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A NEW AETOSAUR (REPTILIA: ARCHOSAURIA) FROM THE UPPER TRIASSIC OF TEXAS AND THE PHYLOGENY OF AETOSAURS

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ABSTRACT—*Coahomasuchus kahleorum,* gen. et sp. nov. is a small (<1 m long) aetosaur from the Upper Triassic Colorado City Member of the Dockum Formation in West Texas. The holotype consists of a nearly complete articulated skeleton, including a well-preserved dorsal and ventral carapace. Several postcranial features diagnose *Coahomasuchus,* including: dorsal paramedian plates considerably (3.25:1) wider than long, unflexed, lack keels or horns, and bear faint sub-parallel to radial ornamentation, and lateral scutes that are also unflexed, flat, and bear a faint radial pattern of pits and grooves. *Coahomasuchus* co-occurs with the aetosaur *Longosuchus* and the phytosaurs *Angistorhinus* and *Paleorhinus,* indicating that it is of Otischalkian (early late Carnian) age.

Detailed phylogenetic analysis reveals that several North American aetosaur taxa are junior subjective synonyms of previously named taxa. *Lucasuchus* was named from material from the type locality of *Longosuchus* and is a junior subjective synonym of that taxon. *Acaenasuchus* is known only from localities that also produce *Desmatosuchus* and probably represents juvenile individuals of *Desmatosuchus. Stegomus,* from various localities in the Newark Supergroup, is a junior subjective synonym of *Aetosaurus,* known previously from the German Keuper and Upper Triassic strata in Italy and Greenland. *Paratypothorax andressi* is properly called *P. andressorum* and is known from strata of Adamanian (latest Carnian) to Apachean (Rhaetian) age.

INTRODUCTION

Although there is significant disagreement regarding the phylogenetic relationships of Triassic archosaurs, all recent authors consider the Aetosauria to be a monophyletic group within the Archosauria (e.g., Gauthier, 1984, 1994; Parrish, 1986, 1993; Benton and Clark, 1988; Sereno, 1991). Currently, aetosaur fossils are known from Upper Triassic strata in Europe, North America, South America, Africa, Greenland, and India (Fig. 1). These quadrupedal, armored, apparently herbivorous animals are among the most commonly recovered fossils in the Chinle Group of western North America (Long and Ballew, 1985) and have been used extensively for correlation, biostratigraphy, and biochronology in the Chinle and elsewhere (e.g., Lucas, 1993, 1997; Lucas and Hunt, 1993; Lucas and Heckert, 1996). Here, we document a new aetosaur, *Coahomasuchus kahleorum,* gen. et sp. nov., from the Colorado City Member of the Dockum Formation in West Texas (Fig. 2).

The Colorado City Member produces the type fossil assemblage of the Otischalkian land-vertebrate faunachron (Lucas, 1993, 1997; Lucas and Hunt, 1993; Lucas et al., 1993). Other aetosaurs known from this time interval are *Longosuchus* and *Desmatosuchus* (Hunt and Lucas, 1990; Lucas, 1993, 1997; Lucas and Hunt, 1993; Long and Murry, 1995; Lucas et al., 1997). Although many new aetosaurs have been recognized and described in the last ten years and their biochronology has been examined (e.g., Long and Ballew, 1985; Hunt and Lucas, 1990, 1991, 1992; Long and Murry, 1995), it is only in the last five years that cladistic analyses of aetosaur phylogeny have been attempted (Parrish, 1994; Heckert et al., 1996).

Anatomical Terms—In this paper the word "column" is used to describe a series of scutes from anterior to posterior, or parallel to the vertebral column, and the word "row" is limited to the description of a series of scutes that stretch across the body transversely, or perpendicular to the vertebral column. Other anatomical abbreviations are detailed in the appropriate figures.

Institutional Abbreviations—NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; **PVL**, Miguel Lillo Institute, Tucumán, Argentina; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor.

SYSTEMATIC PALEONTOLOGY

Superorder ARCHOSAURIA Cope, 1869
Order CROCODYLOTARSI Benton and Clark, 1988
Suborder AETOSAURIA Nicholson and Lydekker, 1889
Family STAGONOLEPIDIDAE Lydekker, 1887

COAHOMASUCHUS, gen. nov.

Type Species—*Coahomasuchus kahleorum,* new species.

Diagnosis—*Coahomasuchus* can be distinguished from all other aetosaurs by the following characteristics: presacral dorsal paramedian scutes with faint ornamentation consisting of subparallel, non-radial grooves and ridges; lateral scutes latero-medially flat, lacking keels, spikes, or flanges with a radial pattern of pits emanating from the center of the medial third of the specimen; small, subcircular to ovate, posteriorly tapering cervical ventral scutes; anterior ventral thoracic scutes hexagonal; thoracic scutes articulated in as few as four and as many as ten columns.

Additionally, *Coahomasuchus* is readily distinguished from all aetosaurs except *Aetosaurus* by its small adult size (1 m body length), with presacral dorsal paramedian scutes averaging approximately 3.2 times wider than long. *Coahomasuchus* is distinguished from *Desmatosuchus, Typothorax, Paratypothorax,* and *Longosuchus* by the lack of spikes on the lateral scutes, from *Desmatosuchus, Typothorax,* and *Longosuchus* by its relatively gracile appendicular skeleton, from *Typothorax* and *Redondasuchus* by the lack of extensive pitting on the dorsal paramedian scutes, from *Desmatosuchus* by anterior bars on its paramedian, lateral, and ventral scutes, and from *Redondasuchus* by the presence of lateral scutes.

Etymology—Named for the town of Coahoma, Texas, near the type locality, and from *suchus,* the Greek word for crocodile.

FIGURE 1. Distribution of aetosaur fossils across Late Triassic Pangea. **1**, Chinle Group, western United States; **2**, Newark Supergroup, eastern United States; **3**, Ischigualasto and Los Colorados Formations, Argentina; **4**, Santa Maria Formation, Brazil; **5**, Fleming Fjord Formation, Greenland; **6**, Lossiemouth Sandstone, Scotland; **7**, Keuper, Germany, and Alpine marine Triassic, Italy; **8**, Timesgadiouine Formation, Morocco; **9**, Zarzaïtine Series, Algeria; **10**, Maleri Formation, India.

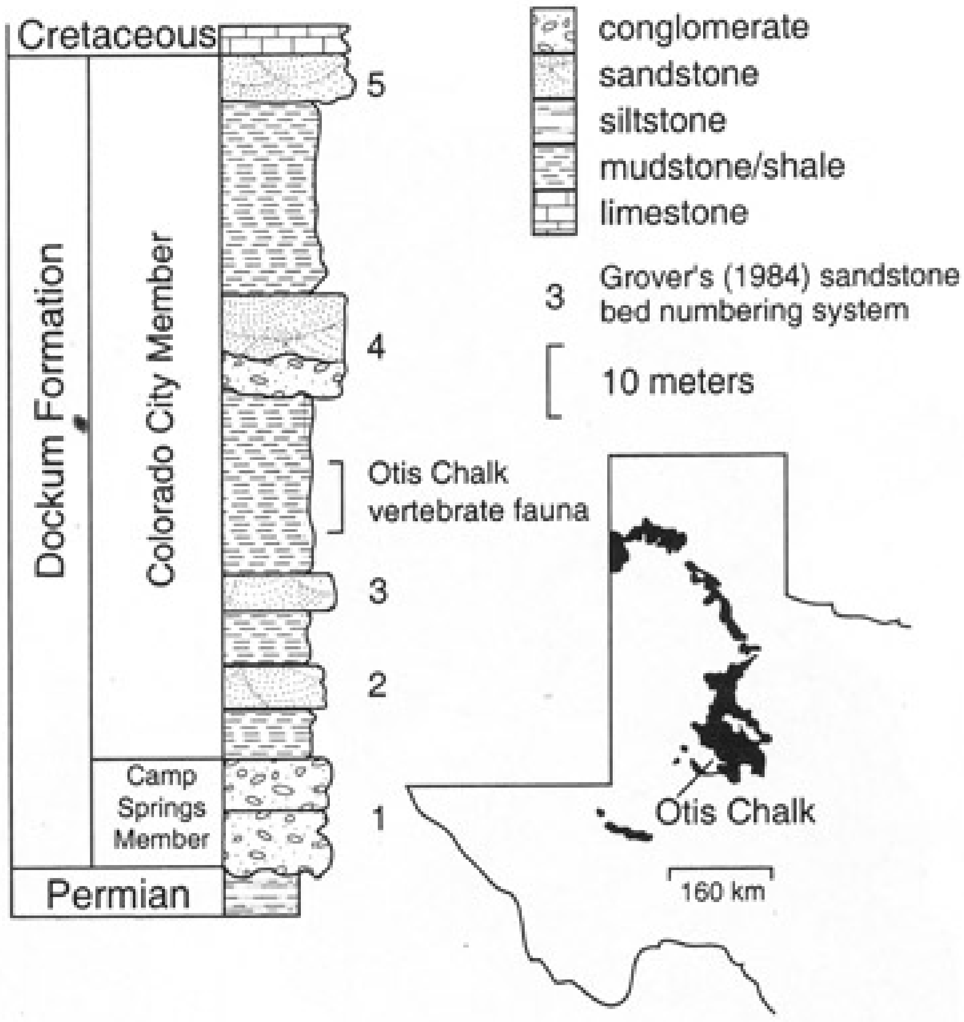

FIGURE 2. Generalized Upper Triassic stratigraphy of the Otis Chalk area and its location in the Dockum Formation outcrop belt of West Texas.

Coahomasuchus kahleorum, sp. nov.
(Figs. 3–8)

Etymology—Named for Mr. Robert Kahle and his son, Mr. Adam Kahle, of Midland, Texas, who together found, collected, and began initial preparation of the holotype specimen, and donated it to the New Mexico Museum of Natural History and Science.

Diagnosis—Same as for genus.

Holotype—NMMNH P-18496, a nearly complete, articulated, dorso-ventrally crushed skeleton, including portions of the skull and jaw, an almost complete carapace, portions of all four limbs, both girdles, and, presumably, a complete vertebral column from the neck through the middle of the tail.

Horizon and Locality—Found in the Colorado City Member of the Chinle Group as defined by Lucas and Anderson (1993, 1995; Lucas et al., 1994) at NMMNH locality 3357, north of the abandoned town of Otis Chalk in Howard County, Texas (Fig. 2). The Colorado City Member is considered late Carnian (Tuvalian) on the basis of vertebrate biostratigraphy, principally the presence of late Carnian index fossils, specifically the labyrinthodont amphibian *Metoposaurus bakeri* and the phytosaurs *Paleorhinus* and *Angistorhinus* (Lucas, 1993, 1997; Lucas et al., 1993, 1994). All these vertebrates are considered typical of the Otischalkian (early late Carnian) land-vertebrate faunachron of Lucas and Hunt (1993) (see Lucas et al., 1997).

DESCRIPTION

Specimen

The holotype specimen of *Coahomasuchus kahleorum*, NMMNH-18496, is a nearly complete, articulated skeleton of a small aetosaur that includes the brain case and posterior margin of the skull roof, the posterior half of the right mandible, a complete armor series from the cervical region to the tail, including paramedian, lateral, and ventral scutes, portions of all four limbs, their respective girdles, appendicular scutes, and much of the vertebral column (Figs. 3–8). As preserved, the skeleton is 71 cm long, with a total length estimated to be approximately 90 cm. The skeleton, while dorso-ventrally flattened, is preserved in such perfect articulation that many limb and most vertebral elements are obscured by the articulated carapace. Consequently, we are able to provide a detailed osteology of the following elements: dorsal skull roof, anterior portion of the braincase, posterior half of the right jaw, including its articulation with a badly damaged quadrate, one cervical, five to six dorsals, a sacral, and three or four caudal vertebrae, the dorsal paramedian armor from the cervical series to the mid-caudal region, lateral scutes from the same area excluding some posterior dorsals, ventral scutes from the head to posterior of the cloaca, most of the left and portions of the right humeri, portions of the left ulna and radius, both femora, right tibia, fibula, and tarsus. Fragments of two ribs can be seen, as can edge surfaces of both scapulae. Both femora are embedded in their respective acetabula, and thus combine with the ventral armor to obscure almost all of the pubes and ischia on both sides. The ilia are almost completely hidden.

In spite of these complications, this specimen is remarkable in that it offers insight into the articulation of the dermal armor, especially in several noteworthy areas such as the base of the skull, neck, pelvic girdle, cloaca, and, in the case of the right hind limb, the appendages. Although appendicular scutes have been reported from several aetosaurs, including *Aetosaurus* (Walker, 1961), *Aetosauroides* and *Argentinasuchus* (Casamiquela, 1961a, b), *Stagonolepis* (Walker, 1961), *Desmatosuchus* (Case, 1922), *Longosuchus* (Sawin, 1947) and *Typothorax* (Hunt et al., 1993), this is the first specimen that demonstrates how these scutes were distributed over the hind limb.

Skull and Mandible

Of the commonly recognized genera of aetosaurs, well-preserved cranial material has been thoroughly described in only three genera, namely *Desmatosuchus* (Case, 1922; Small, 1985), *Stagonolepis* (Walker, 1961), and *Longosuchus* (Sawin, 1947; Parrish, 1994). Preliminary or sketchy information has been published on the skulls of *Aetosaurus* (Fraas, 1877; Huene, 1920; Walker, 1961), *Aetosauroides* (Casamiquela, 1961a, b, 1967), and *Neoaetosauroides* (Bonaparte, 1967, 1971). A complete, articulated skeleton of *Typothorax*, including the skull, awaits final preparation at NMMNH, and has thus far received only a very preliminary description (Hunt et al., 1993). Additional *Typothorax* material was recovered from the Post

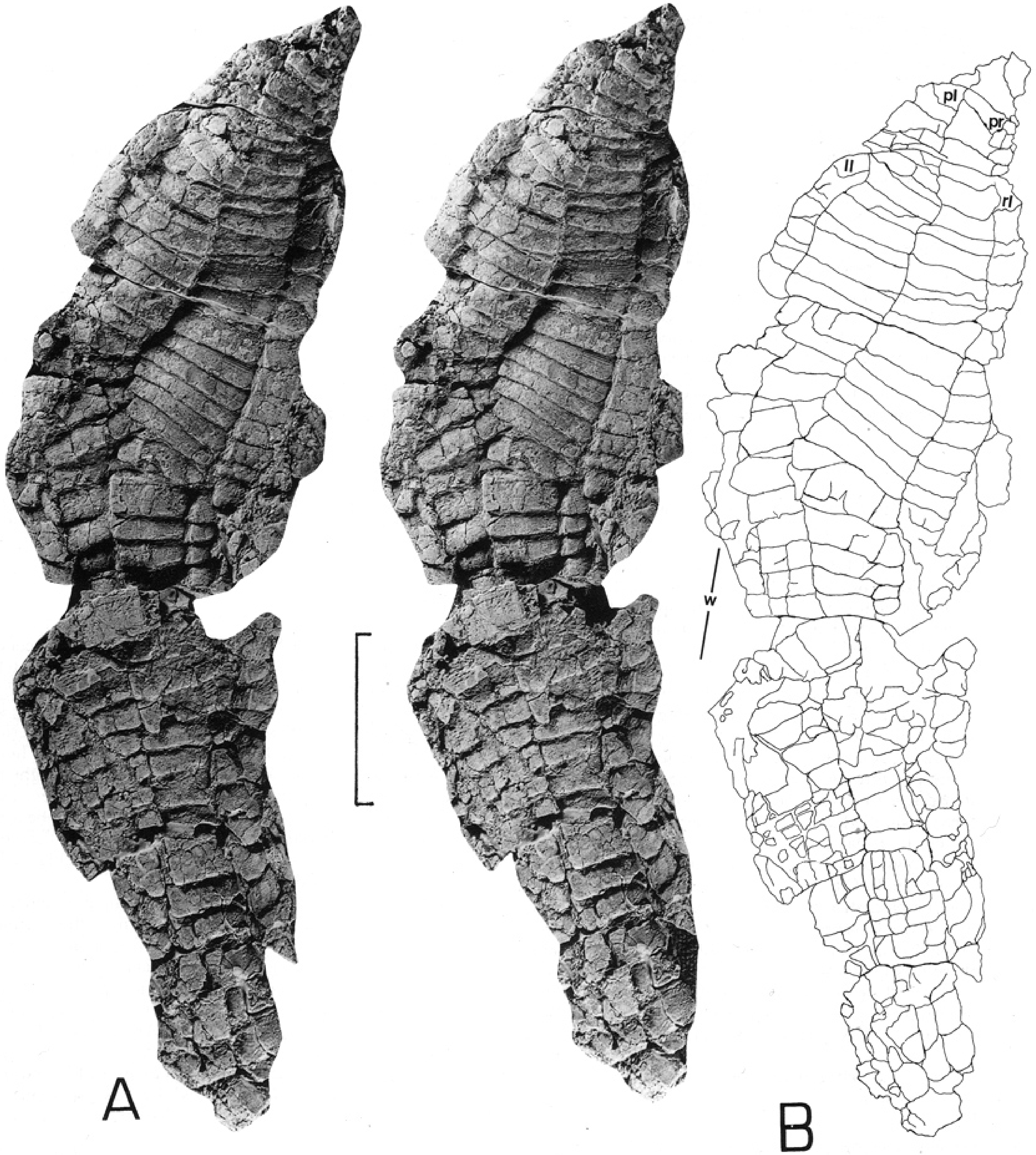

FIGURE 3. Dorsal view of articulated carapace of holotype specimen of *Coahomasuchus kahleorum* (NMMNH P-18496). Stereophotographs, **A**, and interpretative sketch, **B**. **Abbreviations**: **ll**, left column of lateral scutes; **pl**, left column of paramedian scutes; **pr**, right column of paramedian scutes; **rl**, right lateral column of lateral scutes; **w**, "waist," or rows of narrower paramedian scutes immediately anterior to sacrum. Scale bar equals 10 cm.

Quarry in Texas (Murry and Long, 1989), but has never been described other than incidentally in Parrish's (1994) cladistic analysis of the aetosaurs. The dentary and skull of *Paratypothorax* is known from very fragmentary material (Parrish, 1994; Long and Murry, 1995).

The skull of *Coahomasuchus* is badly damaged, and consists of a large fragment containing the posterior dorsal skull roof and braincase, preserved in articulation with both the cervical vertebrae and the cervical scutes, and a smaller fragment that includes portions of the right quadrate, quadratojugal, squamosal, and jugal. The latter fragment, while badly crushed, remains in articulation with the right mandible (Fig. 5). Almost

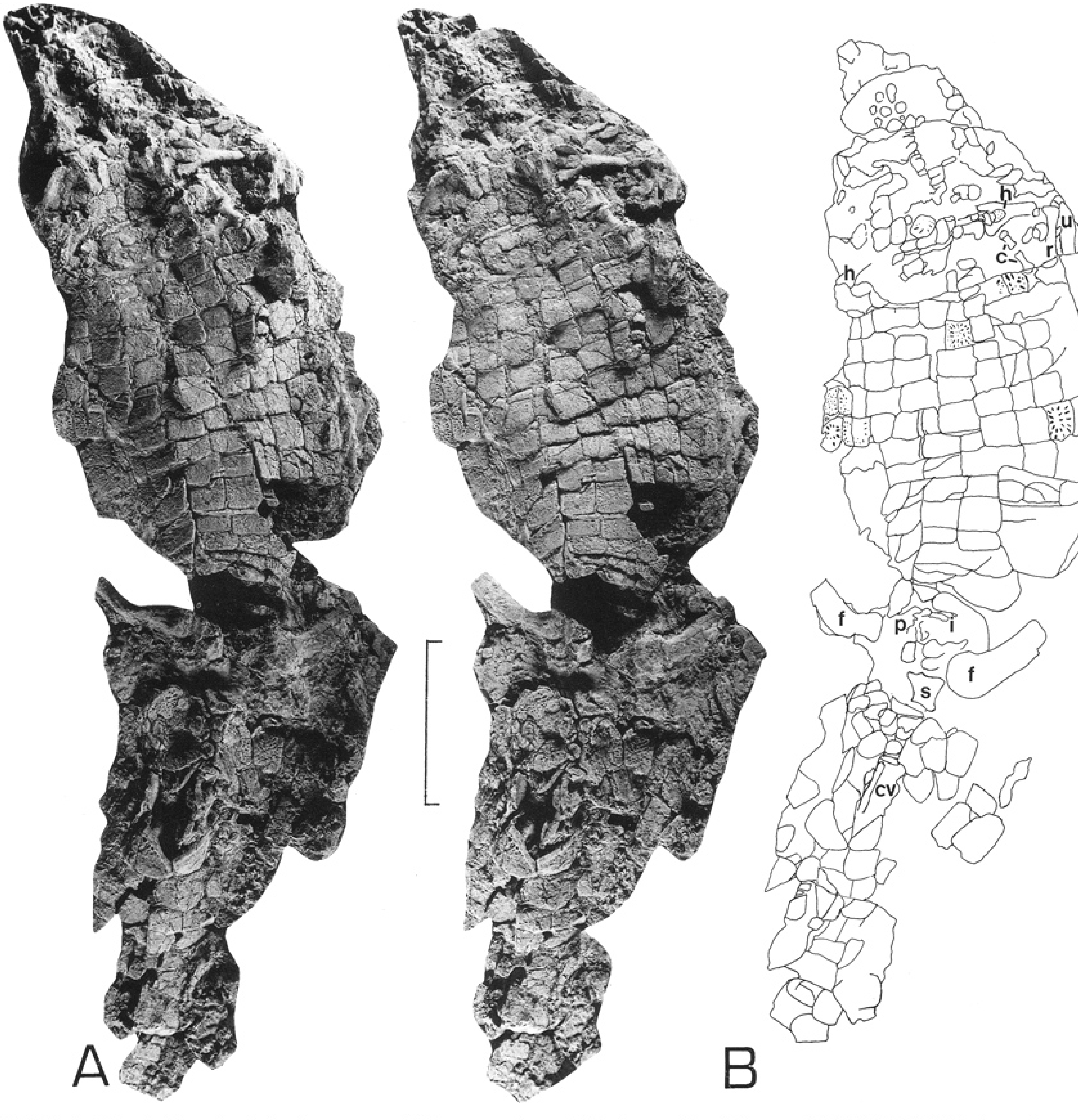

FIGURE 4. Ventral view of articulated carapace of holotype specimen of *Coahomasuchus kahleorum* (NMMNH P-18496). Stereophotographs, **A**, and interpretative sketch, **B**. **Abbreviations**: **c**, centrum; **cv**, cloacal vent; **f**, femur; **h**, humerus; **i**, ilium; **p**, pubis; **r**, radius; **u**, ulna. Scale bar equals 10 cm.

all sutures are obscured. This is almost certainly in part due to preservational processes, but also indicates that although this specimen was small (<1 m), it was probably an adult with fused cranial sutures. If so, this would make it one of the smallest described adult aetosaurs, together with *Aetosaurus* (=*Stegomus*) (Fraas, 1877; Marsh, 1896; Huene, 1920; Jepsen, 1948; Walker, 1961; Baird, 1986; Wild, 1989; Small, 1998).

The most anterior skull bones preserved in the holotype specimen are fragments of the proximal frontals. At an indeterminable point, these are sutured to the next most posterior bone, the postorbital, which is best preserved on the left side. The supratemporal fenestra is obscured by the dorsal-ventral crushing that typifies the entire specimen, whereas the infratemporal fenestra is well preserved on the left side and present but poorly preserved on the right side in the fragment containing the posterior margin of the jaw (Fig. 5A, B). In both pieces, the infratemporal fenestra is crudely quadrangular, with the long axis running from the antero-dorsal corner near the orbit to the postero-ventral corner near the articulation with the jaw on the upper and lower margins.

The braincase is directly observable in ventral view and preserved from the broken anterior process of the parasphenoid

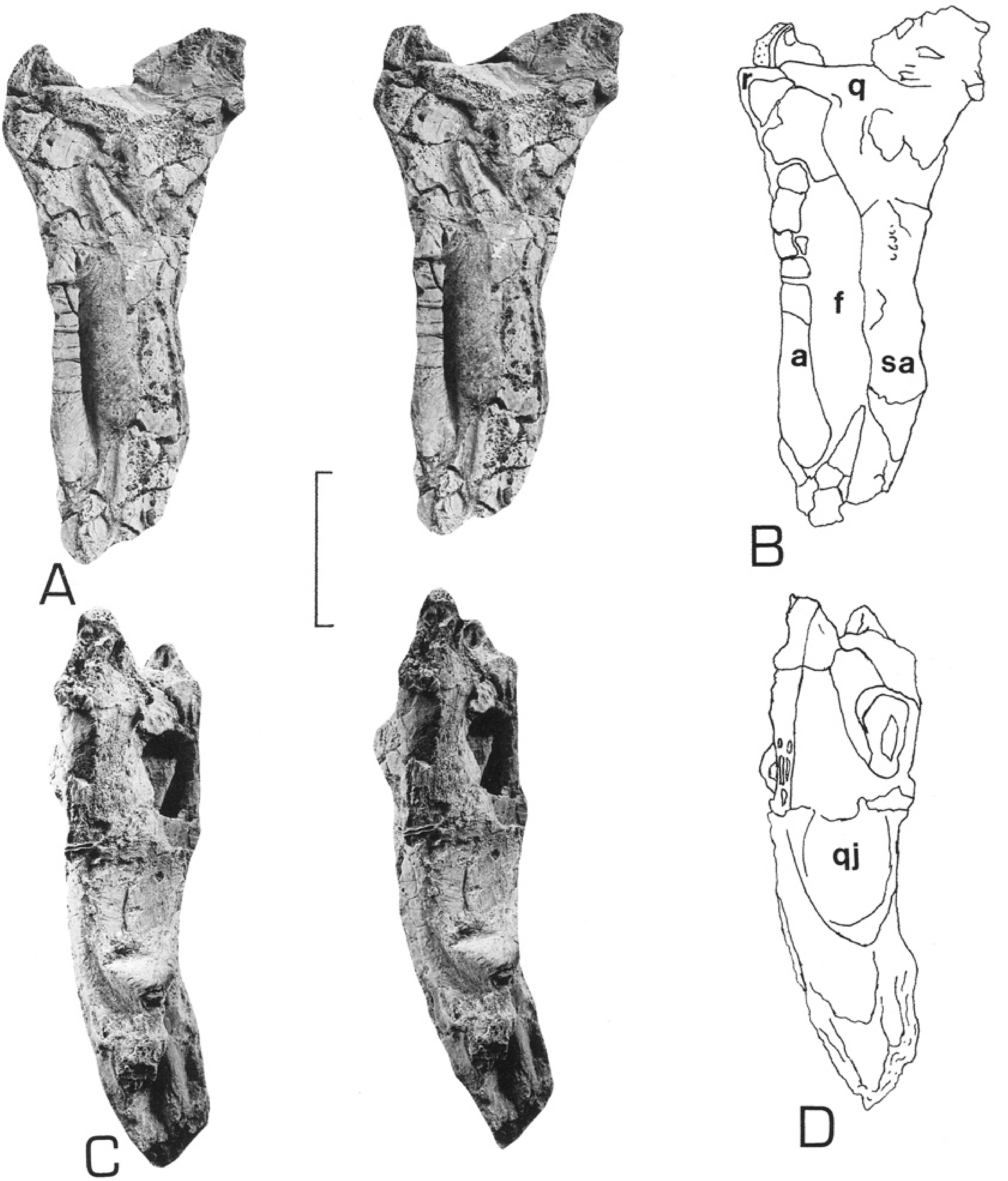

FIGURE 5. Partial right jaw and posterior skull of holotype specimen of *Coahomasuchus kahleorum* (NMMNH P-18496). **A**, **B**: stereophotographs **A**, and interpretive sketch **B**, of jaw fragment in lateral view; **C**, **D**: stereophotographs **C**, and interpretive sketch **D**, of jaw in occlusal view. **Abbreviations**: **a**, angular; **f**, mandibular fenestra; **q**, quadrate; **qj**, quadratojugal; **r**, ramus; **sa**, surangular. Scale bar equals 2 cm.

posteriorly past the basisphenoid to the basioccipital, which is largely hidden by matrix and unprepared bone fragments. The parasphenoid is broken anterior to the basipterygoid processes, which are robust and project anteriorly and ventrally (Fig. 6A, B). Their distal ends are worn and abraded, making precise determination of their shape impossible, although they appear slightly bulbous. There is no clear suture between the basipterygoids and the basisphenoid, but dorso-laterally deflected cracks near the base of the basipterygoid processes may represent this suture. The basisphenoid is very deeply excavated ventrally. This may correspond to the "deep, hemispherical fontanelle in the bottom of the basisphenoid between the basal tuber and basipterygoid processes" that Parrish (1994:204) described in *Longosuchus* and *Desmatosuchus,* also present in *Stagonolepis* (Walker, 1961:fig. 5a). Posteriorly, the suture with the basioccipital is obscured by matrix and unprepared bony plates, several of which appear to be dislocated scutes. Crushed bony surfaces lateral to the basisphenoid probably represent the prootics, but no structural details are preserved. In general, the preserved braincase is relatively more elongate than, but otherwise similar to, that of *Stagonolepis* (Walker, 1961:fig. 5a).

Vertebrae

The axial skeleton is probably preserved in its entirety, but most of it is concealed by the armor (Figs. 4, 6C–F). Neither the atlas nor the axis are discernible, and of the remainder of the cervical series, only the ventral portion of the ?third postatlantal centrum is identifiable. Posterior to the left humerus, three dorsal vertebrae are incompletely exposed. Two posterior dorsals are partially visible in a hole in the ventral armor just anterior to the sacrum. Portions of the ventral surface of the last dorsal are visible immediately anterior to the femora. The ventral surface of the second sacral centrum is very well exposed, together with the anterior margin of the first caudal. Portions of the third through fifth caudal vertebrae, including chevrons, can be discerned through the cloacal vent. Additional disarticulated material included with NMMNH-18496 shows some cross-sections of distal caudal vertebrae. All centra are amphiplatyan to weakly amphicoelous, and no dorsal structures, such as transverse processes or neural spines, can be discerned. Table 1 contains measurements of the exposed vertebrae and associated paramedian scutes.

Cervical Vertebrae—The only exposed cervical centrum lies beneath the third row of paramedian scutes. This centrum is constricted medially, with a mid-centrum diameter less than half as wide as the postero-articular facet. Although damaged, the centrum appears to be keeled as in *Stagonolepis* and other primitive aetosaurs (Walker, 1961; Long and Murry, 1995). All vertebral processes, including the neural spine and transverse processes, are hidden. As preserved, it is slightly shorter than the overlying paramedian scutes. The centrum is longer than wide, not foreshortened as in *Typothorax* (Long and Murry, 1995).

Dorsal Vertebrae—Three dorsal centra are incompletely exposed posterior to the pectoral girdle and offset to the left of the midline (Figs. 4, 6E). These vertebrae correspond to the tenth thorough twelfth pairs of paramedian scutes. The centra are typically 13–16 mm long, respectively, and thus slightly shorter than the overlying scutes (Table 1). Neither these centra nor the extremely posterior dorsals near the second portion of the skeleton are keeled. Like the cervical centrum, they are medially constricted, with the center of the centrum only slightly more than half as wide as the articular facets. The dorsal centrum beneath the twenty-first dorsal paramedian scute is visible through an opening in the ventral carapace (Figs. 4, 6F). This centrum is similar in construction to, but considerably more robust than, the more anterior dorsal centra.

Portions of the anteroventral surface of the last dorsal centrum are visible anterior to the sacrum (Fig. 6C, D). This centrum is also much more massively constructed than the more anterior dorsal centra. It is not the first sacral vertebra, which appears to be missing, for two reasons: (1) it is not in contact with the second sacral, being anterior to it by as much as 30 mm; and (2) this centrum does not resemble the second sacral in morphology, bearing a narrow "waist" with no sacral rib processes or other features typical of sacral vertebrae.

Sacral Vertebrae—The first sacral vertebra appears to be missing. However, just posterior to the two femora, the second sacral centrum lies between the ilia as a large (23+ mm long) and broadly expanded body (Fig. 6C, D). The anterior half of this centrum bears prominent sacral ribs that increase the vertebral width to at least 37 mm. The distal portion of the right sacral rib is well preserved and well exposed, showing an anterolaterally concave surface for articulation with the right ilium. This centrum lacks the ventrally convex surface present on the more anterior vertebrae, and is instead broad and flat.

Caudal Vertebrae—The articular facet of the first caudal vertebra is slightly offset from the second sacral. Although it is almost completely hidden, this centrum appears to be nearly as robust as the second sacral, but is considerably narrower. The third through fifth caudals are exposed through the cloacal vent, although they are partially obscured by their own chevrons. These vertebrae are constructed more delicately than the dorsal centra, and are typically 17–18 mm long. Their relatively small size demonstrates that the caudal vertebrae decreased in size rapidly posterior to the pelvis, in contrast to the overlying scutes, which remain relatively long. The chevrons are oval in cross-section, with the long axis in the dorso-ventral plane, and overlap 50 percent with the succeeding centrum.

Portions of the caudal vertebrae are preserved to the tip of the tail, but this is the most fragmentary portion of the specimen. In the distal reaches of the tail the caudal centra are only visible in cross-section, where they appear to be small (2–3 mm in diameter) and circular. In general, the proximal caudal vertebrae appear to have a 1:1 relationship with the overlying pairs of paramedian scutes.

Appendicular Skeleton

Due to the nearly complete carapace, most of the pectoral girdle, much of the pelvic girdle, and portions of the forelimbs remain buried between articulated dorsal, lateral, and ventral scutes. Therefore, we can describe only a portion of the proximal humerus in the right forelimb and the scapulocoracoid, humerus, ulna, radius, and some metacarpals in the left forelimb. The right hind limb is relatively complete, and consists of an articulated femur, tibia, fibula, astragalus, calcaneum, and several metatarsals, as well as a covering of appendicular scutes (Fig. 7). Only the proximal femur of the left hind limb is preserved. Where possible, we provide measurements of important skeletal features (Table 2).

Scapulocoracoid—The articular socket of the scapulocoracoid is incompletely exposed on the left side of the skeleton, and is otherwise obscured by ventral scutes and the proximal humerus. The exposed distal edge of the coracoid is more robust than in aetosaur skeletons of similar size, such as the holotype specimen of *Stagonolepis* (=*Aetosauroides*) *scagliai,* PVL 2073.

Humerus—The proximal left humerus appears to be articulated with the scapulocoracoid, but the latter is buried beneath ventral scutes and matrix. The humerus is 46 mm long as preserved, and total length probably reached approximately 70 mm. The head of the humerus is 23 mm across, indicating that *Coahomasuchus* possessed a relatively large (3:1) ratio of humerus length:head breadth. This is similar to other lightly built aetosaurs, such as *Stagonolepis* and *Aetosaurus,* and differs from the more robust (approximately 2.25:1) *Longosuchus, Desmatosuchus,* and *Typothorax* (Long and Murry, 1995). The humeral shaft of *Coahomasuchus* is thin, 10 mm across at midlength. The deltopectoral crest is robust and medially deflected, as is common in aetosaurs. Only the ventral surface of the an-

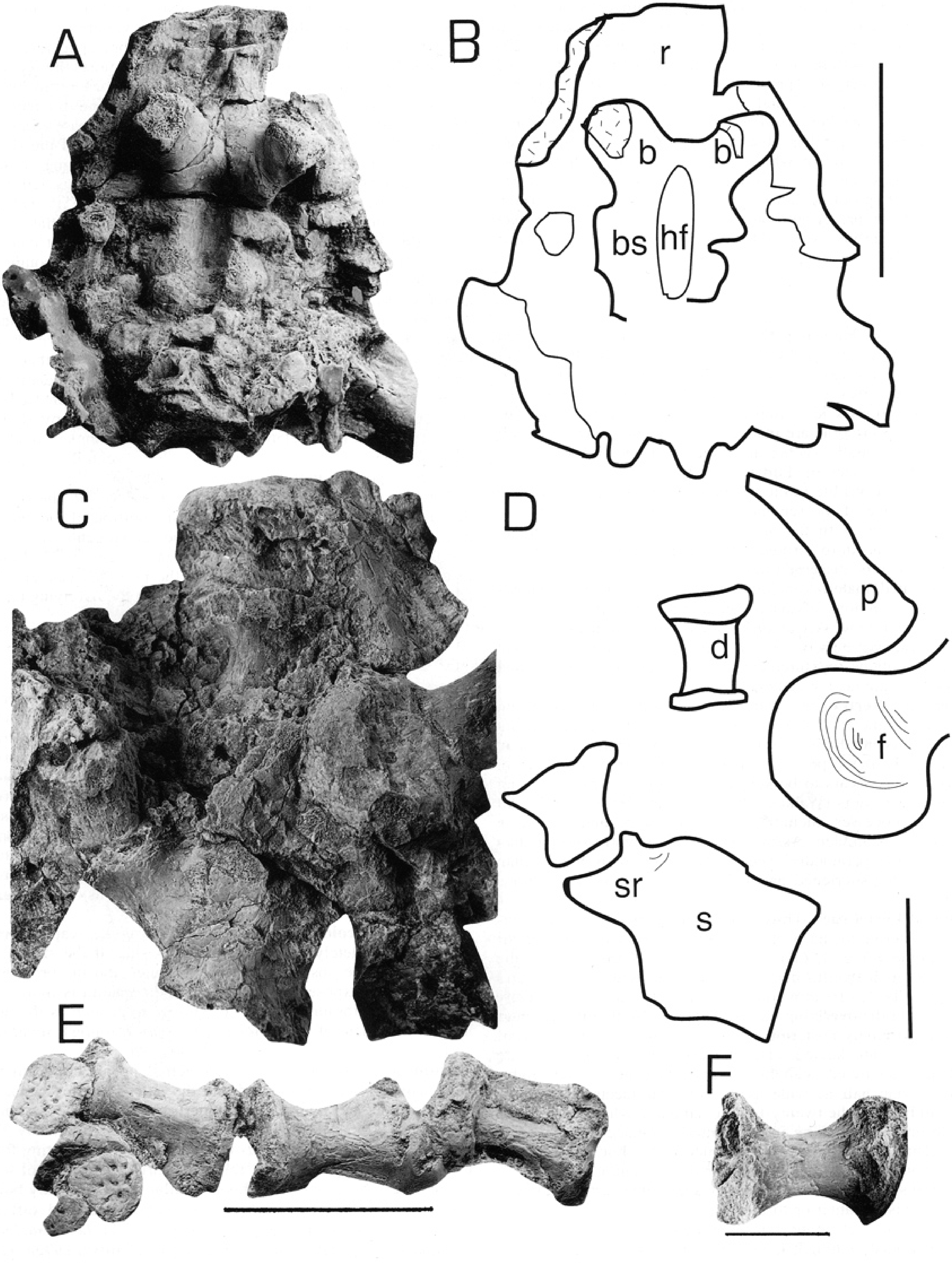
A
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TABLE 1. Measurements of exposed centra and associated scutes.

Centrum	Length	Articular facet width (anterior/ posterior)	Width (waist)	Overlying para- median scute row	Exposed length of over- lying scute
Cervical 3?	9.5	?/7	3	3	11.7
Dorsal 3?	13.3	12?/12	6.2	10	15.5
Dorsal 4?	14.8	11.4/11/1?	6.0	11	15.0
Dorsal 5?	15.8	11.8/11.6?	6.5	12	18
Dorsal 15?	18.0	16?/?	8?	21	18.5
Dorsal 18?	17.0	17.7/?	8+?	24	18
Sacral 2	21.8?	?/21.8	23–37+*	26	19
Caudal 1	18.5?	19.5?/?	?	27	19
Caudal 3	17.9?	11.8/?	?	31	19
Caudal 4	18.7	?	9?	31/32	N/A
Caudal 5	?	13?/?	?	32	19

*The width of the sacral is highly variable due to the flared nature of the sacral ribs. All measurements in mm.

teroproximal portion of the right humerus, including the deltopectoral crest, is exposed.

Ulna—The proximal 36 mm of the left ulna are preserved in a segment that represents just over half the apparent length of the element. The ulna is typical of aetosaurs, with a prominent olecranon process that is both transversely wide (7 mm) and posteriorly extended. An ovoid bone fragment articulated with the manus may represent the distal end of this element. If so, the ulna is approximately 66 mm long.

Radius—The left radius is, like the ulna, broken, and the remaining segment preserves the proximal 32 mm. The proximal surface is ovate and slightly bulbous, unlike that of most other aetosaurs. The bone fragment described above, if it pertains to the radius and not the ulna, indicates a total length of as much as 60 mm for the radius.

Manus—The left manus is folded up against the body and incompletely preserved in a mass of bone associated with the thoracic ventral scutes. Several partial metacarpals, probably metacarpals II–V, are visible, but cannot be observed fully enough to permit detailed description. With the possible exception of metacarpal II?, all are broken. Metacarpal II? measures 10 mm in length in dorsal view. Both ends are slightly expanded relative to the shaft. The proximal end is concave, the distal convex. The other metacarpals are incomplete but appear broadly similar in structure.

Pubes—Other than a fragment of the left pubis, the pubes cannot be characterized adequately, and appear to be crushed and/or missing their distal portions. The left pubis is exposed anterior to the left femur, although only the proximal portion remains (Fig. 6C, D). This element is relatively delicate, with a ventral surface that is ventro-posteriorly concave, bringing the distal end of the pubis down and toward the midline, where one broken edge of bone suggests that *Coahomasuchus* had a pubic "apron" similar to that of other aetosaurs. As preserved, the right pubis is 24–33 mm long proximo-distally.

Ischia—A single fragment of bone prepared separately from the posterior skeleton appears to represent the fused portions (38 mm long) of the ischia along the midline. This fragment is similar in shape and overall morphology to fused ischia we have observed in other aetosaurs. It also bears two columns of small, ovoid scutes that mark the only known armor on the ventral surface of the pelvis of this or any other aetosaur.

Femora—Both femora are firmly embedded in their respective acetabula. The femoral heads are slightly bowed medially (Fig. 6C, D), this offset occurring proximal to the fourth trochanter, approximately 24 mm below the proximal head. The fourth trochanter forms an elongate ridge that is approximately 20 percent of the length of the femur.

Tibia—The right tibia is about 82 mm long, or 75 percent of the length of the femur (Fig. 7A–D). The cnemial crest is very prominent, extending over one-third of the length of the shaft. It may be weakly rugose. The head is robust and triangular, with a maximum mediolateral breadth of 22 mm and an anteroposterior length of 23 mm.

Fibula—The right fibula is only slightly less robust than the tibia, is 79 mm long, and is exposed only in postero-lateral view (Fig. 7A, B). The prominent, elongate, ridge-like anterolateral process is 17 mm long and extends from one-third of the way down the shaft to the bone's mid-length.

Tarsals—Both the astragalus and calcaneum are articulated with more proximal and distal elements of the right pes. This, combined with the presence of several small appendicular scutes, obscures most of the detail on these important elements (Fig. 7A–D). The astragalus is by far the more robust of the two bones. Two ventral concavities are evident in the calcaneum. Distal tarsals are evident, and appear to be associated with metatarsals IV, III, and II–I.

Pes—All five metatarsals are at least partially preserved. They are expanded proximally and constricted in the middle (Fig. 7). Metatarsal I is almost complete, and slightly more robust than metatarsals II–IV. Metatarsals II–IV are thin and rod-like, and among the most gracile of any aetosaur for which the pes is known. Metatarsal V is severely abraded but, as in most aetosaurs, has a broadly expanded proximal process that tapers distally.

Carapace

The holotype specimen of *Coahomasuchus* includes a carapace that is nearly complete and, except for some dorso-ventral crushing, articulated in life position (Figs. 3, 4). As is typical in aetosaurs, this carapace consists of two columns of dorsal paramedian scutes that run the length of the vertebral column from the occiput to the tip of the tail, right and left columns of lateral scutes that coincide with the paramedian scutes throughout the entire length of the carapace, and a series of ventral scutes that includes the first documented cervical ventral scutes of an aetosaur, a nearly complete thoracic carapace, and a well-preserved caudal series that includes the cloacal opening.

Dorsal Paramedian Scutes—Twenty-four pairs of dorsal paramedian scutes are preserved on the presacral portion of the skeleton (Fig. 3). Probably seven or eight of these are cervicals, as opposed to the nine observed in *Stagonolepis* (Walker, 1961), and the remainder are true dorsal paramedian scutes. Posteriorly, dorsal paramedian scutes are heavily damaged in the vicinity of the sacrum, where at least one pair has been juxtaposed on top of another. Thus, a minimum of three and a maximum of five rows of scutes covered the sacral region. The preserved caudal series consists of 11 pairs of articulated para-

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FIGURE 6. Braincase, sacrum, and selected vertebrae of *Coahomasuchus kahleorum* (NMMNH P-18496). **A**, **B**: photograph **A**, and interpretive sketch, **B**, of the braincase in ventral view; **C**, **D**: photograph, **C**, and interpretive sketch, **D**, of the sacral region in ventral view; **E**, dorsal centra 3–5(?) in ventral view, ventral scutes partially cover dorsal 3?; **F**, dorsal centrum 15? in ventral view, anterior end to the left. **Abbreviations**: **b**, basipterygoid processes; **bs**, basisphenoid; **d**, dorsal centrum; **f**, femoral head; **hf**, hemispherical fontanelle; **p**, pubis; **r**, skull roof; **s**, sacral centrum; **sr**, sacral rib. Scale bars equal 2 cm for A–E, 1 cm for F.

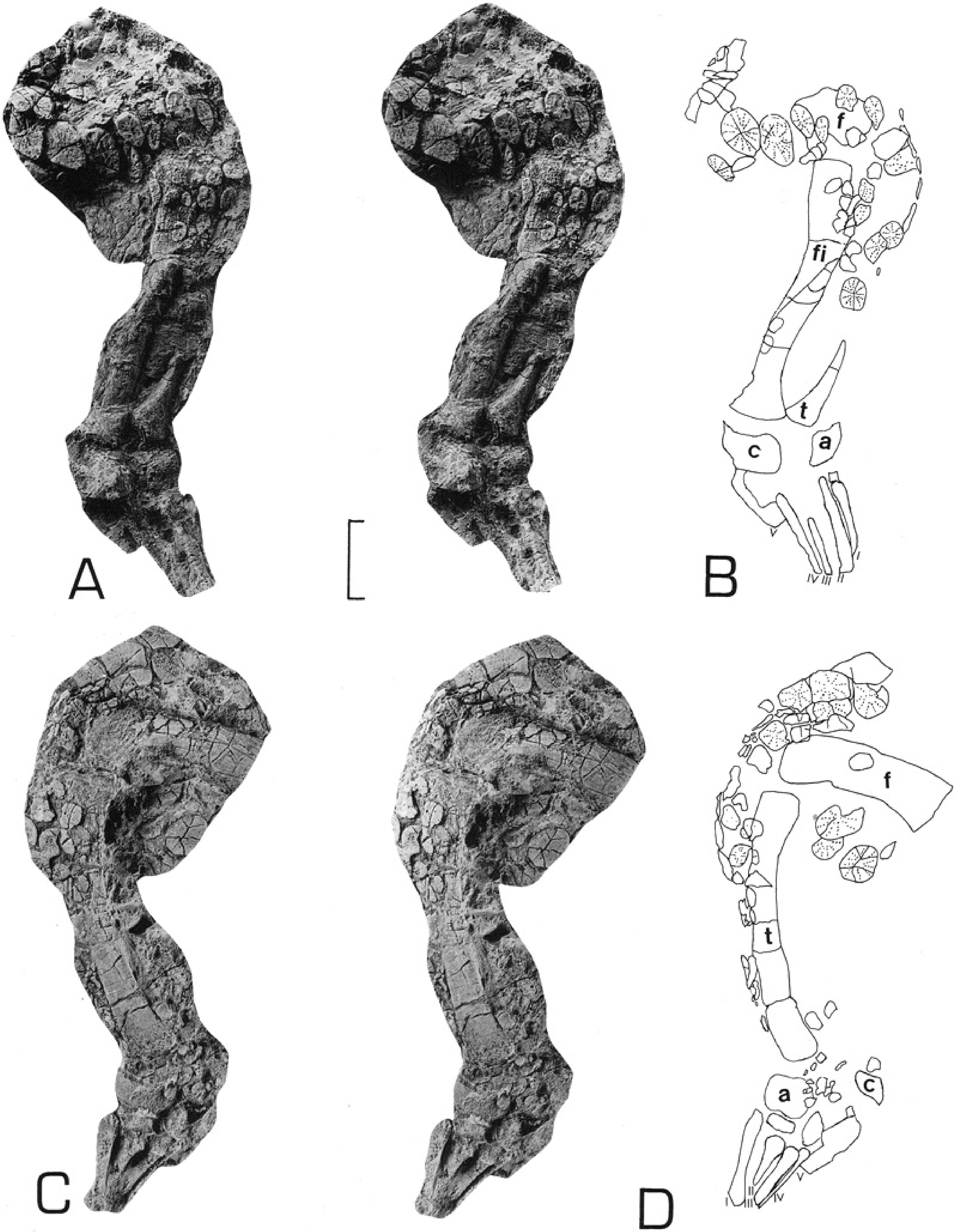

FIGURE 7. Right hind limb of holotype specimen of *Coahomasuchus kahleorum* (NMMNH P-18496). **A**, **B**: stereophotographs **A**, and interpretive sketch, **B**, of right hind limb in lateral view; **C**, **D**: stereophotographs **C**, and interpretive sketch **D**, of right hind limb in medial view. **Abbreviations**: **a**, astragalus; **c**, calcaneum; **f**, femur; **fi**, fibula; **t**, tibia; **I–V**, metatarsals I–V. Scale bar equals 2 cm.

TABLE 2. Measurements of appendicular elements.

Element	Measurements
Left coracoid	23 mm across, 4–6 mm thick
Left humerus	Proximal 43 mm preserved, total length approximately 70 mm; head is 23 mm across
Left ulna	Proximal 34 mm preserved, total length possibly 66 mm; head is 7 mm across
Left radius	Proximal 30 mm preserved, total length possibly 60 mm; head is 11 mm across, shaft tapers to 5 mm across
Left metacarpal II?	Proximal 11 mm preserved
Left metacarpal IV?	10 mm long, articular ends 4 mm wide; shaft 3 mm across
Right femur	109 mm long, mid-shaft diameter 9 × 15.5 mm, head 23.4 mm across
Left femur	Proximal 59.8 mm preserved, head 20 mm across
Right tibia	82 mm long; head 22 mm across mediolaterally, 23 mm anteroposteriorly
Right fibula	79 mm long
Right metatarsal I	21 mm long, 10.5 mm wide proximally; 3.5 distally; shaft 4 mm across
Right metatarsal II	27 mm long, 6 mm wide proximally; shaft 3.5 mm across
Right metatarsal III	25 mm long, 4 mm wide proximally; shaft 3 mm across
Right metatarsal IV	28 mm long; shaft 2 mm across
Right metatarsal V	Proximal 21 mm preserved; 10–12 mm wide proximally; shaft 3 mm across

median scutes, with the maximum width of the tail tapering only gradually over this length. Additional, very fragmentary caudal material is preserved with the specimen, but does not appear to articulate with the remainder of the fossil material, although it is complete enough to include the tip of the tail. Therefore, it is not possible to obtain an exact count of either the rows of the caudal paramedian scutes or the underlying vertebrae. However, the tail, as preserved, demonstrates that there were considerably more than 23 vertebrae and corresponding pairs of dorsal paramedian scutes. This indicates that *Coahomasuchus,* like most aetosaurs, was a long-tailed taxon, unlike *Neoaetosauroides,* which has only 23 caudal vertebrae (Bonaparte, 1967). The proximal caudal scutes remain nearly as broad as the caudal paramedian scutes, even though the underlying vertebrae are considerably smaller than the sacral vertebrae, as described above.

Dorsal paramedian scute morphology has long been used to differentiate aetosaurs, from Cope's (1875) initial description of *Typothorax* to recent descriptions of taxa such as *Paratypothorax* (Long and Ballew, 1985), *Redondasuchus* (Hunt and Lucas, 1991; Heckert et al., 1996), *Lucasuchus* (Long and Murry, 1995), and *Acaenasuchus* (Long and Murry, 1995), some of which are based on holotypes that are fragments of a paramedian scute(s). Primitive aetosaur structures preserved in the paramedians of *Coahomasuchus* (Fig. 8A) include: (1) anterior bars; (2) a faint, radiate pattern of elongate pits, grooves, and ridges (primarily in the caudal series); (3) a presacral "waist" where the dorsal paramedians become less broad before expanding again over the sacrum; (4) a lack of transverse flexure; and (5) a lack of tongue and groove articulations with the lateral scutes. Advanced features include the loss of dorsal bosses anteriorly, the presence of subradial grooves in the anterior series, and the relatively high (3.25:1) width : length ratio.

Walker (1961) documented an increase in relief between the raised surface and the depressed pits and grooves of dorsal paramedian scutes from the anterior to posterior rows of scutes in both *Stagonolepis* and *Aetosaurus,* although perhaps the best illustration of this is in the partial carapace of *Stagonolepis* described by Case (1932:plate 1). We have also observed this increased relief in the type specimen of *Aetosauroides.* The patterns on the dorsal paramedian scutes of *Coahomasuchus* also share this trend. The anterior dorsal paramedian scutes bear a faint pattern of low, sub-parallel ridges and grooves. Further posteriorly, the patterns are deeper, and the caudal paramedian scutes are deeply incised with the typical aetosaurian pattern of radial pits and grooves.

Lateral Scutes—The lateral scute series is much less well-preserved (Fig. 3). Along the right side, 16 lateral scutes are preserved in articulation with their corresponding paramedians (Figs. 3, 8A), with another seven lateral scutes exhibiting varying degrees of damage and disarticulation. On the left side, only 11 well-preserved lateral scutes can be identified, with at least three nearly to completely missing and the remainder badly crushed. At the sacrum, and farther posteriorly, approximately eight lateral scutes are represented from each side, including at least one scute from each row except for the first sacral.

Ornamentation on the lateral scutes of *Coahomasuchus* consists of a pattern of radial, arcuate grooves and ridges with some minor pitting that radiates from the dorso-medial edge of the scute (Fig. 8A). The lateral scutes are not flexed; they are flatter than those of the primitive aetosaurs *Aetosaurus* and *Stagonolepis* (Walker, 1961). Similarly, they bear no indication of a medial boss of the type possessed by *Stagonolepis* (=*Aetosauroides*) (Casamiquela, 1961a, b, 1967; Walker, 1961). Likewise, the lateral scutes are clearly not horn-bearing, as in *Desmatosuchus, Longosuchus, Paratypothorax,* and *Typothorax.* Indeed, an autapomorphy of *Coahomasuchus* is the presence of lateral scutes that are so flat that they cannot be subdivided into dorsal and ventral halves (Fig. 8A).

Ventral Scutes—One of the most important morphological features preserved in NMMNH P-18496 is the well-preserved ventral scute series (Figs. 4, 8B, C). Although ventral scutes have been reported for a number of aetosaur taxa, we believe that this is the best-preserved, articulated ventral carapace of any aetosaur outside of the type material of *Aetosaurus ferratus* (O. Fraas, 1877; Walker, 1961).

The ventral carapace of *Coahomasuchus* consists of four primary regions: (1) the cervical series; (2) the torso, from the posterior pectoral girdle to the anterior pelvic girdle; (3) a largely scute-free area corresponding to most of the pelvis; and (4) the caudal series. The neck and anterior torso armor consists primarily of numerous small, subcircular to polygonal scutes. The main ventral carapace preserves as many as ten transverse columns of larger, equant, almost square scutes that are very similar to the lateral scutes (Figs. 3, 4, 8A–C). Posterior to the largely unarmored ventral surface of the pelvis, the caudal series includes a set of specially modified scutes around the cloacal opening and persists to the tip of the tail, although much of the distal tail is no longer articulated.

The ventral scutes of the cervical series are primarily small (7–10 mm across) oval to polygonal scutes. Unlike most aetosaur scutes, these scutes lack any indication of articular surfaces, and instead appear to have been "floating" in the skin, much as the appendicular scutes covering the limbs (see below). These scutes are typically not articulated, except for two columns of ovate to tear-drop shaped scutes that parallel the mid-

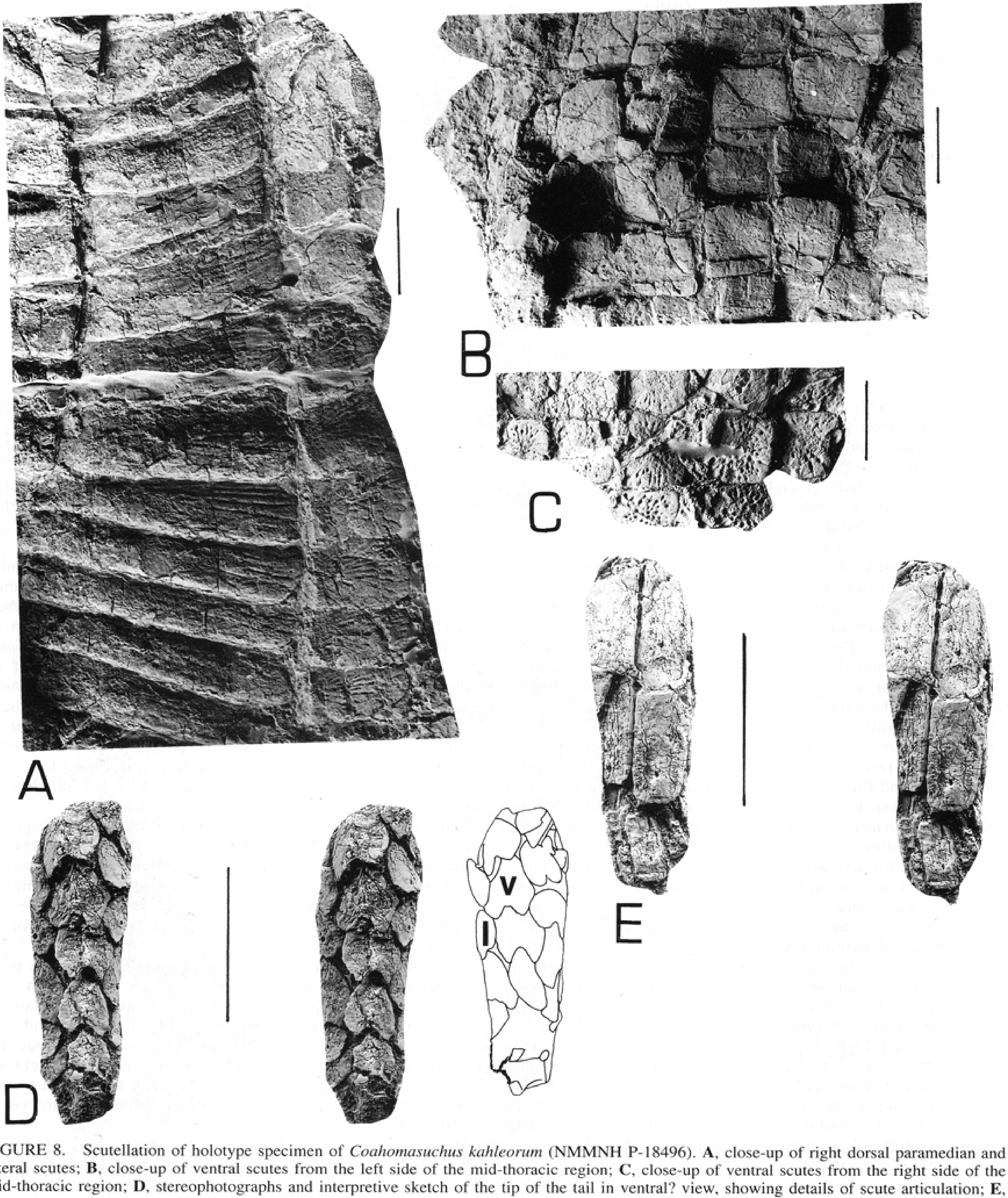

FIGURE 8. Scutellation of holotype specimen of *Coahomasuchus kahleorum* (NMMNH P-18496). **A**, close-up of right dorsal paramedian and lateral scutes; **B**, close-up of ventral scutes from the left side of the mid-thoracic region; **C**, close-up of ventral scutes from the right side of the mid-thoracic region; **D**, stereophotographs and interpretive sketch of the tip of the tail in ventral? view, showing details of scute articulation; **E**, stereophotographs of the tip of the tail in dorsal? view showing details of scute articulation. **Abbreviations**: **l**, lateral? scute; **v**, ventral? scute. All scales are 2 cm.

line. The long axis of each scute usually runs antero-posteriorly, and, in the case of the tear-drop shaped scutes, the wide end is anteriormost. These scutes appear somewhat imbricated, with posterior scutes overlapping the next most anterior scute as in dorsal and lateral scutes, but again, there is no evidence of an articular surface. Other scutes in this region vary from ovate through polygonal to hexagonal. This scutellation pattern appears to persist through the first eight presacral vertebrae, after which it is replaced by the articulated, imbricated ventral scutes of the torso.

In general, the ventral armor of *Coahomasuchus* coincides with Walker's (1961:163, fig. 23) illustrations of *Stagonolepis,* particularly in the torso, where as many as ten columns of scutes extend from the pectoral girdle to a point just anterior to the pelvis in a total of 18 rows (Fig. 4). The first three rows of articulated thoracic ventral scutes are clearly transitional from the largely unarticulated cervical scutes to the articulated thoracic series. In these rows the scutes are typically hexagonal, with the points aligned antero-posteriorly and articular bars on the anterior two edges (Fig. 4). Posteriorly, the scutes in each row become more quadrangular and, by the fourth row of thoracic scutes, all ventral scutes are nearly square, with a thin anterior bar. The anterior scutes are typically 12 mm across and 11–12 mm long. Posteriorly, ventral thoracic scutes can be as much as 21 mm across and 20 mm long. Typically these scutes bear a pattern of pits radiating from the center of the scute. There are no bosses, spikes, or other protuberances on any of these scutes.

The ventral scutes are not well preserved immediately anterior to the pelvis, so it is not clear if the number of columns of thoracic scutes is reduced posteriorly. However, there is no evidence of large, articulated scutes in the pelvic girdle area, so it appears that the thoracic ventral scute series abruptly terminates anterior to the pelvis. The only evidence of ventral scutellation in the immediate vicinity of the pelvic girdle is a series of small, subcircular scutes imbedded in the ventral surface of the fused, paired ischia? If these are ventral pelvic scutes, then *Coahomasuchus* differs from other aetosaurs, including *Stagonolepis,* in possessing ventral pelvic armor (Walker, 1961).

The ventral scute series resumes posterior to the pelvis. The anteriormost caudal scutes are roughly quadrangular and similar to the thoracic scutes. Immediately posterior to this row are three rows of ventral scutes that have been modified to accommodate the cloacal opening. The cloacal vent is located immediately posterior to the second caudal vertebra, underneath the third through fifth pairs of caudal paramedian scutes. Ventrally, the cloaca is surrounded by six ventral scutes, representing the third through fifth pairs of the middle two columns. The actual opening is rhomboid, with the longest axis opening antero-posteriorly, and the surrounding ventral scutes modified accordingly (Fig. 4). Detailed morphology of this region in aetosaurs is otherwise known only from *Aetosaurus.* Walker (1961:120) notes that ventral scutes of *Aetosaurus* also change shape to accommodate the cloacal vent.

Four columns of caudal scutes persist further posteriorly, but little can be determined from them. The caudal series, particularly the proximal portion, consists of quadrilateral scutes similar to those of the thoracic series, with some modification of anterior scutes to accommodate the cloacal opening and posterior modifications to fit the tapering tail. Patterns on the ventral caudal scutes are deeply incised and consist of the typical radiating series of pits and ridges.

The distal tip of the tail is preserved as three pairs of presumed dorsal paramedian scutes, and five pairs of lateral? scutes, as well as a single column of ventral? scutes (Fig. 8D, E). The paramedian scutes are longer than wide, a feature characteristic of the distal extremity of the tail (e.g., Walker, 1961). The lateral? scutes and the ventral column are essentially chevron-shaped. All of the scutes bear faint, almost microscopic, radial patterns of pits, indicating that the patterns established anteriorly persist to the very distal tip of the tail. Because of the single column of ventral? scutes, this is also the only portion of the carapace where the scute columns are not evenly paired across the midline.

Appendicular Scutes—Appendicular scutes cover much of the distal right femur, tibia, and fibula. Some smaller appendicular scutes even persist over portions of the pes. We illustrate here the appendicular scutes of the hind limb of *Coahomasuchus kahleorum* (Fig. 7). Appendicular scutes also covered the forelimbs, but are not as well preserved.

In dorso-lateral view, at least 24 subrounded scutes of various sizes cover the femur, tibia, and fibula. Another 18 scutes are visible in ventro-medial view. Scute size appears to correlate with the size of the underlying elements, with the largest scutes in the vicinity of the distal femur and proximal tibia and the smallest scutes associated with the distal tibia, fibula, and the tarsals. Most appendicular scutes are lightly decorated with faint, very small pits radiating out from the center of the scute. The appendicular scutes are closely spaced, but do not overlap or articulate in the fashion of much of the carapace. Scutellation is particularly thick, with large scutes in the knee region, and appears to taper distally.

Walker (1961:160) described the appendicular armor of *Stagonolepis,* but provided only a single illustration of some armor over the proximal femur (Walker, 1961:155, fig. 20). *Coahomasuchus* differs from *Stagonolepis* in possessing relatively larger, ovoid appendicular scutes over the hind limb, although forelimb scutes of *Stagonolepis* (=*Aetosauroides*) resemble those of *Coahomasuchus,* particularly in South American specimens. We have observed appendicular scutes, or are aware of reports of them, in *Stagonolepis* (Casamiquela, 1961a, b, 1967; Walker, 1961), *Aetosaurus* (Walker, 1961), *Longosuchus* (Sawin, 1947), and *Typothorax* (Hunt et al., 1993). However, we are unwilling to differentiate these taxa on the basis of appendicular scute patterns, especially because these structures are seldom preserved, and we are unable to compare these taxa to others, such as *Desmatosuchus* and *Paratypothorax,* which may also have had appendicular scutes.

PHYLOGENY

Parrish (1994:206) recently proposed the first cladistic phylogenetic hypothesis for the aetosaurs, defining the Aetosauria, and thus the Stagonolepididae, by the following synapomorphies: possession of an anteriorly edentulous premaxilla, reduced, nearly conical teeth, a complete carapace consisting of dorsal and ventral elements, sculptured dorsal paramedian osteoderms that are wider than long (and lacking anteriorly or posteriorly projecting lappets, as seen in the rauisuchians), and "stout" limb bones with hypertrophied trochanters (see also Parrish, 1994:tables 1, 2). We have followed Parrish (1994) in designating the Rauisuchia as an outgroup, and here rely on *Postosuchus* and *Saurosuchus* for comparison.

Long and Murry (1995) recently published a taxon-by-taxon description of the aetosaurs and some other Late Triassic tetrapods of the American Southwest, including characters they use to define the Aetosauria, but provided no phylogeny. Heckert et al. (1996) accepted Parrish's (1994) monophyletic Aetosauria and utilized *Aetosaurus* as an outgroup to all other aetosaur taxa. While we still believe this approach is valid, our goal here in utilizing two genera of rauisuchians as outgroups is threefold: (1) we hope to further test the monophyly of the Aetosauria, including a test of the assumption that *Aetosaurus* represents one of the most primitive aetosaur taxa; (2) we wish to place the new genus *Coahomasuchus* in a meaningful phylogenetic framework within the Aetosauria; and (3) we hope to test the utility of Long and Murry's (1995) characters, obtained primarily from examination of North American specimens, for aetosaurs worldwide.

Parrish (1994) conducted his phylogenetic analysis with 15 characters. Heckert et al. (1996) utilized some of those characters and expanded the total matrix to 22 characters. Long and Murry (1995:66) independently listed a total of 23 characters that they considered diagnostic of the Aetosauria, although they did not conduct their own analysis. Here we integrate these analyses and add new characters, resulting in a data matrix of 60 characters (see Appendix 1 for a description of characters and character states, and Appendix 2 for a data matrix). These characters are ordered by position on the body, with skull and mandible characters listed first, followed by characters of the axial skeleton, appendicular skeleton, and the armor. Armor characters are subdivided into those for dorsal paramedian, lateral, ventral, and appendicular scutes. Within each subdivision, we list characters utilized by Parrish (1994) and Long and Murry (1995) first, followed by characters we have examined.

Unfortunately, many existing aetosaur genera cannot be evaluated for Long and Murry's (1995) characters, as 13 of these characters are found on either the skull or mandible, elements that are infrequently preserved relative to the armor, which we rely on for 32 characters. Furthermore, another six of Long and Murry's characters are synonymous with characters identified by Parrish (1994), with character 3 "premaxilla edentulous anteriorly with an anteroventrally inclined mediolaterally expanded 'shovel' at anterior end" (Parrish, 1994:table 1) accounting for two of Long and Murry's characters. We also did not consider the last character of Long and Murry (1995:66), "tendency toward spinescence within lateral armor" to be quantifiable in cladistic terms, although we do utilize several characters to evaluate changes in lateral scute morphology. Two of Long and Murry's (1995) characters, "anterior portion of dentary edentulous" and "dentary with reduced dentition," are linked, but were maintained as separate characters. We feel this is justified because all aetosaurs with preserved jaw material have an edentulous anterior dentary, but within the aetosaurs, tooth counts in the dentary range from more than ten to as few as five, and we consider the latter condition relatively derived.

We examined specimens or primary literature of the following aetosaurs (important citations listed with each taxon): *Aetosaurus,* including both *A. ferratus* and *A. crassicauda* (O. Fraas, 1877; E. Fraas, 1907; Huene, 1920; Walker, 1961; Wild, 1989; Small, 1998); *Stagonolepis,* including both *S. robertsoni* and *S. wellesi* (Case, 1932; Walker, 1961; Long and Ballew, 1985; Long and Murry, 1995); *Desmatosuchus* (Case, 1922; Long and Ballew, 1985; Small, 1985, 1989; Long and Murry, 1995); *Longosuchus* (Sawin, 1947; Hunt and Lucas, 1990; Parrish, 1994; Long and Murry, 1995); *Paratypothorax* (Long and Ballew, 1985; Hunt and Lucas, 1992; Long and Murry, 1995); *Typothorax* (Long and Ballew, 1985; Hunt et al., 1993; Long and Murry, 1995); *Aetosauroides* (Casamiquela, 1961a, b, 1967); *Neoaetosauroides* (Bonaparte, 1967, 1970, 1971, 1978); *Redondasuchus* (Hunt and Lucas, 1991; Heckert et al., 1996); *Acaenasuchus* (Long and Murry, 1995); and *Lucasuchus* (Long and Murry, 1995). All named aetosaur genera were considered, subject to the following caveats: *Argentinasuchus* (Casamiquela, 1961a) is clearly a junior synonym of the Ischigualasto Formation aetosaur, herein referred to *Stagonolepis* (=*Aetosauroides,* see below). The type specimen of *Chilenosuchus* (Casamiquela, 1978) is lost, is almost certainly not an aetosaur, and may not even be from Triassic rocks (Breitkreuz et al., 1992). A detailed osteology of *Stegomus* (Marsh, 1896; Jepsen, 1948; Baird, 1986) is not possible from the known specimens, which are indistinguishable from *Aetosaurus* (Lucas et al., 1998). Murry and Long (1996) reported a new, "carnivorous" aetosaur from the same horizon as *Coahomasuchus,* but this taxon has not been described enough for us to include it in our phylogenetic analysis.

With these considerations in mind we constructed a data matrix of 60 characters for *Coahomasuchus* and the 11 taxa listed above. Initial runs of PAUP (Swofford, 1993) analyses using both the branch-and-bound and exhaustive algorithms and incorporating all the taxa in the data matrix yielded 16 most parsimonious trees. The strict consensus of these trees bore out our initial suspicions that *Stagonolepis robertsoni* and *Aetosauroides scagliai* are congeneric, as are *Desmatosuchus* and *Acaenasuchus,* and *Longosuchus* and *Lucasuchus.* Accordingly, we removed *Aetosauroides, Acaenasuchus* and *Lucasuchus* from the matrix and here regard them as junior subjective synonyms of *Stagonolepis, Desmatosuchus* and *Longosuchus,* respectively. We also remain skeptical regarding the distinctiveness of the Chinle species *Stagonolepis wellesi* (Long and Ballew, 1985) from the European *S. robertsoni.* Although Long and Ballew (1985) and Long and Murry (1995) note the presence of spikes on the cervical lateral scutes as well as wider transverse processes on *S. wellesi,* these features are not convincingly associated with UMMP 13950, the type specimen of *S.* (=*Calyptosuchus*) *wellesi* (Long and Ballew, 1985). Indeed, the type specimen is a mid-dorsal to mid-caudal carapace, associated vertebrae, pelvis, and miscellaneous appendicular scutes, and thus lacks cervical lateral scutes entirely. Otherwise, these taxa score almost identically throughout the matrix. The same is true of the two distinct German species of *Aetosaurus, A. ferratus* and *A. crassicauda,* which differ primarily in size (O. Fraas, 1877; E. Fraas, 1907; Huene, 1920; Wild, 1989; Small, 1998). Although we consider *Redondasuchus* distinct from *Typothorax* (Heckert et al., 1996; contra Long and Murry, 1995; Small, 1998), we determined that it was too incompletely known (only 29 of 60 characters could be coded) to include in our analyses. Therefore, in our final analysis we chose to include only a single species of *Stagonolepis* (*S. robertsoni*) as well as the taxa *Aetosaurus ferratus, Coahomasuchus kahleorum, Desmatosuchus haplocerus, Longosuchus meadei, Neoaetosauroides engaeus, Paratypothorax andressorum,* and *Typothorax coccinarum,* and utilized the rauisuchians as an outgroup.

The result of this analysis was a single most parsimonious tree (Fig. 9). This tree has a treelength of 76, a consistency index of 0.74, and a retention index of 0.56. This analysis demonstrates that the aetosaurs are a monophyletic group, with *Aetosaurus* a sister taxon to the other aetosaurs, composed of two clades, (*Coahomasuchus* + *Stagonolepis*) and (*Neoaetosauroides* + ((*Typothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratypothorax*))). The conclusions of this analysis are broadly similar to those reached by other workers, both using cladistics (Parrish, 1994; Heckert et al., 1996) and older, non-cladistic phylogenetic hypotheses (e.g., Walker, 1961). The following is our systematic description of the results of this analysis.

Suborder AETOSAURIA Nicholson and Lydekker, 1889
Family STAGONOLEPIDIDAE Lydekker, 1887

We present a new diagnosis of the Aetosauria, and thus the Stagonolepididae, based on the following 18 synapomorphies:

1. Premaxilla edentulous anteriorly, with an anteroventrally inclined, mediolaterally expanded "shovel" at the anterior end (unknown in *Coahomasuchus* and *Paratypothorax*).
2. Teeth reduced in size, conical or nearly conical (unknown in *Coahomasuchus* and *Paratypothorax*).
8. External nares longer than antorbital fenestra (unknown in *Coahomasuchus* and *Paratypothorax*).
10. Supratemporal fenestra exposed laterally, not dorsally (unknown in *Coahomasuchus* and *Paratypothorax*).

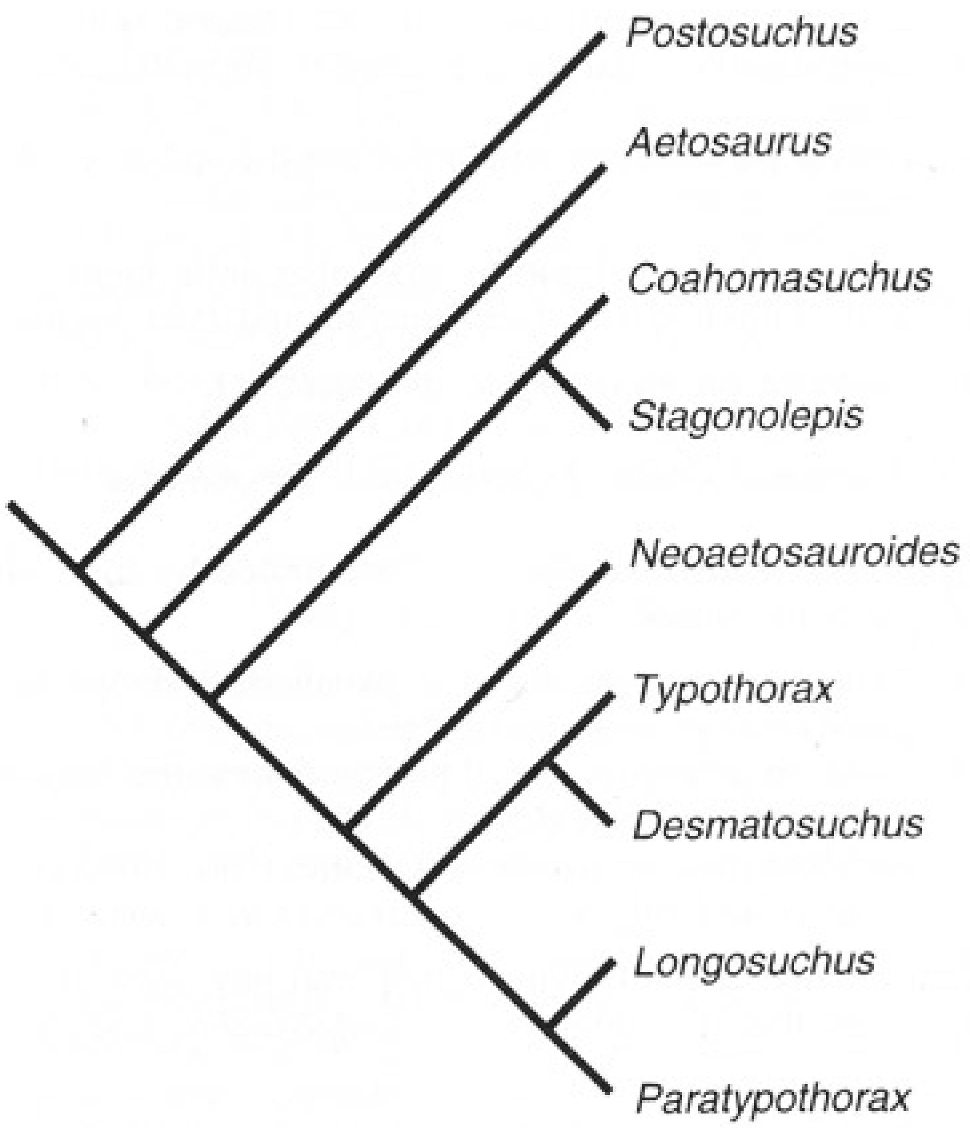

FIGURE 9. Single most parsimonious tree of the eight best-known aetosaur genera, with the rauisuchian *Postosuchus* used as an outgroup. Treelength is 76, consistency index is 0.74, retention index is 0.56. See text for details and appendices for character lists and data matrix.

11. Parietal short (unknown in *Coahomasuchus* and *Paratypothorax*).
12. Posterior margin of parietal modified to receive paramedian scutes (unknown in *Coahomasuchus* and *Paratypothorax*).
13. Maxilla included in external nares (unknown in *Coahomasuchus, Paratypothorax,* and *Neoaetosauroides*).
14. Jugal downturned (unknown in *Coahomasuchus* and *Paratypothorax*).
15. "Slipper-shaped" mandible, consisting of robust posterior bones and processes with dorsally concave, less robust dentary.
17. Presacral vertebral column massively constructed (unknown in *Paratypothorax*).
22. Apex of scapula broadly expanded (unknown in *Coahomasuchus* or *Paratypothorax*).
23. Manus short, broad, and small, effectively wider than long (unknown in *Paratypothorax*).
24. Well-developed, robust, short anterior iliac blade (unknown in *Paratypothorax*).
27. Pubes broadened transversely and fused, forming a "pubic apron" in anterior view (unknown in *Coahomasuchus, Longosuchus, Neoaetosauroides* and *Paratypothorax*).
28. Dorsal paramedian plates wider than long, sculptured, lacking anteriorly or posteriorly projecting lappets.
57. Dermal lateral scutes articulating with larger paramedian plates.
59. Dermal ventral scutes articulating with each other to form a ventral carapace (unknown in *Typothorax, Desmatosuchus,* and *Paratypothorax*).
60. Dermal scutes covering the appendages, at least in part (unknown in *Desmatosuchus, Neoaetosauroides* and *Paratypothorax*).

AETOSAURUS O. Fraas, 1877

Aetosaurus was named by O. Fraas (1877) for 22 articulated skeletons collected from the Lower Stubensandstein in Germany. This aetosaur is widely considered the most primitive member of the Stagonolepididae, a conclusion borne out by our analysis. Of the two species, *A. ferratus* and *A. crassicauda* (E. Fraas, 1907), *A. ferratus* is the best known. Wild (1989) summarized the evidence demonstrating the validity of the two species (see below). The aetosaur *Stegomus,* from several localities in the Newark Supergroup in the eastern U.S.A., is indistinguishable from *Aetosaurus* (Lucas et al., 1998). Recently Jenkins et al. (1994) reported *Aetosaurus* from the Fleming Fjord Formation in Greenland and Heckert and Lucas (1998) and Small (1998) have reported *Aetosaurus* from the Chinle Group in the western U.S.A. All occurrences of *Aetosaurus* are from strata of Norian age (Lucas and Heckert, 1996).

AETOSAURUS FERRATUS O. Fraas, 1877

Aetosaurus ferratus is known from the type locality in the Lower Stubensandstein and the Calcare di Zorzino Formation near Bergamo, Italy (Wild, 1989). Wild (1989) differentiates *A. ferratus* from *A. crassicauda* based on its smaller size (90 cm maximum adult length), elongate keels on the dorsal paramedian scutes, and densely packed, deeply incised radial patterns of pits and grooves. The Greenland specimens represent *A. ferratus* (Jenkins et al., 1994), as do at least some of the Chinle specimens (Heckert and Lucas, 1998; Small, 1998).

AETOSAURUS CRASSICAUDA E. Fraas, 1907

E. Fraas (1907) described *A. crassicauda* from the Middle Stubensandstein in Germany. As Wild (1989) noted, the most obvious differences between *A. ferratus* and *A. crassicauda* are the latter's larger size (up to 150 cm adult length), shallow and lightly incised pitting, development of the dorsal keel on the paramedian scutes into a knob, and the strong transverse arching of the anterior caudal paramedians. At least one of the Newark Supergroup specimens of *Aetosaurus* (Lucas et al., 1998) probably represents *A. crassicauda.*

Unnamed Clade: (*Coahomasuchus* + *Stagonolepis*) + (*Neoaetosauroides* + ((*Desmatosuchus* + *Typothorax*) + (*Longosuchus* + *Paratypothorax*)))

All aetosaurs except for *Aetosaurus* are united by the following three synapomorphies:

3. Teeth conical, not recurved (unknown in *Coahomasuchus*).
4. Anterior part of dentary edentulous (unknown in *Coahomasuchus*).
5. Maxillary tooth row does not extend anterior to the posterior end of the external naris (unknown in *Coahomasuchus, Neoaetosauroides,* and *Paratypothorax*; reversed in *Desmatosuchus*).

Unnamed Clade: (*Coahomasuchus* + *Stagonolepis*):

Coahomasuchus and *Stagonolepis* are united by the following two synapomorphies:

7. Presence of a deep, hemispherical fontanelle in the bottom of the basisphenoid between the basal tubera and basipterygoid processes (unknown in *Neoaetosauroides* and *Paratypothorax*; convergent with *Longosuchus* and *Desmatosuchus*).
36. Absence of raised bosses on cervical paramedian scutes (convergent with *Typothorax*).

STAGONOLEPIS ROBERTSONI Agassiz, 1844

Stagonolepis, from the Lossiemouth Sandstone in Scotland, was the first aetosaur to be described, albeit as a fish (Agassiz, 1844). This relatively primitive aetosaur is slightly more derived than *Aetosaurus,* based on the synapomorphies listed for the clade of (*Coahomasuchus* + *Stagonolepis*), as well as numerous other skeletal features (see Walker, 1961). Three genera of aetosaurs, namely *Argentinasuchus* Casamiquela, 1961a, *Aetosauroides* Casamiquela, 1961a, and *Calyptosuchus* Long and Ballew, 1985, are all congeneric with *Stagonolepis.* At this time, we only recognize one species of *Stagonolepis, S. robertsoni.* Long and Murry (1995) argued that *Calyptosuchus wellesi* from the Chinle Group is congeneric with *Stagonolepis,* but reiterated the position of Murry and Long (1989) that the Chinle form is a different species, *S. wellesi.* We have maintained the distinction in the appendices based on their descriptions, but note here that we are not convinced that these characteristics are demonstrably associated with their holotype of *S. wellesi.* Including *S. wellesi* in the analysis results in no change in tree topology (it is a sister taxon to *S. robertsoni*), but lowers the consistency and retention indices due to the reported presence of lateral spikes, indicating convergence with the derived clade of ((*Typothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratypothorax*). All reported specimens of *Stagonolepis* occur in strata of latest Carnian age (Lucas and Heckert, 1996).

COAHOMASUCHUS KAHLEORUM, gen. et sp. nov.

Coahomasuchus was described in detail previously in this paper.

Unnamed clade: *Neoaetosauroides* + ((*Typothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratypothorax*))

Various characters loosely tie *Neoaetosauroides* to the more derived aetosaurs by the overlap of some derived character states. Additionally, these aetosaurs are slightly more robust (lower length:width limb bone ratios) than the other aetosaurs. This clade is weakly supported by the following synapomorphy:

9. Infratemporal fenestra equant to square (unknown in *Typothorax, Coahomasuchus,* and *Paratypothorax*).

NEOAETOSAUROIDES ENGAEUS Bonaparte, 1967

Neoaetosauroides is known from three specimens in the Los Colorados Formation in Argentina (Bonaparte, 1967, 1970, 1971, 1978). This taxon is notable for its postglenoid process on the coracoid and reduction of the fifth metatarsal (Parrish, 1994) as well as its greatly reduced dentary tooth count. Characters we have observed but which were not included in the phylogenetic analysis that may support inclusion of *Neoaetosauroides* with more derived aetosaurs listed below are its relatively stout limb proportions. Recently one of us (ABH) restudied the type specimen and currently we are preparing a manuscript redescribing the taxon. *Neoaetosauroides* is of probable latest Norian (Rhaetian) age (Lucas and Heckert, 1996).

Unnamed Clade: (*Typothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratypothorax*)

These aetosaurs share the following seven synapomorphies:

39. Dorsal bosses form a distinct knob.
41. Dorsal paramedian caudal scutes not transversely arched.
48. Posterior emargination of lateral scute, revealing hollow on the posterior side of the lateral spike (reversed in *Typothorax*).
49. Lateral spikes on cervical lateral scutes.
50. Lateral spikes on dorsal ("trunk") lateral scutes.
52. Lateral scutes sharply angulated to approximately 90° or more.
54. Dorsal paramedian scutes not constricted anterior to sacrum.

The following synapomorphy may also unite these taxa, except that it is unknown in *Longosuchus* and *Paratypothorax*:

6. Posterior premaxillary teeth absent (1).

Unnamed Clade: *Typothorax* + *Desmatosuchus*

Typothorax and *Desmatosuchus* are united by the following three synapomorphies:

32. Random pitting on cervical paramedian scutes, no elongate radial grooves and ridges.
33. Random pitting on dorsal paramedian scutes, no elongate radial grooves and ridges.
47. Random pitting on lateral scutes, no elongate radial grooves and ridges.

Additionally, the following synapomorphy may unite these taxa, except that it is unknown in *Longosuchus* and *Paratypothorax*:

6. Posterior premaxillary teeth absent.

TYPOTHORAX COCCINARUM Cope, 1875

Typothorax, known from numerous localities in the Chinle Group, was the first aetosaur described from the U.S.A. (Cope, 1875). This genus is easily distinguished by, among other features, its very broad dorsal paramedian scutes with ornamentation consisting of a random pattern of pits. The dorsal paramedian scutes also possess prominent ventral keels. The limb bones are very short and stout, and the dorso-ventrally tall ilium is particularly diagnostic. *Typothorax* is restricted to the Chinle, where it is one of the most abundant vertebrate fossils in strata of early–mid Norian age (Lucas and Heckert, 1996).

DESMATOSUCHUS HAPLOCERUS (Cope, 1892)

Gregory (1953) demonstrated that the holotype of *D. spurensis* Case (1920) is congeneric with *Episcoposaurus haplocerus* Cope (1892) and that the type of *Episcoposaurus, E. horridus* (Cope, 1875), is probably a synonym of *Typothorax coccinarum* (1875). Thus, the type and only species of *Desmatosuchus* is *D. haplocerus. Desmatosuchus* is one of the best known Chinle aetosaurs, and is easily diagnosed by the giant recurved lateral spikes developed on anterior lateral scutes and the lack of anterior bars on the dorsal and lateral scutes. This latter feature, as well as the random pitting on dorsal paramedian scutes, also occurs in the small aetosaur *Acaenasuchus,* which is one of the reasons we consider it to represent juveniles of *Desmatosuchus.* Recent descriptions of *Desmatosuchus* include Small (1985, 1989), and Long and Murry (1995). *Desmatosuchus* occurs in strata from late Carnian to early–mid Norian age (Lucas and Heckert, 1996), including a possible record in the Zarzaitine Series in Algeria (Jalil et al., 1995).

Unnamed Clade: (*Longosuchus* + *Paratypothorax*)

35. Bosses on dorsal paramedian scutes touching to overlapping posterior margin of scute (shared with *Stagonolepis*).

LONGOSUCHUS MEADEI (Sawin, 1947)

Hunt and Lucas (1990) separated the holotype of *Typothorax meadei* from *Typothorax* as a new genus, *Longosuchus,* based on numerous characteristics, including the extremely different armor. Parrish (1994) recently redescribed the skull of *Longosuchus.* Long and Murry (1995) named *Lucasuchus* for topotypic material of *Longosuchus.* Although some of the material they referred to *Lucasuchus* probably represents a different species, little if any of this material is associated with the holotype of *Lucasuchus. Longosuchus* is a relatively derived aetosaur, most readily diagnosed by the faceted lateral spikes and prominent dorsal bosses projecting from the paramedian scutes. All occurrences of *Longosuchus* (=*Lucasuchus*) are from strata of early late Carnian age (Lucas and Heckert, 1996).

PARATYPOTHORAX ANDRESSORUM
Long and Ballew, 1985

Long and Ballew (1985) named this aetosaur for very distinctive specimens collected from the Lower Stubensandstein in Germany. They, and Hunt and Lucas (1992), noted the presence of this aetosaur in the Chinle Group in the southwestern U.S.A. Jenkins et al. (1994) reported *Paratypothorax* from the Fleming Fjord Formation in Greenland. *Paratypothorax* is easily diagnosed by its wide, strap-like paramedian scutes with a deeply incised pattern of radial pits and grooves and prominent knob that overlaps the rear of the scute. Unfortunately, little of the skeleton is known outside of the armor, although Long and Murry (1995) illustrate much associated material.

We note here that this analysis produces results broadly similar to those of studies by Walker (1961), Parrish (1994) and Heckert et al. (1996). The phylogenetic analysis described here supports the hypotheses that: (1) the aetosaurs are monophyletic; and (2) *Aetosaurus* is the most primitive aetosaur. It also places *Coahomasuchus* into a phylogenetic framework indicating that it is an autapomorphic, yet relatively primitive aetosaur. We use this last hypothesis to suggest that *Coahomasuchus* fills an important gap in the record of aetosaur evolution, as it is the oldest relatively primitive aetosaur, and is significantly older than *Aetosaurus.* Therefore, it is evident from this analysis that aetosaurs diversified rapidly before the late Carnian, splitting into at least three distinct lineages: (1) a primitive lineage that gave rise to *Aetosaurus* in the Norian; (2) a more derived lineage that includes the late Carnian *Coahomasuchus* and the latest Carnian *Stagonolepis;* and (3) a derived lineage that quickly diversified to give rise to *Longosuchus, Desmatosuchus,* and *Paratypothorax,* all of which make their first appearance in the late Carnian.

CONCLUSIONS

Using characters defined and utilized by both ourselves and previous authors, we demonstrate that *Coahomasuchus kahleorum* is an autapomorphic, yet relatively primitive, aetosaur. Recent hypotheses of aetosaur phylogeny (Parrish, 1994; Heckert et al., 1996) have shown that certain early-appearing forms, such as *Longosuchus* and *Desmatosuchus,* are among the most derived aetosaurs, whereas more primitive aetosaurs, particularly *Aetosaurus,* have their first appearance much later. This study indicates that *Coahomasuchus* fills a gap in the aetosaurian record by demonstrating the presence of primitive aetosaurs in the early late Carnian, synchronous with the first appearance of aetosaurs in the fossil record.

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APPENDIX I

Description of Characters Used for Phylogenetic Analysis of the Aetosaurs

Characters 1–7 taken almost verbatim from Parrish (1994:204, table 1), with Parrish's character number in parenthesis.

1.(3) Premaxilla edentulous anteriorly, with an anteroventrally in-

clined, mediolaterally expanded "shovel" at the anterior end: absent (0) or present (1).
2.(4) Teeth unreduced, mediolaterally compressed (0) or reduced in size, nearly conical (1).
3.(8) Teeth recurved (0) or conical (1).
4.(9) Anterior part of dentary with teeth (0) or edentulous (1).
5.(11) Maxillary tooth row does (0) or does not (1) extend anterior to the posterior end of the external naris.
6.(12) Posterior premaxillary teeth: present (0) or absent (1).
7.(14) Absence (0) or presence (1) of a deep, hemispherical fontanelle in the bottom of the basisphenoid between the basal tubera and basipterygoid processes.

Characters 8–15 modified from Long and Murry (1995:66).

8. External nares longer than antorbital fenestra: no (0) or yes (1).
9. Infratemporal fenestra antero-posteriorly short, dorso-ventrally elongate (0) or more equant to square (1).
10. Position of supratemporal fenestra: dorsally exposed (0) or lateral (1).
11. Length of parietal: long (0) or short (1).
12. Posterior margin of parietal: unmodified (0) or modified to receive paramedian scutes (1).
13. Position of maxilla relative to external nares: excluded (0) or included (1).
14. Jugal: not downturned (0) or downturned (1).
15. "Slipper shaped" mandible, consisting of robust posterior bones and processes with dorsally concave, less robust dentary: absent (0) or present (1).
16. Dentary tooth count: 10 or more (0) or fewer than 10 (1).
17. Presacral vertebral column: gracile (0) or massively constructed (1).
18. Width of presacral transverse processes: less than twice as wide as centrum (0) or several times wider than centrum (1).
19. Height of presacral neural spines: low, less than height of centrum (0) or high, greater than height of centrum (1).
20. Ventral keel on cervical centra: present (0) or absent (1).

Character 21 is also from Parrish (1994:table 1, character 6).

21.(7) Limb bones very stout, with hypertrophied trochanters for muscle attachment on the humerus (deltopectoral crest), femur (fourth trochanter), tibia (intracondylar ridge) and fibula (iliofibularis trochanter): absent (0) or present (1).

Characters 22–25 modified from Long and Murry (1995:66).

22. Apex of scapula: un- or modestly expanded (0) or broadly expanded (1).
23. Manus gracile and elongate (longer than wide) (0) or short, broad, and small (wider than long) (1).
24. Well-developed, robust, short anterior iliac blade: absent (0) or present (1).
25. Openings in pubis: none or one (0) or two (1).
26. Coracoid: shallow (0) or robust (1).
27. Pubes broadened transversely and fused, forming a "pubic apron" in anterior view: absent (0) or present (1).

Character 28 is also from Parrish (1994:table 1, character 6).

28.(6) Dorsal paramedian plates wider than long, sculptured, lacking anteriorly or posteriorly projecting lappets: absent (0) or present (1).
29. Anterior bars on dorsal paramedian scutes: present or not applicable (0), or absent (1).

Character 30 is modified from Parrish (1994:table 1, character 15).

30.(15) Width to length ratio of dorsal paramedian scutes: maximum of less than 4 (0) or more than 4 (1).
31. Shape of cervical dorsal paramedian scutes: wider than long (0); equant or longer than wide (1).
32. Patterning of cervical paramedian scutes: radiate (0) or random (1).
33. Patterning of dorsal paramedian scutes: radiate (0) or random (1).
34. Ornamentation of dorsal paramedian scutes: mixture of pits, elongate pits, grooves, and ridges (0) or small, subcircular pits only (1).
35. Position of bosses: not in contact with posterior margin of scute (0) or touching to overlapping posterior margin of scute (1).

Characters 36–38 are expanded from Parrish (1994:table 1, character 10).

36. Raised bosses on cervical paramedian scutes: present (0) or absent (1).
37. Raised bosses on dorsal paramedian scutes: present (0) or absent (1).
38. Raised bosses on caudal paramedian scutes: present (0) or absent (1).
39. Shape of dorsal bosses: anterior-posterior elongate keel (0) or knob (1).
40. Dorsal boss incised: (0) no or yes, forms two convergent flanges (1).
41. Dorsal paramedian caudal scutes transversely arched: yes (0) or no (1).
42. Lateral portion of dorsal paramedian scutes strongly downturned: no (0) or yes (1).
43. Ventral keel or strut on dorsal paramedian scutes: absent (0) or present (1).
44. Ventral keel or strut continuous across width of scute: yes (0) or no (1).
45. Cervical paramedian scutes dorso-ventrally thickened: yes (0) or no (1).
46. Tongue and groove articulations for lateral scutes in dorsal presacral paramedian scutes: absent (0) or present (1).
47. Patterning of lateral scutes: radiate (0) or random (1).
48. Posterior emargination of lateral scute, revealing hollow on the posterior side of the lateral spike: absent/not applicable (0) or present (1).

Characters 49–51 are expanded from Parrish (1994:table 1, character 13).

49. Lateral spikes on cervical lateral scutes: absent (0) or present (1).
50. Lateral spikes on dorsal ("trunk") lateral scutes: absent (0) or present (1).
51. Lateral spikes on caudal lateral scutes: absent (0) or present (1).
52. Lateral scute angles: flat to slightly angulated (0) or sharply angulated to approximately 90° or more (1).
53. Lateral spike angles: up to approximately 90° or not applicable (0) or acutely angled (1).
54. Dorsal paramedian scutes constricted anterior to sacrum, resulting in a "waist": yes (0) or no (1).
55. Anterior bars on lateral scutes: present (0) or absent, replaced by laminae (1).
56. Incision of ornamentation: shallow or faint (0) or deeply incised (1).
57. Dermal lateral scutes articulating with larger paramedian plates: absent (0) or present (1).
58. Patterning of ventral scutes: radiate (0) or random (1).
59. Dermal ventral scutes articulating with each other to form a ventral carapace: absent (0) or present (1).
60. Dermal scutes covering the appendages, at least in part: absent (0) or present (1).

APPENDIX 2. Distribution of character states used for phylogenetic analysis of the aetosaurs.

Character:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Rauisuchia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coahomasuchus	?	?	?	?	?	?	1	?	?	?	1	1	?	?	1	?	1	?	?	?	1	?	1	1	?	?	?	1	0	0
Aetosaurus	1	1	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	?	0	?	1	1	1	1	?	?	1	1	0	0
S. robertsoni	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0	0	1	1	1	1	1	0	1	1	0	0
S. wellesi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	?	?	?	?	0	1	1	0	0
Longosuchus	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	?	0	?	1	1	1	1	0	0	?	1	0	0
Lucasuchus	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	0	1	1	0	0
Desmatosuchus	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	?	1	1	1	1	0
Acaenasuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
Typothorax	1	1	1	1	0	1	0	1	?	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	?	0	1	1	0	1
Aetosauroides	1	1	1	1	1	0	?	1	?	1	1	1	?	?	?	0	1	1	0	0	1	1	1	1	?	0	1	1	0	0
Neoaetosauroides	1	1	1	1	0	0	?	1	1	1	1	1	?	1	1	1	1	?	?	1	1	1	1	1	?	?	?	1	0	0
Paratypothorax	?	?	1	1	?	?	?	?	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	1	0	1
Redondasuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0

Character:	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Rauisuchia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coahomasuchus	0	?	0	0	0	1	1	1	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Aetosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	1	1
S. robertsoni	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
S. wellesi	0	0	0	0	1	?	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1
Longosuchus	1	0	0	0	1	0	0	0	0	0	?	0	0	0	0	1	0	1	1	1	1	1	0	1	0	0	1	?	1	1
Lucasuchus	1	0	0	0	0	0	0	0	1	0	?	0	0	0	1	1	?	1	1	1	1	1	0	0	0	0	1	?	?	?
Desmatosuchus	1	1	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1	1	0	1	0	1	1	1	1	?	?	?
Acaenasuchus	1	1	1	0	0	0	0	0	0	1	?	0	0	0	?	0	1	0	1	1	?	0	0	?	1	1	1	?	?	?
Typothorax	0	1	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	0	1	0	0	1	1	1	0	0	1	?	?	1
Aetosauroides	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
Neoaetosauroides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	?
Paratypothorax	?	0	0	0	1	?	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	?	?	?
Redondasuchus	0	1	1	1	0	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	?	0	0	0	?	?	?