002).

"ACAENASUCHUS GEOFFREYI"

(Figures 3,5; Tables 1-2—see Appendix)

Holotype: UCMP 139576, a dorsal paramedian scute, probably from the left side

Type Locality: UCMP 7308, in the Blue Hills, northeast of St. Johns, Apache County, Arizona.

Type Horizon: Lower Blue Mesa Member of the Petrified Forest Formation (Fig. 2). The Blue Mesa Member is of well-established Adamanian (latest Carnian) age (Lucas and Heckert, 1996a; Lucas et al. 1997).

Description

Long and Murry (1995, p. 114) provided the following diagnosis of "*Acaenasuchus*:"

Paramedian scutes with anterior laminae (as in *Desmatosuchus*), but in *Acaenasuchus* are greatly developed throughout the presacral series; paramedian eminences include thorn-like processes bearing lateral and medial branches paralleling the posterior margin of the scute; random ornamentation consists of intricate latticework of deep hollows and fine ridges; posterior margin of paramedian scutes beveled; cervical paramedian scutes longer (antero-posterior) than wide (medio-lateral); lateral plates with thorn-like lateral ridges or conical recurved horns

To date, in the UCMP collection approximately 95 scutes or partial scutes represented by 90 catalog numbers have been assigned to *Acaenasuchus*. The MNA collection is considerably smaller, consisting of 14 fragmentary scutes (Table 1). Long and Murry (1995, p. 114-115) also refer a single specimen from "Rincon Basin East" near Winslow, Arizona, to *Acaenasuchus*. This specimen may be in private hands (Long and Murry, 1995, p. 115). Our descriptions draw most heavily from the more extensive and better-preserved UCMP material, which appears to include at least two individuals, a smaller individual that is probably represented by most of the scutes identified by Long and Murry (1995), and a larger individual not as well represented in their collection. Notably, several of the lateral scutes are markedly larger and wider than others. Scutes we tentatively assign to the larger individual(s) are marked by a "LG" in Table 1.

Paramedian Scutes

Paramedian scutes are generically distinctive among the aetosaurs, and the holotype or lectotype specimens of *Desmatosuchus*, *Typpothorax*, *Paratyppothorax*, *Redondasuchus* and

Acaenasuchus are all paramedian scutes in varying states of preservation (Heckert and Lucas, 2000). We illustrate here the holotype (Fig. 3A-E) and several of the best-preserved paramedian scutes assigned to *Acaenasuchus* (Fig. 3F-H) by Long and Murry (1995). These scutes lack anterior bars, possess a pattern of very faintly radiate to random pitting, a raised boss emanating from the postero-medial surface of the scute, and weakly developed interdigitating lateral margins for tongue-and-groove articulation with the lateral scutes. The center of the boss is slightly medial and posterior to the center of the scute, as in *Desmatosuchus*. The width:length ratios of the three complete or nearly complete specimens are low—1.6-1.87:1 (Table 2A)—a feature that also coincides with *Desmatosuchus*, and differs from *Paratyppothorax*, *Aetosaurus* and *Typpothorax*. Most dorsal paramedian scutes are sigmoid in lateral or medial views, including the holotype (Fig. 3B, D) and UCMP 139585-139588. As Long and Murry (1995) noted, the lateral margin of several of these scutes is dorso-ventrally thickened, and this corresponds well to the medial thickening observed on the lateral scutes. All of these features also occur in *Desmatosuchus* (Fig. 4D-H). The presence of an anterior lamina (*in lieu* of an anterior bar) is an autapomorphy of *Desmatosuchus* (Long and Ballew, 1985). *Desmatosuchus* is also characterized by ornamentation consisting of a raised boss from which a random to faintly radial array of irregularly shaped pits emanates anteriorly, medially, and laterally.

The development of the anterior lamina varies among the UCMP paramedian scutes. In the holotype, the relative length of the scute to the lamina is 15:1, whereas in the other specimens this measurement varies from 2.5:1 to 10:1 (Table 2A). We agree with Long and Murry (1995, p. 114) that low ratios probably indicate a higher degree of flexibility in the carapace, but we suspect that this is largely an artifact of position within the scute column. We also differ from Long and Murry (1995) in that we do not recognize any cervical paramedian scutes of *Acaenasuchus*, as all of the scutes are clearly much wider than long (W:L 2:1), a condition unlike the cervicals of *Desmatosuchus* (W:L < 1:1) or most other aetosaurs (W:L < 2:1)

"Tongue-and-groove" or interdigitating articulations with the lateral scutes are best preserved on UCMP 139588 (Fig. 3G). The anterior lamina on this partial dorsal paramedian scute flares anteriorly along the edge, as is typical on the lateral margin of aetosaur scutes. Along the lateral margin the anterior portion of this scute is slightly recessed anteriorly. The scute possesses a modest embayment in the middle of the lateral margin, so that the dorsal surface overlaps the ventral edge, a condition that is nearly reversed at the posterior portion of the scute, which is almost convex. Furthermore, careful examination of the paramedian scutes of *Acaenasuchus* (e.g., Fig. 3B,D) reveals irregular margins that we interpret as the early development of the "tongue-and-groove" articulation between lateral (tongue) and paramedian (groove) scutes of *Desmatosuchus*.

The only characteristics of the scutes of *Acaenasuchus* that differ from those of *Desmatosuchus* are their small size, the relatively deeply incised pitting, and the triradiate division of the raised boss into distinct anterior, lateral and medial flanges. Given the preponderance of other features shared with *Desmatosuchus*, we suspect that these are ontogenetic or, at most, species-level differences. We have observed aetosaurs in different size classes of *Aetosaurus* and *Stagonolepis*, and in both genera the smaller individuals preserve a relatively more deeply incised ornamentation (resulting in more distinct patterns) than larger individuals (see Heckert and Lucas, 2002b). Examples include juvenile individuals, particularly specimen IX of the *Aetosaurus ferratus* block (Fraas, 1877, 1896) and the juveniles of *Stagonolepis* we illustrate elsewhere in this volume. Therefore, we suspect that the deeply

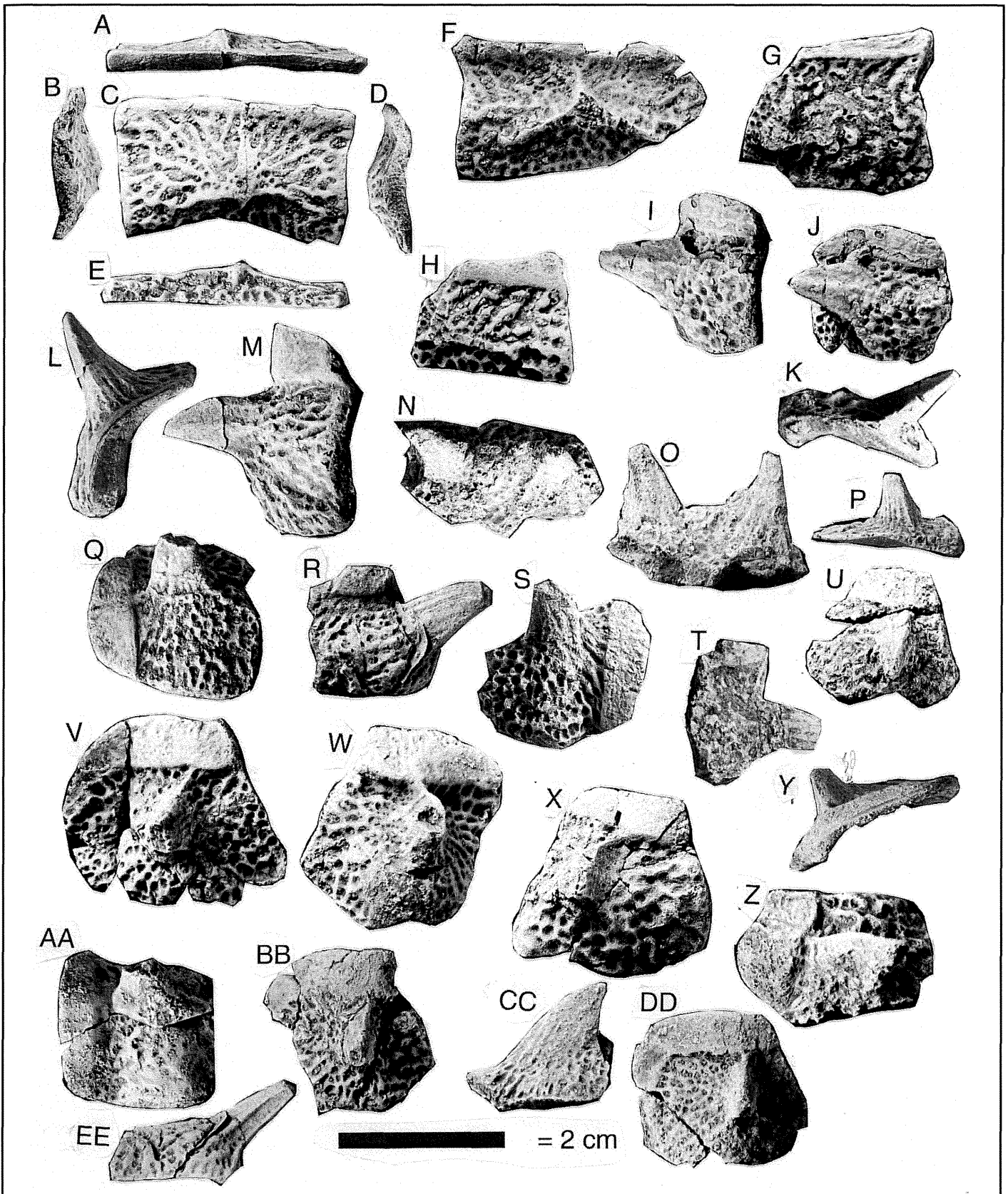


FIGURE 3. Dorsal paramedian (A-H) and lateral (I-EE) scutes of juvenile *Desmatosuchus haplocerus* previously assigned to "*Acaenasuchus*." A-E, UCMP 139576, holotype scute of *Acaenasuchus geoffreyi* in anterior (A), lateral? (B), dorsal (C), medial? (D), and posterior (E) views; F, UCMP 139586 in dorsal view; G, UCMP 139588, in dorsal view; H, UCMP 139584 in dorsal view; I, UCMP 13959 in dorsal? view; J-K, UCMP 139579, left cervical lateral scute in dorsal (J) and anterior (K) views; L-M, UCMP 139577, left cervical lateral scute in anterior (L) and dorsal (M) views; N-O, UCMP 139582, two right cervical lateral scutes in lateral (N) and ventral (O) views; P, UCMP 139580 in anterior view; Q, UCMP 139598 in lateral view; R, UCMP 139583 in

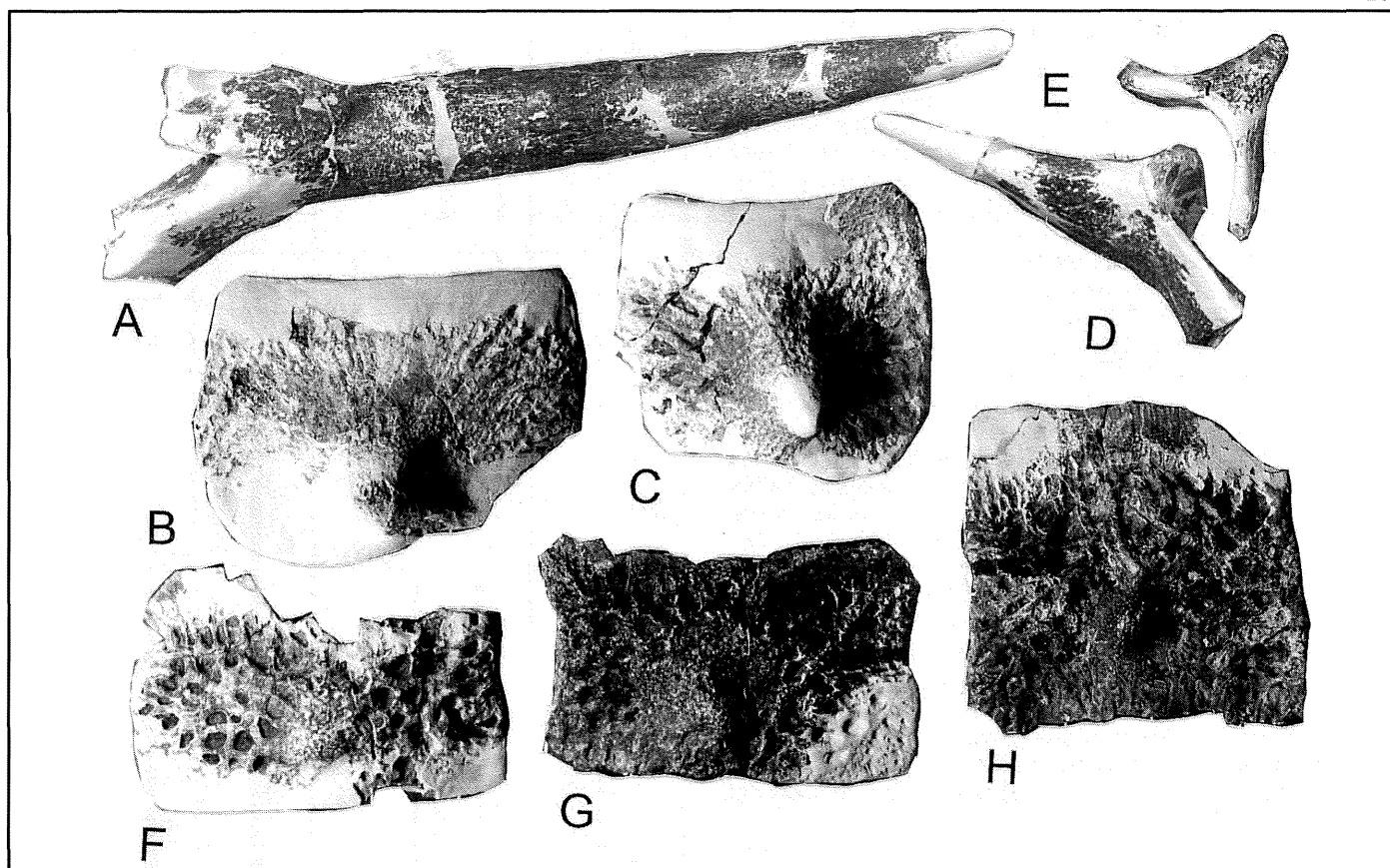


FIGURE 4. Selected scutes of adult *Desmatosuchus* (all UCMP 33200 from the *Placerias* quarry) for comparison with scutes assigned to "*Acaenasuchus*" (Fig. 3). A-C, Lateral scutes in posterior view, A = 5th? scute, C = 4th? or 6th? scute; D-H, Paramedian scutes, all in dorsal view. All scale bars = 2 cm.

incised pitting that typifies scutes assigned to *Acaenasuchus* reflects ontogenetic variation.

The triradiate flanges on the boss of *Acaenasuchus* also appear to represent the juvenile morphology of *Desmatosuchus*. Notably, published photographs show indications of triradiate bosses on paramedian scutes UCMP 269/126833 (Long and Ballew, 1985, fig. 2C) and UMMP 7476 (Long and Murry, 1995, fig. 88), UCMP 269/33200 (Fig. 4D). We suspect that the marked triradiate division of the boss in specimens of "*Acaenasuchus*" becomes less prominent as the boss develops ontogenetically. That is, the distinct flanges of the boss coalesce with increased size.

Lateral Scutes

As in the paramedian scutes, lateral scutes are generically distinctive among the aetosaurs. All of the well-preserved lateral scutes assigned to *Acaenasuchus* by Long and Murry (1995) lack anterior bars, are sharply angulated in anterior or posterior view (Figs. 3K-L, Y), and possess a prominent spike or horn that projects dorso-laterally. In many of these scutes the spike is strongly recurved posteriorly in a manner identical to the cervical lateral scutes of *Desmatosuchus*—the medial margin is thickened and sigmoidal in medial view, and clearly articulates with the lateral scutes, and may represent the incipient development of the tongue in a tongue-and-groove articulation with the paramedian scutes. In these respects, lateral scutes of *Acaenasuchus* are identical to

Desmatosuchus (Fig. 4A-C), but distinct from other aetosaurs.

The presence of anterior laminae *in lieu* of anterior bars on these scutes is another autapomorphy of *Desmatosuchus*. Among the aetosaurs, only *Desmatosuchus* and *Longosuchus* bear lateral scutes with dorsal and lateral flanges that meet at an approximate right angle (Long and Murry, 1995; Heckert et al., 1996; Heckert and Lucas, 1999, 2000). Although *Longosuchus*, *Typothorax* and *Paratypothorax* bear spikes on at least some lateral scutes, only *Desmatosuchus* bears spikes that are longer than the width of the dorsal flange of the lateral scute (Table 2B). *Desmatosuchus* and *Acaenasuchus* are identical in all of these respects, providing further evidence that they are congeneric.

As Long and Murry (1995) noted, a large number of the lateral scutes assigned to *Acaenasuchus* bear strongly recurved lateral spikes. Although the number of specimens that bear such spikes appears disproportionately large (Table 1) for *Desmatosuchus*, which typically only exhibits strongly recurved spikes on lateral scutes 3-6, the possibility that there may be several individuals present makes this less problematic. The total of nine scutes we identify from Long and Murry's (1995) material as possible third, fourth, or sixth lateral scutes are almost evenly distributed (four from the right side and five from the left side) (Table 1). Similarly, the two scutes we identify as likely fifth lateral scutes are both from the right side, and probably correspond to the smaller and larger individual(s) described earlier.

FIGURE 3. (Continued from previous page) dorsal view. S, UCMP 139578, T, UCMP 139594 in dorsal view; U, UCMP 139600 in dorsal? view; V, UCMP 139592 in dorsal? view; W, UCMP 139589 dorsal view; X, UCMP 139593 in dorsal view; Y, UCMP 139600 in anterior view; Z, UCMP 139601 in lateral view, AA, UCMP 139590 in lateral view; BB, UCMP 139597 in dorsal? view; CC, UCMP 139595 in lateral? view; DD, UCMP 139581 in dorsal view; EE, UCMP 139596. Photographs approximately 1.5x natural size. For a complete list of scute positions, see Table 1.

PROVENANCE, DISTRIBUTION AND AGE

The vast majority of catalogued specimens attributed to "*Acaenasuchus*" by Long and Murry (1995) come from two localities, the *Placerias*-Downs' quarry complex and the Blue Hills, both near St. Johns, Arizona (Figs. 1-2). The *Placerias* and Downs' quarries are only 100 m apart and less than 1.5 m separates them stratigraphically (Jacobs and Murry, 1980; Kaye and Padian, 1994; Lucas et al., 1997; Fiorillo et al., 2000). Both quarries are stratigraphically low in the Bluewater Creek Formation (Lucas et al., 1997). The UCMP localities in the Blue Hills are all either very high in the Bluewater Creek Formation or low in the Blue Mesa Member of the overlying Petrified Forest Formation (Camp, 1930; Camp and Welles, 1956; Long and Murry, 1995; Lucas and Heckert, 1996a; Heckert and Lucas, 1997, 2001). Of these localities, both the *Placerias* and the Downs' quarry yield numerous specimens of adult *Desmatosuchus* (Jacobs and Murry, 1980; Kaye and Padian, 1994; Long and Murry, 1995). The Blue Hills localities, albeit slightly higher stratigraphically (Fig. 2) otherwise produce vertebrate assemblages largely identical to those of the *Placerias*-Downs' quarries and the Blue Mesa Member of the Petrified Forest National Park, which also produces abundant *Desmatosuchus* (e.g., Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 1997; Lucas et al., 1997). This is consistent with the conclusion advanced by Long and Ballew (1985) and further supported by us, that the scutes assigned to *Acaenasuchus* simply represent juveniles of *Desmatosuchus*. In addition, we suspect that the apparent rarity of *Acaenasuchus* relative to *Desmatosuchus* is an artifact of the combined biases of the preservational environments and collectors focused on larger animals.

A case in point is the apparent rarity of *Acaenasuchus* (14 catalogued specimens, all at MNA) relative to the several hundred specimens of *Desmatosuchus* (Long and Murry, 1995: p. 232) from the *Placerias* quarry. This is almost certainly a collecting bias, as Camp and Welles (1956, p. 259) noted that "[m]ost of the numerous isolated dermal scutes of *Typothorax* [=all aetosaurus]...were not collected." Therefore, we are confident that the catalogued UCMP collection is not representative of the relative abundance of either taxon or of the size classes actually present in the quarry. Furthermore, known juvenile specimens of aetosaurus are exceedingly rare in the fossil record. The slab containing the type specimen of *Aetosaurus ferratus* includes the remains of at least 23 individuals, of which no more than two are juveniles (O. Fraas, 1877; E. Fraas, 1896; Walker, 1961; pers. obs.). Significantly, the only other juvenile aetosaur scutes we have observed in the American Southwest are juveniles of the aetosaur *Stagonolepis* also collected by Camp in the Blue Hills (Heckert and Lucas, 2002b) and a very few scutes from the Snyder quarry in the Petrified Forest Formation of north central New Mexico. Juvenile scutes of *Typothorax* from the Post quarry in the Bull Canyon Formation of West Texas were also reported by Small (1989).

There is a marked "gap" in size between the smallest "adult" *Desmatosuchus* scutes and the largest *Acaenasuchus* scutes. However, such a gap also exists for all other Chinle Group aetosaurus of relatively large size (*Stagonolepis*, *Paratypothorax*, *Typothorax*, *Redondasuchus*, *Longosuchus*). Clearly, all of these taxa did not exist solely at large (2.5-m+) body size, so the record of juvenile aetosaurus from the Chinle is clearly exceedingly poor. We suspect that "*Acaenasuchus*" is an exception to the rule in part because juvenile *Desmatosuchus* lateral scutes, with their solid bases and relatively thick cross-sections, may have been less susceptible to breakage during transport and other taphonomic processes than the scutes of other aetosaurus.

Both the *Placerias*-Downs quarry complex and the UCMP Blue Hills localities are of well-established Adamanian (latest

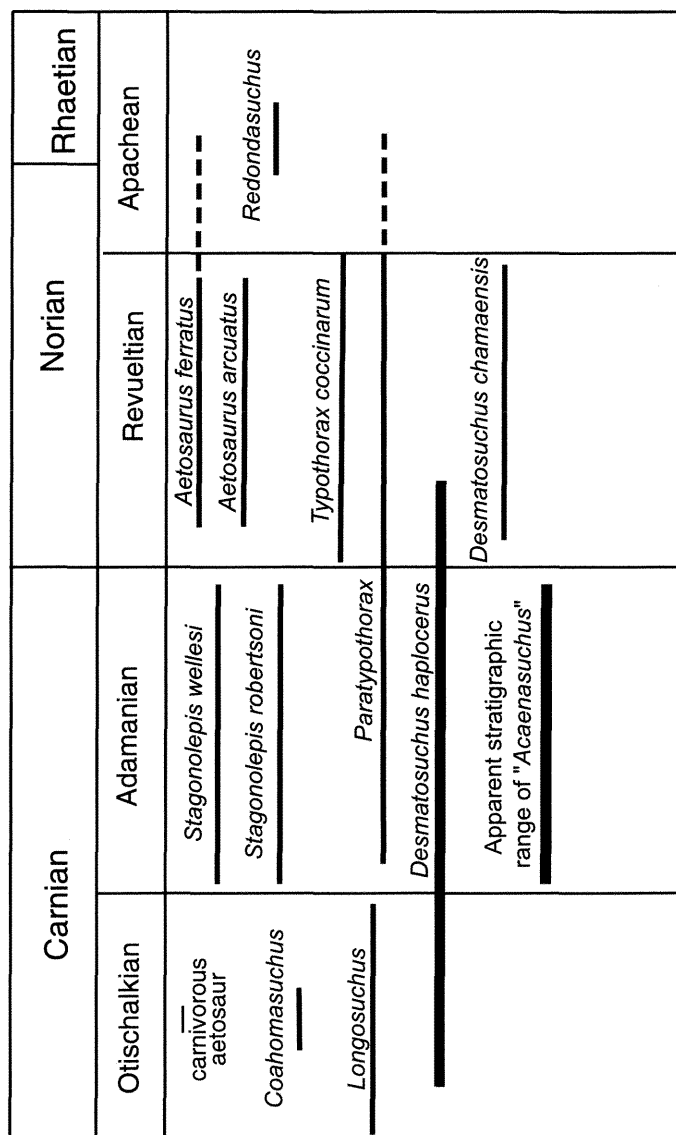


FIGURE 5. Biochronology of Chinle Group aetosaurus. Note the overlap of "*Acaenasuchus*" and *Desmatosuchus haplocerus*.

Carnian) age (Lucas and Hunt, 1993; Lucas and Heckert, 1996a; Heckert and Lucas, 1997, 2001; Lucas et al., 1997). Particularly important are the occurrence of the aetosaur *Stagonolepis* and the phytosaur *Rutiodon*, both of which are index taxa of the Adamanian land-vertebrate faunachron of Lucas and Hunt (1993; Lucas, 1998). Specimens of *Desmatosuchus haplocerus* are known from strata both older and younger than Adamanian; in the Chinle Group of southwestern North America they occur in strata ranging from early-late Carnian (Otischalkian) to early Norian (early Revuelitian) age (Long and Ballew, 1985; Long and Murry, 1995; Lucas and Heckert, 1996b). Within this long (approximately 15 myr) time span, however, *D. haplocerus* is most common in strata of Adamanian age. This is in part because of the large collections in the *Placerias*-Downs' quarries and from the type Adamanian assemblage at Petrified Forest National Park (Long and Ballew, 1985), but also from the type localities in West Texas (Cope, 1892; Case, 1920, 1922). In the past we have referred to this as the "abundance biochron" of *Desmatosuchus* (Lucas and Heckert, 1996b; Lucas et al., 1997; Heckert and Lucas, 2000). Given the well-documented bias of early collectors towards larger and more complete animals and the abundance of *D. haplocerus* in Adamanian strata,

it is hardly surprising that: (1) there are far fewer known specimens of *Acaenasuchus* than *D. haplocerus* than might be expected if *Acaenasuchus* represents a juvenile of *D. haplocerus*; (2) juvenile specimens of *D. haplocerus* are known from a narrower stratigraphic interval than adult *D. haplocerus* (Fig. 5); and (3) the geographic range of *Acaenasuchus* appears more restricted than that of *D. haplocerus*.

CONCLUSIONS

Almost all diagnostic features of the scutes of *Acaenasuchus* are also present in scutes of *Desmatosuchus*. In particular, these two aetosaurs are the only named taxa that share the following synapomorphies: (1) presence of anterior laminae *in lieu* of anterior bars on both dorsal paramedian and lateral scutes; (2) sharply angulated (approximately 90°) lateral scutes, some of which bear prominent, posteriorly recurved spikes; and (3) incipient tongue-and-groove articulations for paramedian scutes with lateral scutes. Both taxa also possess paramedian scutes with raised bosses and ornamentation consisting of faintly radiate to a random pattern of irregular pits, although these features have a broader distribu-

tion among the aetosaurs (Long and Murry, 1995; Heckert and Lucas, 1999, 2000). These features, combined with the presence of *Acaenasuchus* and *Desmatosuchus* at the *Placerias* and Downs' quarries, strongly suggest that *Acaenasuchus* represents juveniles of *Desmatosuchus*, as Long and Ballew (1985) originally suggested. The rarity of specimens assigned to *Acaenasuchus* relative to adult *Desmatosuchus* is probably an artifact of preservational and collecting biases.

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APPENDIX—TABLES OF SPECIMEN DESCRIPTIONS AND MEASUREMENTS

TABLE 1. Anatomical position and description of specimens assigned to *Acaenasuchus* by Long and Murry (1995).

Specimen #	Description (Figure)	Long & Murry (1995) Figure(s)
UCMP 27049	Incomplete right? dorsal paramedian scute	
UCMP 139576	Holotype left dorsal paramedian scute (Fig. 3A-E)	117A-C, 118L
UCMP 139577	Nearly complete right anterior dorsal lateral scute (Fig. 3L-M)	117D-G, 118A
UCMP 139578	Incomplete right cervical (3 rd -4 th) lateral scute (Fig. 3S)	117H-I
UCMP 139579	Nearly complete left cervical (3 rd -4 th ?) lateral scute (LG) (Fig. 3J-K) 117J-K	
UCMP 139580	Incomplete mid-dorsal to caudal right lateral scute (LG)	118C
UCMP 139581	Incomplete left dorsal lateral scute (small)	117N-O
UCMP 139582	2 Incomplete right lateral scutes (3 rd -4 th ?) (Fig. 3N-O)	117P-Q, 118D
UCMP 139583	Incomplete right cervical lateral scute (5 th)	117R-S, 118J
UCMP 139584	Half of left? mid-dorsal paramedian scute (Fig. 3H)	118K
UCMP 139585	Nearly complete right dorsal paramedian scute	
UCMP 139586	Incomplete right? paramedian scute (Fig. 3F)	
UCMP 139587	Incomplete? left? dorsal paramedian scute	
UCMP 139588	Incomplete right dorsal paramedian scute w/ incipient tongue and groove articulation (Fig. 3G)	
UCMP 139589	Incomplete right cervical (3 rd -4 th ?) lateral scute (LG) w/ incipient tongue & groove articulation (Fig. 3W)	
UCMP 139590	Incomplete left cervical lateral scute (LG)—counterpart to 139590	
UCMP 139591	Incomplete left lateral scute w/incipient tongue & groove articulation	
UCMP 139592	Incomplete left antero-dorsal lateral scute (lateral flange) (Fig. 3V, 3AA)	
UCMP 139593	Incomplete left cervical (3 rd -4 th ?) lateral scute (Fig. 3X)	
UCMP 139594	Incomplete right cervical lateral scute (5th)	117L-M, 118E
UCMP 139595	Incomplete left? mid-dorsal lateral scute (Fig. 3CC)	118B
UCMP 139596	Incomplete left? cervical-dorsal lateral scute	
UCMP 139597	Incomplete left? cervical lateral scute (Fig. 3BB)	

TABLE 1 (continued)

Specimen #	Description (Figure)	Long & Murry (1995) Figure(s)
UCMP 139598	Incomplete left? cervical-dorsal (3 rd -4 th or 6 th) lateral scute (Fig. 3Q)	118G(?)
UCMP 139599	Incomplete left cervical (3 rd -4 th) lateral scute (LG)	
UCMP 139600	Incomplete left? cervical? (2 nd) or dorsal lateral scute (blade-like) (Fig. 3U)	
UCMP 139601	Incomplete mid-dorsal left lateral scute (LG) (Fig. 3Z)	
UCMP 139602	Small incomplete right? anterior caudal? lateral scute	
UCMP 139603	Incomplete left? cervical? lateral? scute (LG)	
UCMP 139604	Incomplete right? cervical lateral scute	
UCMP 139605	Fragmentary left? cervical? lateral scute	
UCMP 139606	Fragmentary left? cervical? lateral scute (LG?)	
UCMP 139607	Fragmentary left? cervical (1 st -2 nd) lateral scute (LG)	
UCMP 139608	Incomplete left cervical (4 th ?) or dorsal (6 th ?) lateral scute?	118F
UCMP 139609	Fragmentary left? lateral scute	
UCMP 139610	Lateral flange of left caudal lateral scute	
UCMP 139611	Fragmentary lateral scute	
UCMP 139612	Incomplete left? lateral scute	
UCMP 139613	Fragmentary dorsal to caudal? lateral spike	
UCMP 139614	Fragmentary lateral spike	
UCMP 139615	Incomplete left cervical (2 nd) lateral scute	118H
UCMP 139616	Fragmentary right? lateral scute	
UCMP 139617	Fragmentary right? cervical (1 st -2 nd ?) lateral scute	
UCMP 139618	Fragmentary lateral spike	
UCMP 139619	Fragmentary mid-dorsal to caudal lateral spike	
UCMP 139620	Fragmentary mid-dorsal to caudal lateral spike	
UCMP 139621	Fragmentary mid-dorsal to caudal lateral spikes (2)	
UCMP 156046	4 scute fragments—2 lateral spikes, 2 unassignable	
UCMP 175100	Incomplete right? dorsal paramedian? scute	

TABLE 1 (continued)

Specimen #	Description (Figure)	Long & Murry (1995) Figure(s)
UCMP 175101	Incomplete left? dorsal paramedian scute	
UCMP 175102	Incomplete left? dorsal paramedian scute	
UCMP 175103	Incomplete left? dorsal paramedian scute	
UCMP 175104	Incomplete dorsal paramedian? scute	
UCMP 175105	Fragmentary right dorsal paramedian scute	
UCMP 175106	Incomplete left? lateral scute	
UCMP 175107	Incomplete right cervical (3 rd , 4 th or 6 th) lateral scute	
UCMP 175108	Left cervical lateral (5 th) scute	
UCMP 175109A	Articulated left lateral (6 th ?) scute	
UCMP 175109B	Articulated left lateral (7 th ?) scute	
UCMP 175110	Incomplete right lateral (3 rd ?) scute	
UCMP 175111	Incomplete left lateral scute	
UCMP 175112	Incomplete right lateral scute	
UCMP 175113	Right lateral scute	
UCMP 175114	Incomplete lateral scute	
UCMP 175115	Incomplete lateral scute	
UCMP 175116	Incomplete left? lateral scute	
UCMP 175117	Incomplete right? lateral scute	
UCMP 175118	Incomplete lateral scute	
UCMP 175119	Incomplete lateral scute	
UCMP 175120	Incomplete lateral scute	
UCMP 175121	Incomplete paramedian scute	
UCMP 175121	Incomplete lateral scute	
UCMP 175122	Incomplete lateral scute	
UCMP 175123	Incomplete lateral scute	
UCMP 175124	Incomplete lateral scute	
UCMP 175125	Incomplete lateral scute	
UCMP 175126	Incomplete left? lateral scute	
UCMP 175127	Incomplete dorsal paramedian scute	
UCMP 175128	Fragments	
UCMP 175129	Incomplete probable dorsal paramedian scute	
UCMP 175130	Incomplete right? lateral? scute	
UCMP 175131	Incomplete lateral scute	
UCMP 175132	Incomplete left? dorsal paramedian scute	
UCMP 175133	Fragment	
UCMP 175134	Left lateral (dorso-caudal) lateral scute	
UCMP 175135	Distal caudal right lateral scute	
UCMP 175136	Caudal right? dorsal paramedian? scute	

UCMP 175138	Incomplete dorsal paramedian scute
UCMP 175139	Right? lateral? scute
UCMP 175140	Caudal lateral? scute
UCMP 175141	Fragment
UCMP 175142	Caudal lateral? scute
UCMP 175143	Fragment
MNA V-2912	Fragment
MNA V-2952	Fragment
MNA V-3002	Fragment
MNA V-3007	Fragment
MNA V-3040	Fragment
MNA V-3045	Fragment
MNA V-3046	Fragment
MNA V-3050	Fragment
MNA V-3066	Fragment
MNA V-3067	Fragment
MNA V-3113	Fragment
MNA V-3668	Fragment
MNA V-3679	Fragment
MNA V-3714	Fragment

TABLE 2A. Measurements of UCMP dorsal paramedian scutes assigned to *Acaenasuchus* by Long and Murry (1995).

Specimen #	Length	Width	W:L	Lamina Length	L:L
UCMP 27049	14.4	12+	—	3.0	4.8
UCMP 139576	18.1	29.7	1.6:1	1.2	15
UCMP 139584	16.0	—	—	5.0	3.2
UCMP 139585	17.4	32.5+	1.87:1	3.1	5.6
UCMP 139586	18.1	31.2	1.72:1	3.7	4.9
UCMP 139587	19.8	20.5*	—	3.0	6.6
UCMP 139588	20.6	23.2*	—	3.3	6.2
UCMP 175100	14.9*	12.9*	—	—	—
UCMP 175101	10.8	12.1*	—	1.6	6.75
UCMP 175102	15.3	14.8*	—	2.8	5.5
UCMP 175103	14.0	19.0*	—	1.4	10.0
UCMP 175104	22.0	17.6*	—	6.1	3.6
UCMP 175127	12.6	14.1*	—	2.0	6.3
UCMP 175132	10.0	21.1*	2.1	4.0*	2.5
UCMP 175136	16.5	6.0+7.8	—	1.7	9.7

+measurement very slightly low due to wear on specimen.

*measurement significantly low due to breakage of specimen.

TABLE 2B. Measurements of UCMP lateral scutes assigned to *Acaenasuchus* by Long and Murry (1995).

Specimen #	Length	Width (D/L)	L. Ant. Lamina	L. Lateral Spike
UCMP 139577	18.7	8.0/10.5	3.7	8.7
UCMP 139578	19.0	—/13.3	5.0	7+
UCMP 139579	24.2	13.0/13.4	7.0	10.4+
UCMP 139580	14.1*	5.5/12.2	—	7.5*
UCMP 139581	20.8	5.7+/13/8	5.4	5.7+
UCMP 139582	24.1** (13+, 8+)—	—	—	—(10*, 10+)
UCMP 139583	15.7	10.5/—	5.2	10.4*
UCMP 139585	17.4	32.5+	3.1	1.87:1
UCMP 139589	23.2	15.5*/13.1	7.1	3*
UCMP 139590	24.6	12.8/15.6	6.0	7*
UCMP 139591	22.4	8.3/15.2	6.2	3*
UCMP 139592	20.2	5*/14.0	4.9	*
UCMP 139593	21.2	13.0/9.8	5.5	4.5*
UCMP 139594	17.8	9.1/7+	3.1	8.7+
UCMP 139595	17.4	5.5*/11.3	3.6	6.2
UCMP 139596	21.2	—/12.7	5.4	12.2
UCMP 139597	22.0	11.3*/11.3*	6.8	6.8*
UCMP 139598	20.2	7.4/10.8	5.6	7.8*
UCMP 139599	26.6	13.4/10.2	8.8	4*
UCMP 139600	18.0	9.2/13.3	3.2	6.8
UCMP 139601	22.5	11.3/11.0*	8.2	9.5
UCMP 139602	15.9*	—/8.6	—	4.5
UCMP 139603	24.3	10.3/—	7.3	—
UCMP 139604	16.5	8.0/—	2.8	6.7*
UCMP 139605	—	—	—	8.6*
UCMP 139606	—	—	—	11.5*
UCMP 139607	18.1	—	—	6.3*
UCMP 139608	15.8	—	3.0	11.3+
UCMP 139609	—	—	—	—
UCMP 139610	14.9	—/9.7	2.9	5.4
UCMP 139611	12.2	—	—	6.2
UCMP 139612	11.0*	—/11.4	—	5.4*
UCMP 139613	10.9*	—	—	9.1
UCMP 139614	10.0*	—	—	10.3+

TABLE 2B. (continued)

Specimen #	Length	Width (D/L)	L. Ant. Lamina	L. Lateral Spike
UCMP 139615	12.9	4.8/6.8	1.0+	11.4
UCMP 139616	10.9*	4.1*/7.4	—	7.9+
UCMP 139617	12.1*	—/7.9	—	8.2+
UCMP 139618	—	—	—	11.5+
UCMP 139619	8.4*	—	—	6.4+
UCMP 139620	10.0*	—/5.0	—	4.5*
UCMP 139621A	9.4*	—/6.4*	—	6.0
UCMP 139621B	6.4*	—	—	8.6*
UCMP 156046A	9.5*	—/4.5	—	6.2*
UCMP 156046B	9.8*	—	—	6.5*
UCMP 156046C	—	—	—	—
UCMP 156046D	—	—	—	—
UCMP 175106	15.3*	10.5*/11.4*	—	7.0*
UCMP 175107	14.5*	6.0*/4.5	4.5+	7.1*
UCMP 175108	21.2	12.1/6.7	7.6	8.0
UCMP 175109A	—	—	—	6.0*
UCMP 175109B	—	5.7/5.7	—	4.3*
UCMP 175110	18.0*	9.2*	—	10.0
UCMP 175111	10.1*	3.4*/7.7	—	7.3*
UCMP 175112	17.1	5.8/15.0	—	4.1
UCMP 175113	11.0	4.8/7.5	1.4	5.2
UCMP 175131	14.3	—/13.1	—	—
UCMP 175134	15.1	7.6/9.3	1.7+	6.0+
UCMP 175135	12.7	4.4+/9.2	1.9+	4.0+
UCMP 175138	33.5*	26.9*	6.0	—
UCMP 175139	13.7*	8.5/6.7	?	—
UCMP 175140	20.0	12.0/6.5/6.2	2.3	—
UCMP 175141	—	—	—	—
UCMP 175142	18.8	4.7/5.7	2.3	—
UCMP 175143	19.4	10.0*/5.6*/4.5	—	—

D/L = Dorsal/Lateral flange of lateral scute

+measurement very slightly low due to wear on specimen.

*measurement significantly low due to breakage of specimen.

**total length of two articulated scutes, numbers in parenthesis refer to first and second scute, respectively.