Articulated Skeletons of the Aetosaur Typothorax coccinarum Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: Early-Mid Norian), Eastern New Mexico, USA

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FEATURED ARTICLE

ARTICULATED SKELETONS OF THE AETOSAUR *TYPOTHORAX COCCINARUM* COPE (ARCHOSAURIA: STAGONOLEPIDIDAE) FROM THE UPPER TRIASSIC BULL CANYON FORMATION (REVUELTIAN: EARLY-MID NORIAN), EASTERN NEW MEXICO, USA

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ABSTRACT—We report two nearly complete, articulated skeletons of the crurotarsan archosaur *Typothorax coccinarum* from the Upper Triassic Bull Canyon Formation of east-central New Mexico. These are the most complete, articulated aetosaurs from North America and provide a wealth of new anatomical and paleobiological data, including articulated presacral armor that confirms the distinctiveness of *T. coccinarum* from the closely related *T. antiquum* and from *Redondasuchus*. Cervical vertebrae are small, but the corresponding reduction in armor is accomplished by a reduced number of cervical osteoderms. The third row of osteoderms includes a thin, elongate, lateral spike. The ventral armor consists of 10 thoracic columns and four caudal columns of osteoderms. Spiked osteoderms near the cloacal vent are the first spikes reported in aetosaurian ventral osteoderms. The forelimb of *T. coccinarum* was very short, only ~0.65 the length of the hind limb, possesses some adaptations found in digging taxa, and was held in a sprawling or 'semi-erect' position. In contrast the hind limb is much more robust, 'pillar erect,' and functionally mesotarsal. The articulated pes, including unguals, has, minimally, the phalangeal formula 2-3-3?-4?-3? with relative digit lengths III > II > IV > I > V, digits I–IV equally as wide as long and other characteristics of the footprint ichnogenus *Brachychirotherium*, often attributed to an aetosaurian trackmaker. Both specimens are ~2.5 m long and the preserved armor and limb bones are as large or larger than known *Typothorax* fossils, suggesting that this approximates the upper size limit of *T. coccinarum*, and we calculate body mass estimates of ~100–104 kg for both specimens.

INTRODUCTION

Aetosaurs are an extinct clade of crurotarsan archosaurs known from Upper Triassic strata in North and South America, Greenland, Europe, North Africa, and India (Heckert and Lucas, 2000). The common Late Triassic footprint ichnogenus *Brachychirotherium* has been considered by some to be the track of an aetosaur, and shares a similarly Pangean distribution (Haubold, 1971, 1986; Heckert and Lucas, 2000; Hunt and Lucas, 2007). Aetosaurs were quadrupedal, heavily armored animals variously thought to be herbivorous, omnivorous, or even scavengers (Sawin, 1947; Walker, 1961; Bonaparte, 1978). Because the typical aetosaur bore two columns of dorsal paramedian osteoderms, two additional columns of lateral osteoderms, and various ventral and appendicular osteoderms, their fossils are among the most commonly recovered bones in Upper Triassic strata where they are known. Long and Ballew (1985) recognized many taxonomically significant characteristics of aetosaur osteoderms, and subsequent studies confirmed the distinctiveness of various aspects of aetosaur dorsal and lateral armor (e.g., Long and Murry, 1995; Heckert and Lucas, 1999, 2000; Parker, 2007). Thus, many aetosaur taxa have been named primarily or even solely on the basis of osteoderms (Long and Ballew, 1985; Hunt and Lucas, 1991; Long and Murry, 1995; Zeigler et al., 2002; Martz and Small, 2006; Lucas et al., 2007a). Although our knowledge of aetosaur diversity has grown considerably since reviews by Long and Murry (1995) and Heckert and Lucas (2000), skeletal material is known for only a handful of taxa, little of which is articulated, with very few reasonably complete specimens. This leaves our understanding of aetosaurian paleobiology unsatisfactory, because most recent synthetic work has focused on phylogenetic analyses (Heckert and Lucas, 1999, 2000, 2003; Harris et al., 2003a, 2003b; Parker, 2007), and even thorough osteological studies (Walker, 1961; Schoch, 2007) have not addressed aetosaurian paleobiology in detail. Accordingly, our aim here is to reconstruct *Typothorax coccinarum* Cope based on newly available fossils. In so doing we present a novel skeletal reconstruction of *Typothorax*, including details related to the distribution of armor, limb orientation and proportions, the probable footprint of *Typothorax*, cloacal vent morphology, and the apparently unique adaptations of this aetosaur.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; **MCZ**, Museum of Comparative Zoology, Cambridge; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque; **PEFO**, Petrified Forest National Park, Arizona. **TTUP**, Texas Tech University, Lubbock; **UCMP**, University of California Museum of Paleontology, Berkeley.

MATERIALS AND METHODS

Our observations and descriptions are based primarily on two relatively complete, articulated skeletons of *Typothorax*, the Badlands Ranch specimen (NMMNH P-56299, Figs. 2–5) and the Revuelto Creek specimen (NMMNH P-12964, Figs. 6–8). Other comparative specimens we utilized included both previously studied and unpublished specimens of *T. coccinarum* housed at various institutions, including the partial skeletons recently described by Nesbitt and Stocker (2008). For comparative purposes, we measured many specimens using the protocols of

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Martz (2002) where applicable, to facilitate comparisons across the maximum number of specimens, so specimens measured as part of this study (and not measured by Martz) are included in the supplementary tables of measurements. Some elements (ulna, radius, pes) were unavailable to Martz, so we developed our own protocols for measuring these bones.

Specimens were photographed primarily with a Nikon D60 digital camera, with subsequent image processing by Nikon ViewNX 1.0.3 and Adobe Photoshop CS 3 (version 10.0). Specimen illustrations were accomplished using overlays in Adobe Illustrator CS 3 (version 13.0) as well. Rock colors are described using Goddard et al. (1984).

PREVIOUS STUDIES

Typothorax coccinarum Cope (1875) was the first aetosaur reported from the Americas and the second aetosaur named, following *Stagonolepis robertsoni* Agassiz (1844). Because of the fragmentary nature of the type material and the fact that isolated osteoderms of aetosaurs in the American Southwest were routinely assigned to *Typothorax*, the genus has a long and complex taxonomic history that has been reviewed at length by Huene (1915), Gregory (1953a, 1953b), Heckert and Lucas (2002), and Lucas et al. (2002, 2007b). Heckert and Lucas (2000, 2002) provided lists of synonymies of the taxonomic literature, and we append updated versions of these in the Supplementary Data (www.vertpaleo.org/jvp/JVPcontents.html). Other salient published reviews of *Typothorax coccinarum* include Long and Murry (1995) and Heckert and Lucas (2000). Martz (2002) produced an osteology of *T. coccinarum* as part of his M.S. thesis. The most recent phylogenetic analysis incorporating *Typothorax coccinarum* is that of Parker (2007). Even so, at least one recent article (Kubo and Benton, 2008) still identified *Longosuchus meadei* (Sawin, 1947) as congeneric with *Typothorax*, *contra* all published literature since Hunt and Lucas (1990).

In spite of these many studies, no described specimen of *Typothorax* has been more than perhaps 25% complete—the best available materials were an articulated presacral vertebral column (AMNH 2713, type of *Episcoposaurus horridus*—Long and Murry, 1995; Lucas et al., 2007b), with some associated limb elements potentially belonging to the same individual (see Lucas et al., 2007b, for further discussion), and a variety of partially articulated tail segments with associated postcrania (Long and Murry, 1995; Martz, 2002; Nesbitt and Stocker, 2008). Indeed, although aetosaur osteoderms are relatively common fossils, reasonably complete and/or articulated remains are rare (see Supplementary Table 1). Hunt et al. (1993) provided a very preliminary description and photographs of one side of the Revuelto Creek specimen, and it was also the focus of an abstract (Sealey et al., 1995). Hunt's (1994, 2001) synthetic work on the Bull Canyon Formation also made reference to this specimen. Heckert and Lucas (1999, 2000) relied on this specimen for some coding in their cladistic analyses, but made no attempt to describe it otherwise, nor has any subsequent author.

GEOLOGIC SETTING AND AGE

Both *Typothorax* skeletons were recovered from strata low in the Upper Triassic Bull Canyon Formation of the Upper Triassic Chinle Group in eastern New Mexico (Fig. 1). The more complete Revuelto Creek specimen was collected from NMMNH locality 2640 in the badlands east of Revuelto Creek under the direction of A.P.H. The less complete Badlands Ranch specimen was collected from NMMNH locality 5806, a richly fossiliferous channel deposit in the badlands east of Barranca Creek, approximately 8 km to the west-northwest of the Revuelto Creek specimen, by a crew directed by A.B.H.

The Revuelto Creek specimen was found isolated in a silty mudstone typical of the more fine-grained strata in the Bull

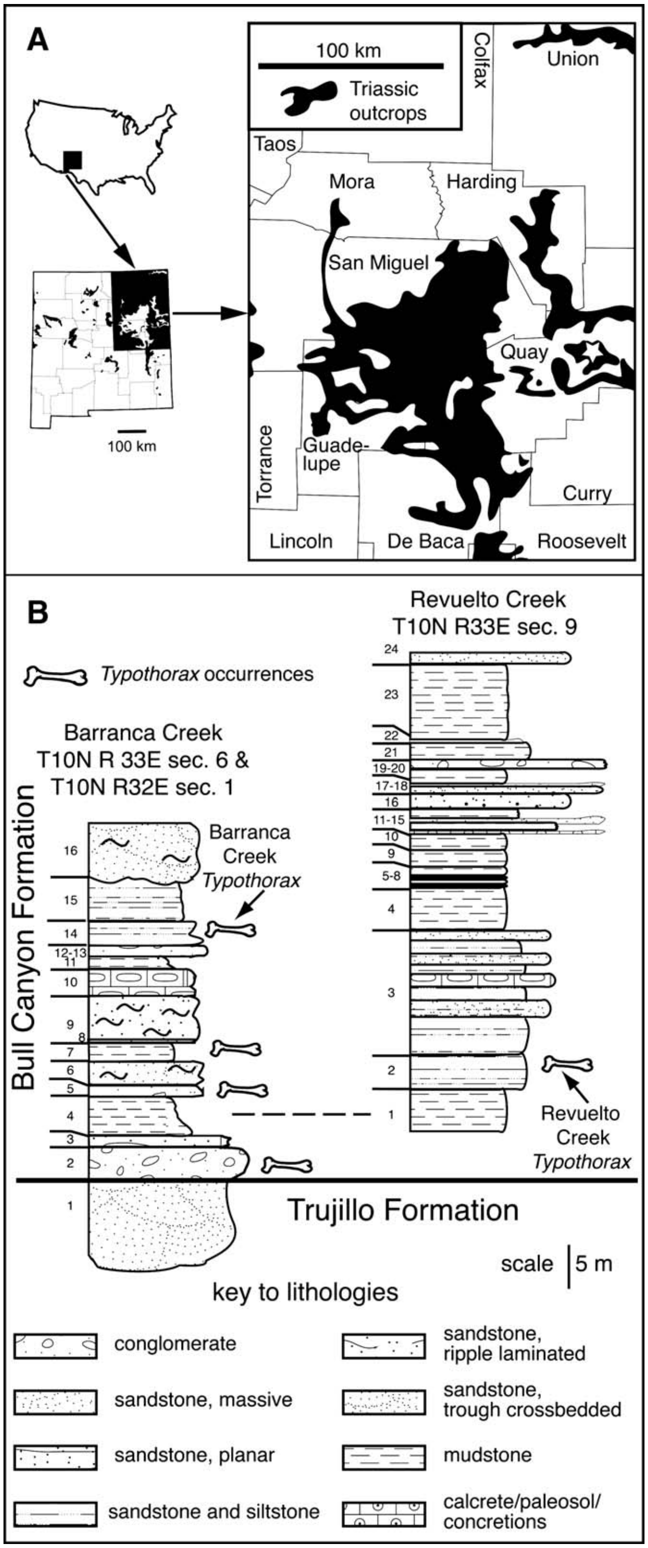

FIGURE 1. *Typothorax* localities in eastern New Mexico described in this paper. **A**, index maps and **B**, measured stratigraphic sections showing the location of the Revuelto Creek and Barranca Creek badlands outcrop belt (star) and the stratigraphic distribution of vertebrate fossils in these outcrops. For detailed descriptions of numbered stratigraphic units and correlations, see Lucas et al. (2001).

Canyon Formation. The Badlands Ranch specimen is preserved in a poorly sorted, conglomeratic, very coarse-grained sandstone, with the largest clasts ~1 cm diameter. Typical clasts are very coarse sand to pebble (2–4 mm) sized, in a matrix that is primarily medium sand. It appears that the body cavity was somewhat intact upon burial, because the conglomerate is present between the limbs and the carapace, but the ventral osteoderms and gastralia are embedded in a finer, muddier matrix (Figs. 2–3). The conglomeratic matrix is grayish red (10R4/2, coarser grains) to pale reddish brown (10R5/4, finer grains) with reduced zones that are grayish yellow green (5G7/2) to light greenish gray (5G8/1). The muddier matrix in the thorax is similarly colored but includes regions that are more of the pale reddish brown than the grayish red. This is the primary matrix visible in dorsal view (Fig. 2).

The Bull Canyon Formation in eastern New Mexico yields abundant vertebrate fossils, including redfieldiid and coelacanth fish, temnospondyl amphibians, and a variety of primarily archosaurian amniotes (Hunt, 2001). Key among these are occurrences of *T. coccinarum* and of relatively derived, pseudopalatine phytosaurs such as *Pseudopalatus*. Throughout the American Southwest these taxa typically first occur in or above the medial sandstone (Trujillo Formation in eastern New Mexico and West Texas, Sonsela Member of the Petrified Forest Formation in western New Mexico and Arizona, Moss Back Formation in Utah) of the Chinle Group (Lucas et al., 2001; Heckert et al., 2005). The vertebrate fauna of the Bull Canyon Formation in this region characterizes the Revueltian land-vertebrate faunachron (LVF) of Lucas and Hunt (1993; Lucas, 1998).

Hunt (2001) subdivided the Revueltian LVF, and the *Typothorax* skeletons described here were obtained from strata that pertain to Hunt's (2001) Barrancan sub-LVF of the Revueltian, characterized by the co-occurrence of the phytosaur *Pseudopalatus*, *Typothorax coccinarum*, and the crurotarsan *Revueltosaurus callenderi*. The Revueltian almost certainly correlates to part of the Norian on the standard global chronostratigraphic timescale (SGCS), and is traditionally considered early-mid Norian (e.g., Lucas, 1998; Lucas et al., 2007c). Riggs et al. (2003) published a U-Pb date on zircons of 211 ± 1.7 Ma for the Black Forest Bed in the Petrified Forest National Park that they considered a maximum depositional age for that unit. The Black Forest Bed overlies the first appearance datum (FAD) of *T. coccinarum* in Arizona, which is in strata correlative with the Bull Canyon Formation (e.g., Heckert and Lucas, 2002; Parker, 2006) but underlies occurrences of *Typothorax* from the Owl Rock Formation that are likely younger than those from the Bull Canyon Formation (Heckert et al., 2005; Spielmann et al., 2007). Thus these specimens are likely Norian, and probably slightly older than Riggs et al.'s (2003) estimate of the Black Forest Bed.

TAPHONOMY

Newell (1993) provided a detailed sedimentology of the Bull Canyon Formation in east-central New Mexico identifying four facies associations (A–D), from which Hunt (2001) recognized three primary taphofacies for vertebrate body fossils: (1) fragmentary, disarticulated to isolated bones in channel sandstones (Newell's [1993] facies A); (2) more complete, associated to articulated, specimens in proximal floodplain facies, including crevasse splays (facies B, C); and (3) distal floodplain/paleosol facies bearing the fossils of smaller, more terrestrial tetrapods (facies D).

The Revuelto Creek specimen was found in Newell's (1993) facies association C, which consists of fine-grained strata with numerous features (desiccation cracks, rootlet structures, reduction halos, etc) that indicate a floodplain origin (Fig. 1). Newell (1993:362) interpreted the silty mudstone encasing the specimen and others found in this facies as typical of the "distal facies equivalents of the levee deposits accumulating off the channel-belt slope during overbank and flooding episodes." In contrast, the Barranca Creek specimen does not fall neatly into any of Newell's (1993) facies. The specimen was found on a nearly stripped surface above a thin (≤1.5 m) but prominent intraformational pebble conglomerate that is overlain by a complex multistoried set of finer-grained strata, up to 6 m thick, dominated by mudstones with subordinate amounts of sandstone and conglomerate (Fig. 1). Although this is superficially similar to Newell's (1993) facies association B, we interpret this as a channel that incised into nearby floodplains and then rapidly aggraded, resulting in the burial of numerous vertebrates. This is most similar to the 'channel-hosted' assemblages of Hunt (2001) but is remarkable in that it hosts relatively complete specimens, and thus is more akin to the 'abandoned channel fill' of Behrensmeyer et al. (1992). Indeed, the 1.5-m-thick interval from the base of the conglomerate into the lowest overlying finer-grained strata has yielded at least three phytosaur skulls, the Barranca Creek *Typothorax* specimen, and at least one other incomplete carapace of *Typothorax* from a narrow ribbon of outcrop <300 m on strike across and less than 2 m thick.

The skeleton of P-56299 was collected in a single jacket, and all bones preserved except a few surface fragments remain associated as they were found during either the excavation or subsequent preparation (Figs. 2–3). Obviously, the elements that were not preserved, including the skull and much of the anterior carapace, must have weathered away prior to discovery or else were lost to scavenging and other taphonomic processes earlier. Based on the shape and condition of the skeleton in dorsal view, we hypothesize that the body was partially scavenged during Late Triassic time, with the carapace opened, probably in the vicinity of the 16th row of dorsal osteoderms (see Description) and much of the dorsal skeleton (dorsal vertebrae, ribs, and osteoderms) was therefore lost during Late Triassic time. Most of the remaining elements were probably buried with the specimen. We further hypothesize that the skeleton was actually first exposed at least once prior to the 1980s, and subsequently re-buried beneath material eroding from the south and carried across the flats by the local ephemeral drainage. Indeed, we strove to divert that drainage after discovery of the specimen in 2005, and yet by spring of 2006 not only had it reestablished itself, but also removed much of the material placed on the temporary plaster cap protecting the specimen. Supplementary Figure S1 highlights these hypotheses.

The Badlands Ranch specimen was discovered in life orientation, with the dorsal side facing upwards (Figs. 2–3). Preparation revealed that the fossil is dorsoventrally crushed but otherwise essentially undistorted (Figs. 4–5). This is in contrast to the more complete Revuelto Creek specimen, which was found lying on its right side, largely articulated, and mediolaterally crushed (Figs. 6–8). The weathered fragments of the left forelimb led to the discovery of the Revuelto Creek specimen (P-12964), so an ulna and radius were recovered as loose elements, as was a dorsal rib and vertebra found approximately 1 m away—the remainder of the specimen was collected in a single jacket (Hunt et al., 1993). Subsequent preparation revealed that the body cavity was disturbed during Late Triassic time, with much disruption and distortion of the ribs and carapace that we consider most likely the result of scavenging and, possibly, postmortem bloating (Hunt et al., 1993).

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
ARCHOSAURIA Cope, 1869
AETOSAURIA Marsh, 1884
STAGONOLEPIDIDAE Lydekker, 1887
TYPOTHORAX Cope, 1875
TYPOTHORAX COCCINARUM Cope, 1875
(Figs. 2–9)

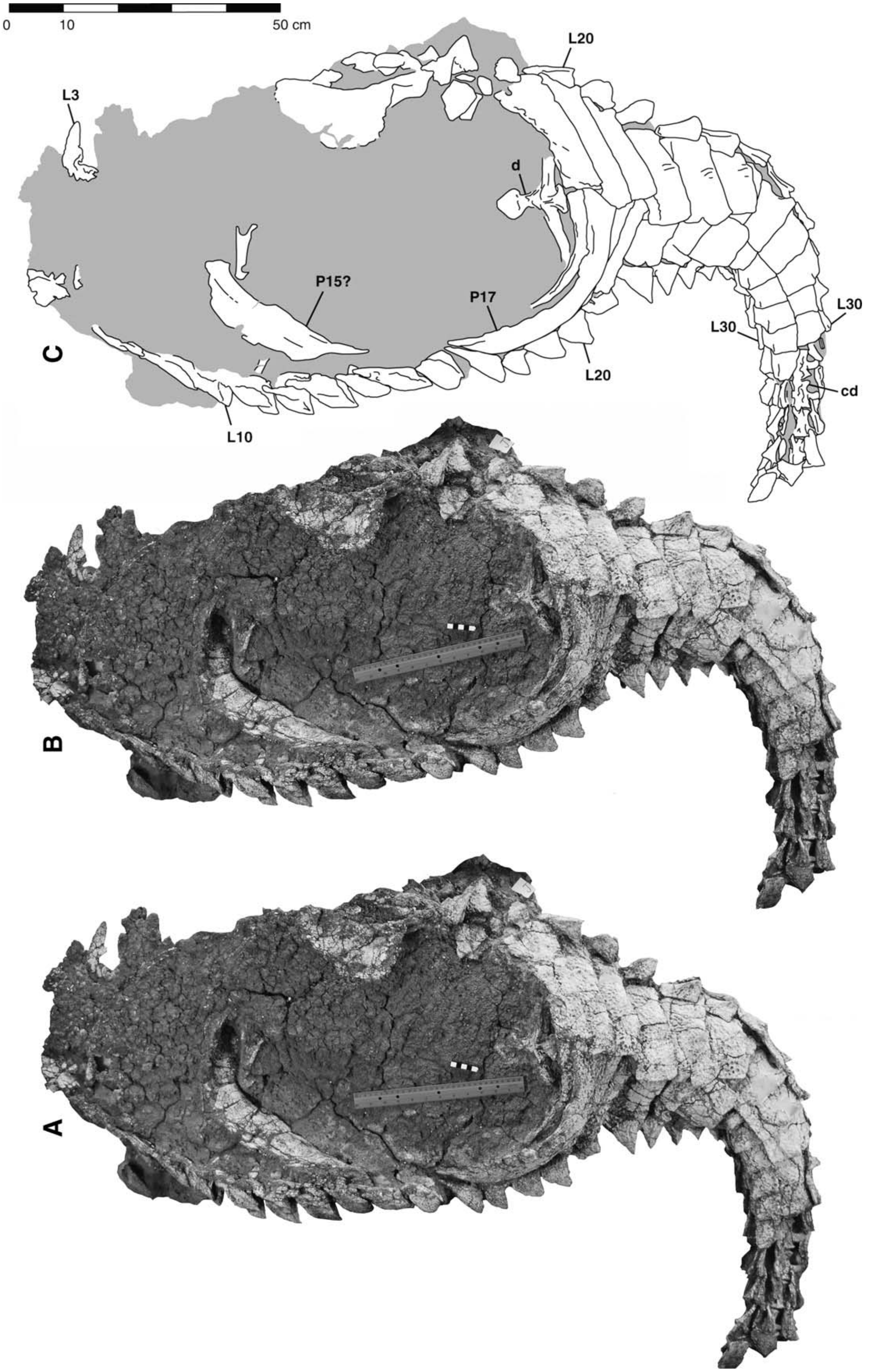

FIGURE 2. Badlands Ranch *Typothorax coccinarum*, NMMNH P-56299. **A**–**B**, stereopair in dorsal view, **C**, interpretive sketch. **Abbreviations**: **cd**, caudal vertebrae; **d**, dorsal vertebra; **L3**, third lateral (cervical 'spike') osteoderm; **L10**, tenth lateral (thoracic) osteoderm; **L20**, twentieth lateral (sacral) osteoderms; **L30**, thirtieth lateral (mid-caudal) osteoderms; **P15?**, ?fifteenth paramedian (mid-thoracic) osteoderm; **P17**, seventeenth paramedian (posterior thoracic) osteoderm. Scale in 10-cm increments.

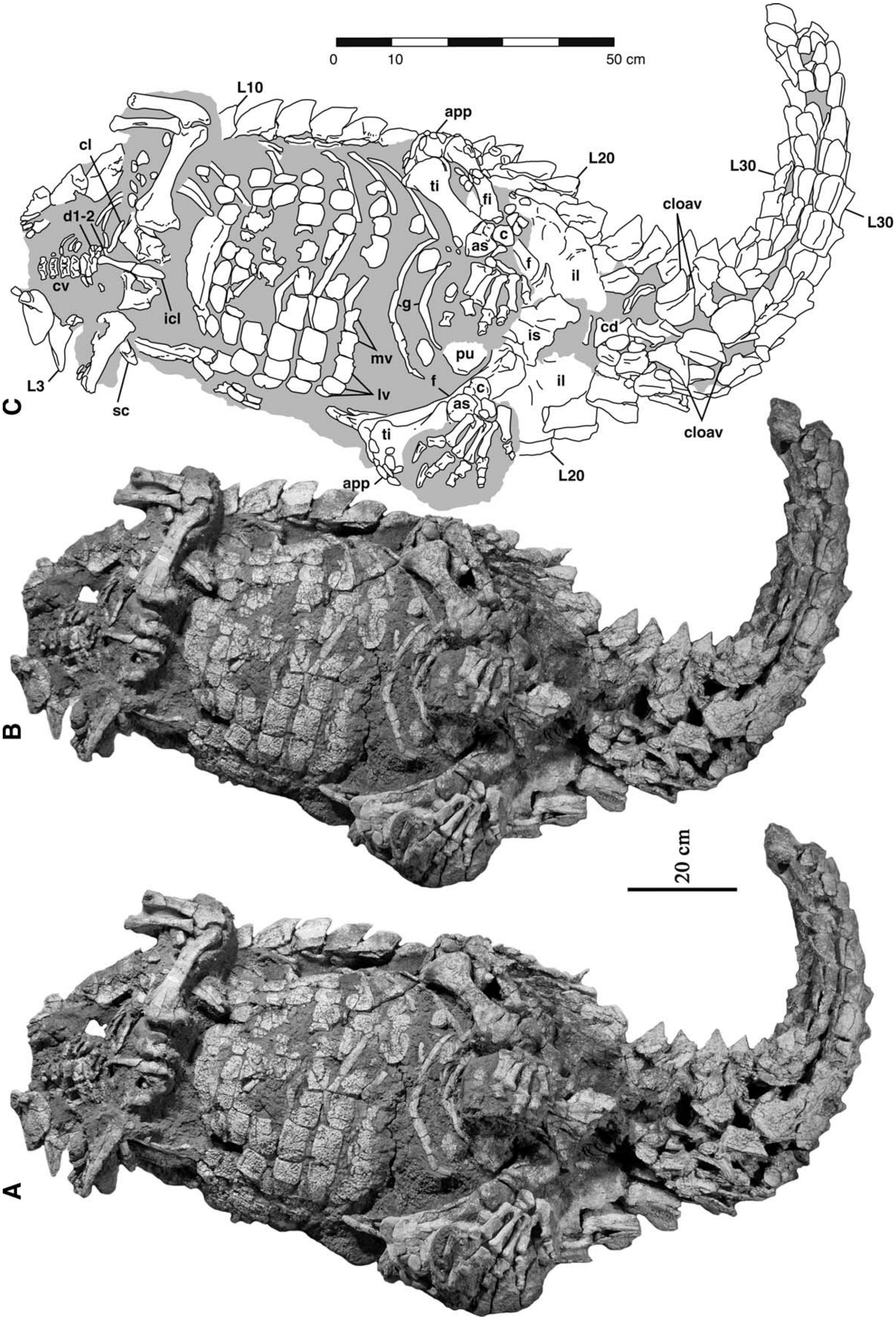

FIGURE 3. Badlands Ranch *Typothorax coccinarum*, NMMNH P-56299. **A**–**B**, stereopair in ventral view, **C**, interpretive sketch. **Abbreviations**: **app**, appendicular osteoderms; **as**, astragalus; **c**, calcaneum; **cd**, caudal vertebrae; **cl**, clavicle; **cloav**, ‘spiked’ cloacal ventral osteoderms; **cv**, cervical vertebrae; **d1–2**, dorsal vertebrae 1 and 2; **f**, femora; **fi**, fibula; **g**, gastralia; **icl**, interclavicle; **il**, ilia; **is**, ischia; **L3**, third lateral (cervical ‘spike’) osteoderm; **L10**, tenth lateral (thoracic) osteoderm; **L20**, twentieth lateral (sacral) osteoderms; **L30**, thirtieth lateral (mid-caudal) osteoderms; **lv**, lateral thoracic ventral osteoderms (three columns per side); **mv**, medial thoracic ventral osteoderms (two columns per side); **pu**, pubis; **sc**, scapula; **ti**, tibia. Scale in 10-cm increments.

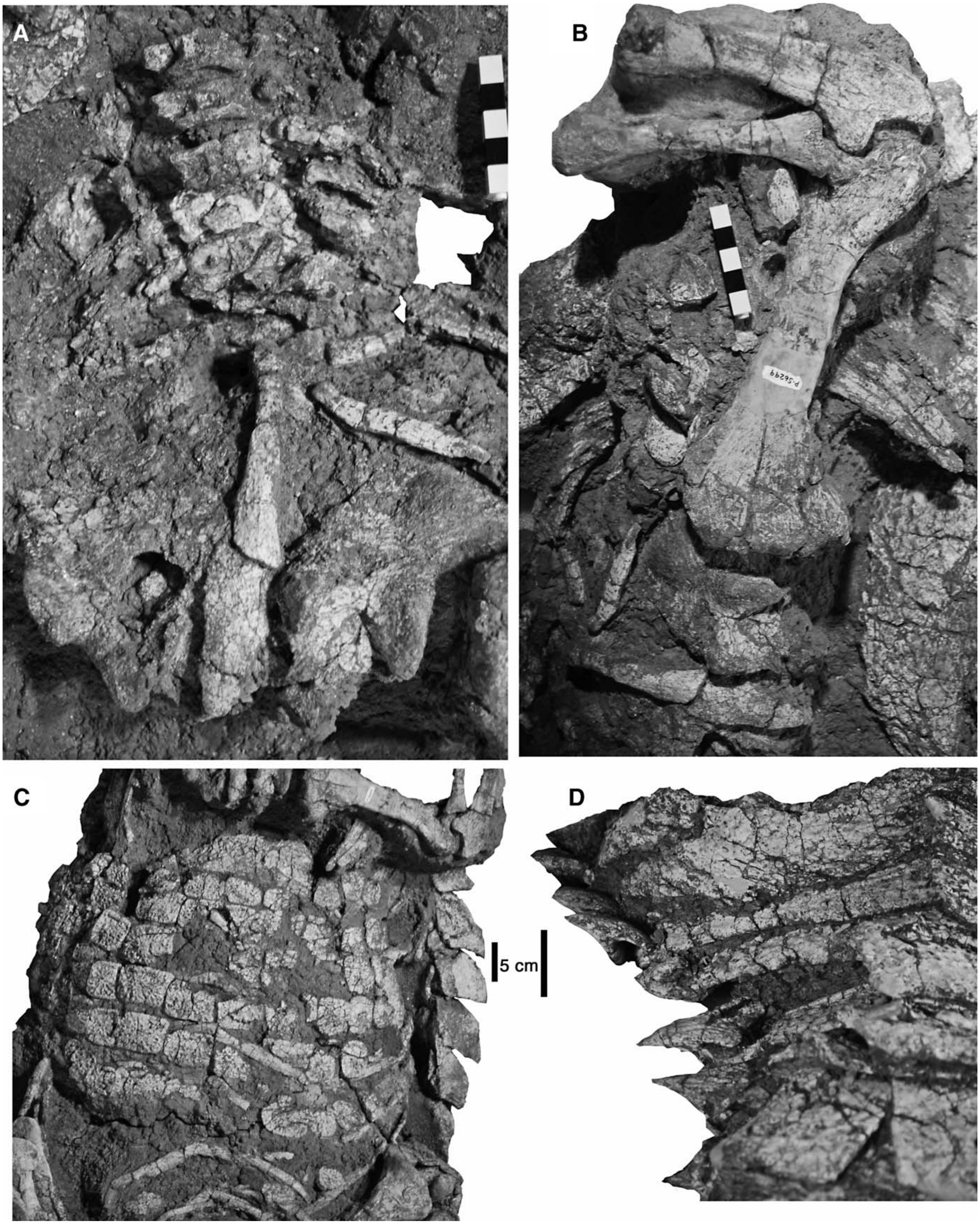

FIGURE 4. Badlands Ranch *Typothorax coccinarum*, NMMNH P-56299. **A**, close-up of cervical vertebral series and pectoral girdle in ventral view. **B**, close-up of left forelimb in ventral view. **C**, ventral thoracic ('belly') osteoderms and gastralia in ventral view. **D**, oblique posterior view of left lateral armor showing tight angle between dorsal and lateral flanges of lateral osteoderms. Scale bars in A and B are in 1-cm increments, scales in C–D equal 5 cm.

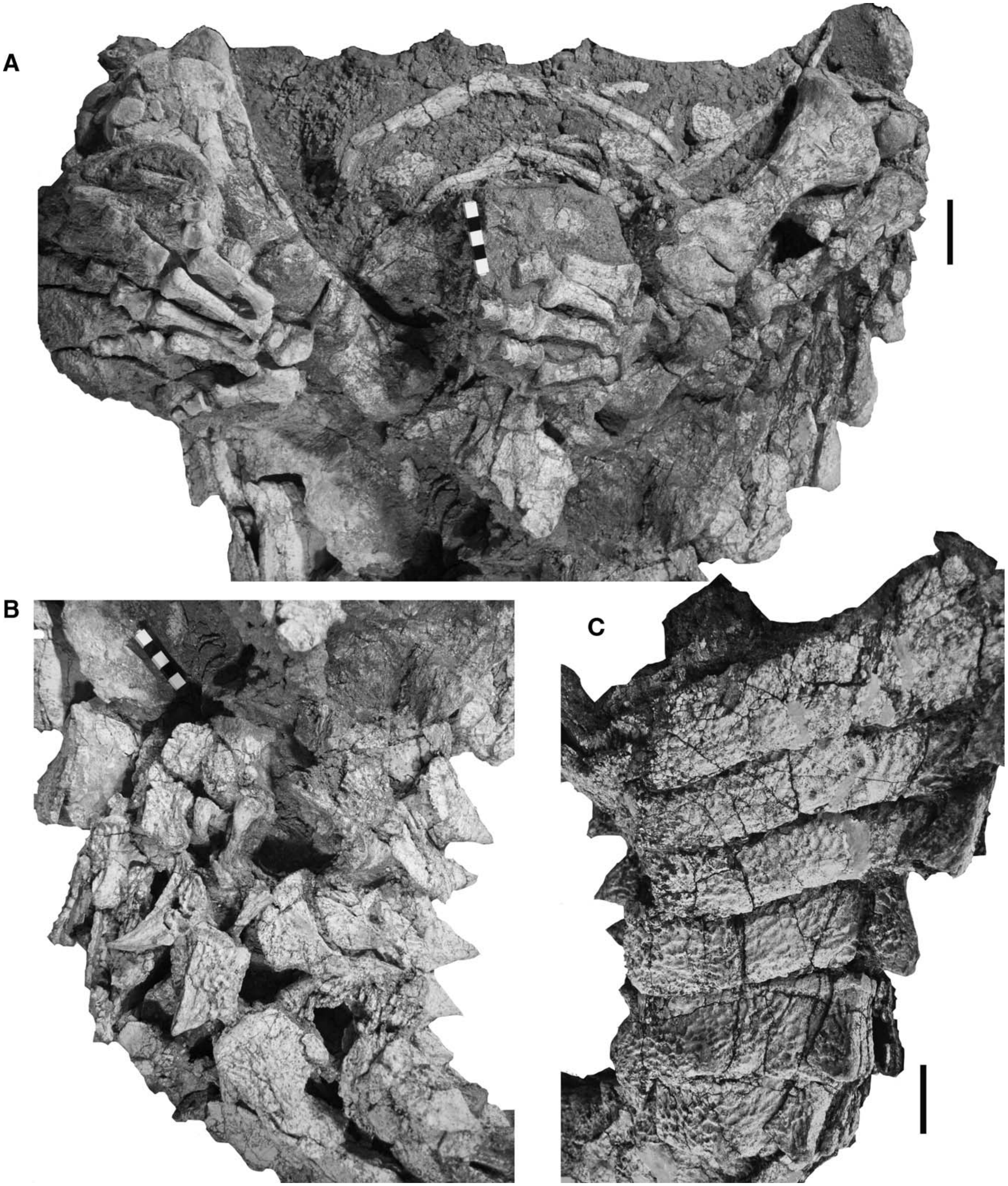

FIGURE 5. Badlands Ranch *Typothorax coccinarum*, NMMNH P-56299. **A**, close-up of hind limbs in ventral view. **B**, close-up of armor in the region of the cloacal vent in ventral view. **C**, Close-up of caudal osteoderm armor at the base of the tail in dorsal view. Scale bars in A and B are in 1-cm increments, scale in C equals 5 cm.

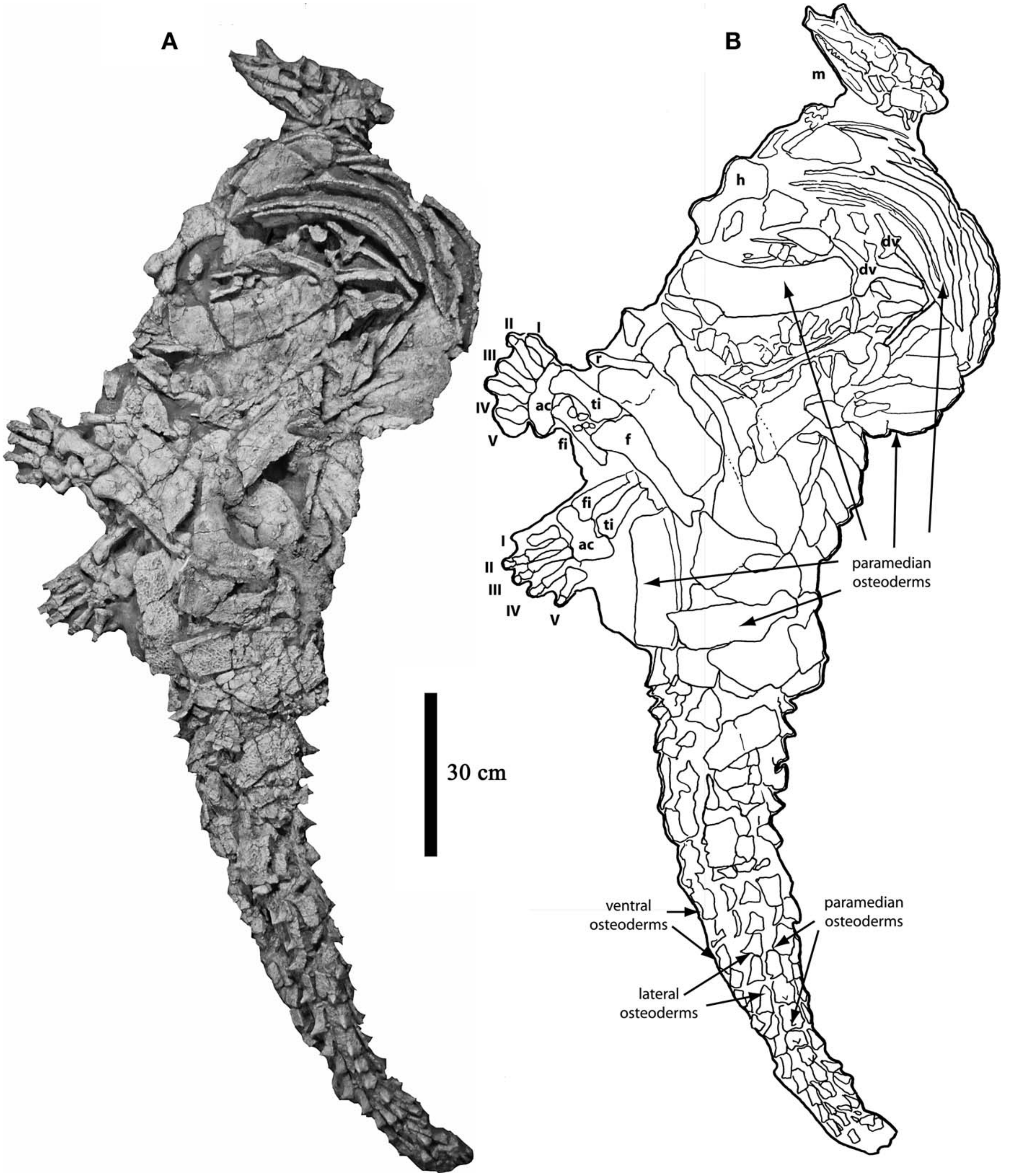

FIGURE 6. Revuelto Creek *Typothorax coccinarum*, C-4638, cast of NMMNH P-12964 in left lateral view. **A**, photograph, and **B**, interpretive sketch. **Abbreviations**: **ac**, astragalus and calcaneum; **dv**, dorsal vertebra; **f**, femur; **fi**, fibula; **h**, humerus; **m**, mandible; **r**, radius; **ti**, tibia. Pedal digits indicated with Roman numerals.

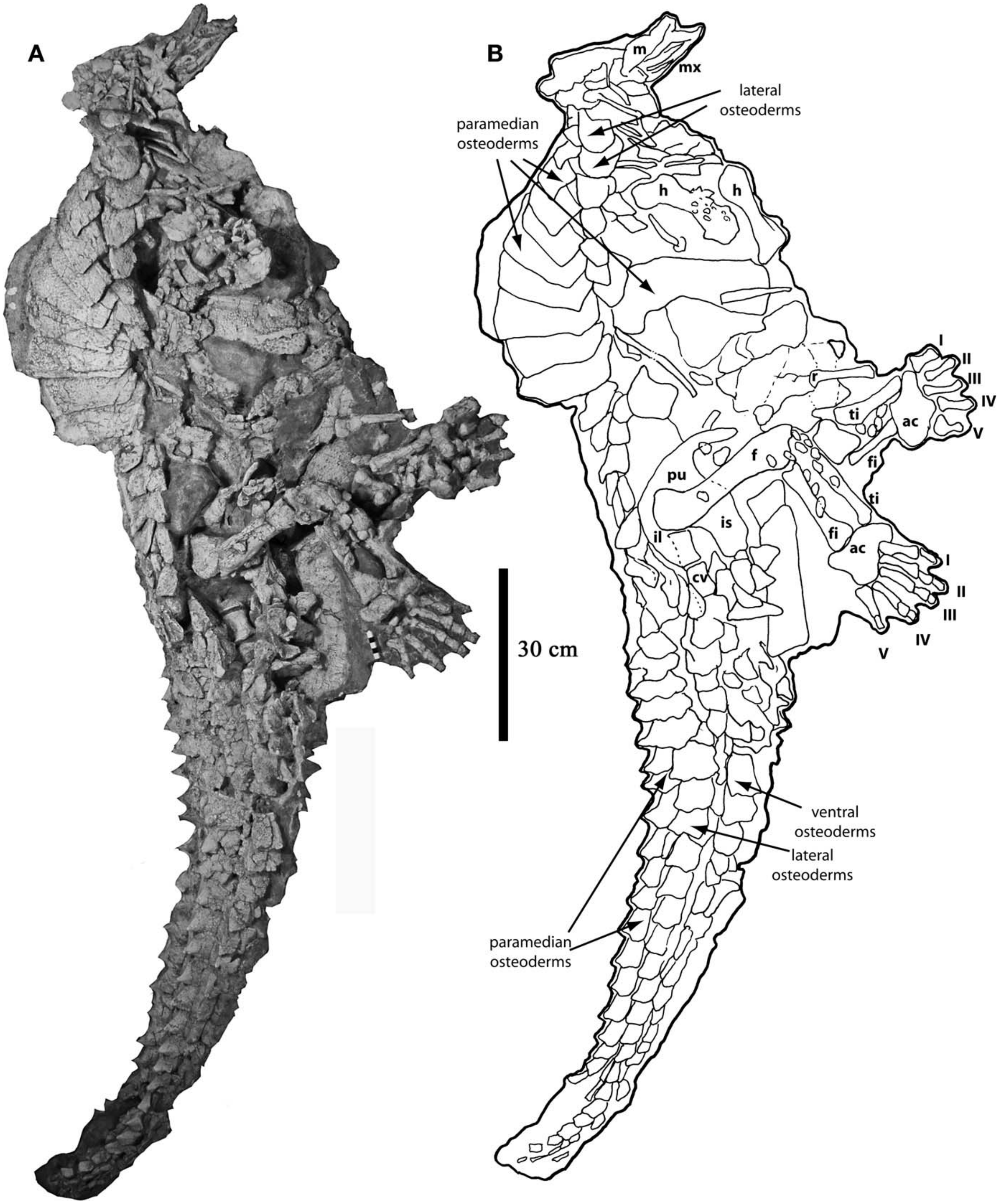

FIGURE 7. Revuelto Creek *Typothorax coccinarum*, C-4638, cast of NMMNH P-12964 in right lateral view. **A**, photograph, and **B**, interpretive sketch. **Abbreviations**: **ac**, astragalus and calcaneum; **cv**, caudal vertebra; **f**, femur; **fi**, fibula; **h**, humerus; **il**, ilium; **is**, ischium; **m**, mandible; **mx**, maxillae, **pu**, pubis; **r**, radius; **ti**, tibia. Pedal digits indicated with Roman numerals.

Revised Diagnosis—This species is distinguished from other aetosaurs by: very broad dorsal paramedian osteoderms (maximum width:length > 4:1) with ornamentation consisting of a random pattern of pits and prominent ventral keels that extend across the entire width of the osteoderm; no more than five rows of cervical paramedian and lateral osteoderms; caudal ventral osteoderms that begin posterior to the fused ischiatic symphysis and have recurved, ventrally directed spikes; spiked caudal ventral osteoderms in close proximity to the cloacal opening (vent); and dorsoventrally tall ilium with its highly unusual constriction above the acetabulum. Also differs from *Coahomasuchus* and *Aetosaurus* in that there is almost no ventral armor over the pelvic area and has a more open cloacal vent (modified from Heckert and Lucas, 2000).

Referred Specimens—NMMNH P-12964, nearly complete, largely articulated skeleton termed the Revuelto Creek specimen from NMMNH locality 2640; NMMNH P-56299, nearly complete, articulated skeleton termed the Badlands Ranch specimen lacking the skull from NMMN locality 5806.

Locality and Horizon—Both NMMNH locality 2640 and 5806 are low in the Upper Triassic Bull Canyon Formation of Quay County, eastern New Mexico (Fig. 1). These specimens are of Revueltian (Norian) age.

Comment—Although the Badlands Ranch specimen is less complete, it is the principal fossil described here because much of what is preserved is essentially in life position. The more complete Revuelto Creek specimen was, regrettably, irrevocably damaged during an attempt to mold and cast it, and thus requires repreparation before meriting a full osteological description of the surviving material. Accordingly, we reconstruct *Typothorax coccinarum* Cope based on the available materials, which include the Badlands Ranch specimen (P-56299—Figs. 2–5), high-fidelity casts of the Revuelto Creek specimen (NMMNH C-4638, complete part/counterpart—Figs. 6–8; C-4639, skull, incomplete dorsal armor, and incomplete tail) and, in some cases, its surviving bones (NMMNH P-12964).

Discussion—The lack of a 1:1 correspondence between cervical vertebrae and cervical rows of paramedian and lateral osteoderm is demonstrated in *Typothorax*, but may have a wider distribution within Aetosauria (Parker, 2008; see description of cervical lateral osteoderms below for a complete discussion). This feature can only be assessed with continued collection of more complete material of all aetosaur taxa.

DESCRIPTION OF NEW MATERIAL

Long and Murry (1995) provided a serviceable osteology of elements of *Typothorax* known to them, and Martz (2002) expanded upon this and wrote extensively on additional elements, although these were largely isolated or at best associated and, in some cases, may not pertain to *T. coccinarum*. Lucas et al. (2002) described a partial skeleton of *T. antiquum*, highlighting similarities and differences between *T. coccinarum* and the holotype and referred material of *T. antiquum*. Thus, we do not attempt to provide a comprehensive osteology of *Typothorax* here, but instead highlight morphology not available to previous authors and its paleobiological implications.

The Badlands Ranch specimen (NMMNH P-56299) is preserved on a block that is ~148 cm long and ~66 cm wide across the pelvis. The preserved skeletal length is approximately 177.5 cm from the anterior-most edge of the first preserved cervical vertebra to the end of the articulated armor. Comparison to the similar-sized NMMNH P-12964 indicates that the skull would have been approximately 30 cm long and that the tail should have continued for another 45 cm, yielding a total skeletal length of approximately 2.5 m.

In ventral view P-56299 preserves all or part of five cervical vertebrae and ribs (but not the atlas-axis complex), two dorsal vertebrae, the interclavicle, much of the left and fragments of the right clavicle, both coracoids, scapulae, and humeri, the left ulna and radius, at least six dorsal ribs and six axial gastralia, all or part of several lateral gastralia, much of the pelvis (but only parts of both ilia, both ischia, and the right pubis are visible), both femora, both tibiae, the left fibula, both astragali, both calcanea, some tarsals, all metatarsals, some phalanges, and parts of three caudal vertebrae in addition to extensive armor (Fig. 3). The osteoderms visible in ventral view include parts of at least three dorsal paramedians and several cervical lateral osteoderms, a continuous series of 29 left lateral osteoderms from the cervical series to the distal tail, 10 columns of thoracic ventral osteoderms in as many as six rows and four columns of ventral osteoderms extending down the tail as well as abundant appendicular armor on all of the appendages.

Much less of the specimen is visible in dorsal view (Fig. 2). Anteriorly a few cervical and thoracic paramedian osteoderms are evident, as the extensive series of left lateral and some right lateral osteoderms. Paired dorsal paramedian osteoderms are only complete from slightly anterior to the sacrum through the mid-caudal region, but both lateral columns of caudal osteoderms are well preserved, and parts of one dorsal and four caudal vertebrae are visible on this side. Subsequent to preparation of the ventral side, the dorsal side was prepared as far as possible, but it was deemed necessary to leave a thin veneer of matrix to retain the structural integrity of the specimen.

Anatomical Regions

In the following sections we describe the skeleton by region, beginning with the axial skeleton, followed by the appendicular skeleton and concluding with the armor. We describe the armor separately from the axial skeleton, as its origin is dermal bone so it is distinct from the endoskeletal elements, even though there are obvious links between, for example, some vertebrae and the armor as well as various appendages and the armor covering them. We also feel justified in treating the armor separately because it is the basis of much taxonomic and phylogenetic information, and has been the focus of much recent work on aetosaurs (e.g., Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 2000, 2003; Harris et al., 2003a, 2003b; Parker, 2007). Tables of measurements are provided in the Supplementary Data.

Axial Skeleton

Five cervical centra and parts of two dorsal centra are visible in ventral view (Fig. 4A). The neural arch of a single dorsal (apparently the last presacral) vertebra is visible in anterior view on the dorsal side (Fig. 2). Parts of three proximal caudal vertebrae are visible from the ventral side (Figs. 3, 5B), and parts of several mid-to-distal caudal vertebrae are visible in lateral view from the dorsal side (Fig. 4).

Cervical Vertebrae—Neither the atlas nor the axis is preserved. The first three preserved centra are clearly cervicals, and are less than half as long as wide, with the prominent longitudinal ventral keels separating deep ventral excavations (sulci) (Fig. 4). The parapophyses are robust with a deep excavation between them and the corresponding diapophyses. Hunt et al. (1993:209) described the Revuelto Creek cervicals as “80% shorter than the longest dorsal,” which Hunt (2001) clarified as only 20% as long as the longest dorsal. Long and Murry (1995) also indicated that in *Typothorax coccinarum* the cervical vertebrae are extremely short and thus more than twice as wide as long. We also note that they are extremely small relative to other vertebrae, particularly the proximal caudal centra, which are approximately four times longer. Indeed, the cervical vertebrae are so small that they would likely be mistaken for juveniles, if not another taxon, if found disarticulated from the rest of the skeleton. Remnants of small, thin cervical ribs are evident, especially on the left side of these centra. The first preserved centrum shows that the

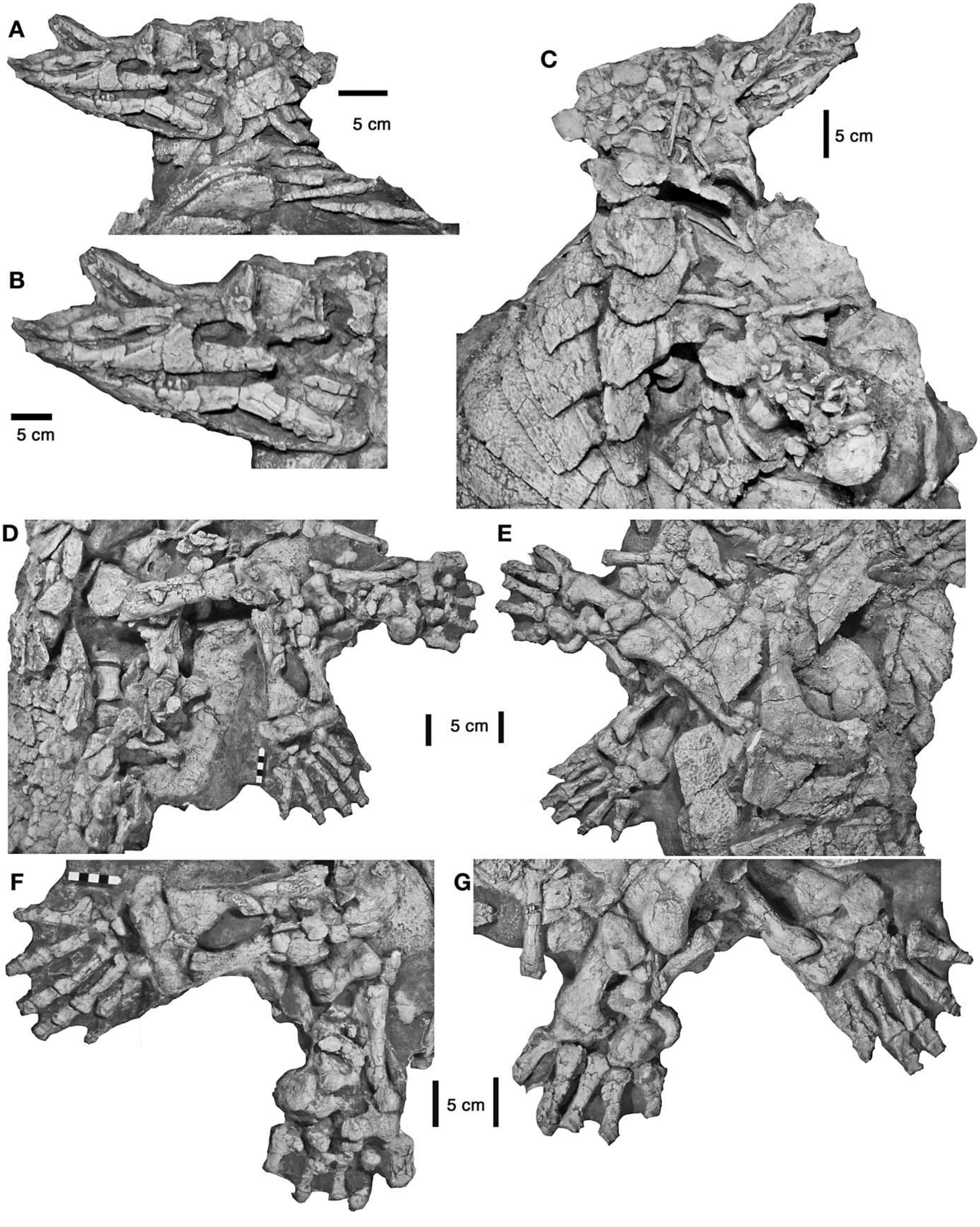

FIGURE 8. Revuelto Creek *Typothorax coccinarum*, C-4638, cast of NMMNH P-12964. **A**–**B**, left lateral views of the skull and anterior torso; **C**, skull and anterior torso in right lateral view; **D**–**E**, hind limbs in **D**, right lateral to dorsal views and **E**, left lateral views; **F**–**G**, close-ups of the feet in **F**, right lateral, and **G**, left lateral views. All scales equal 5 cm.

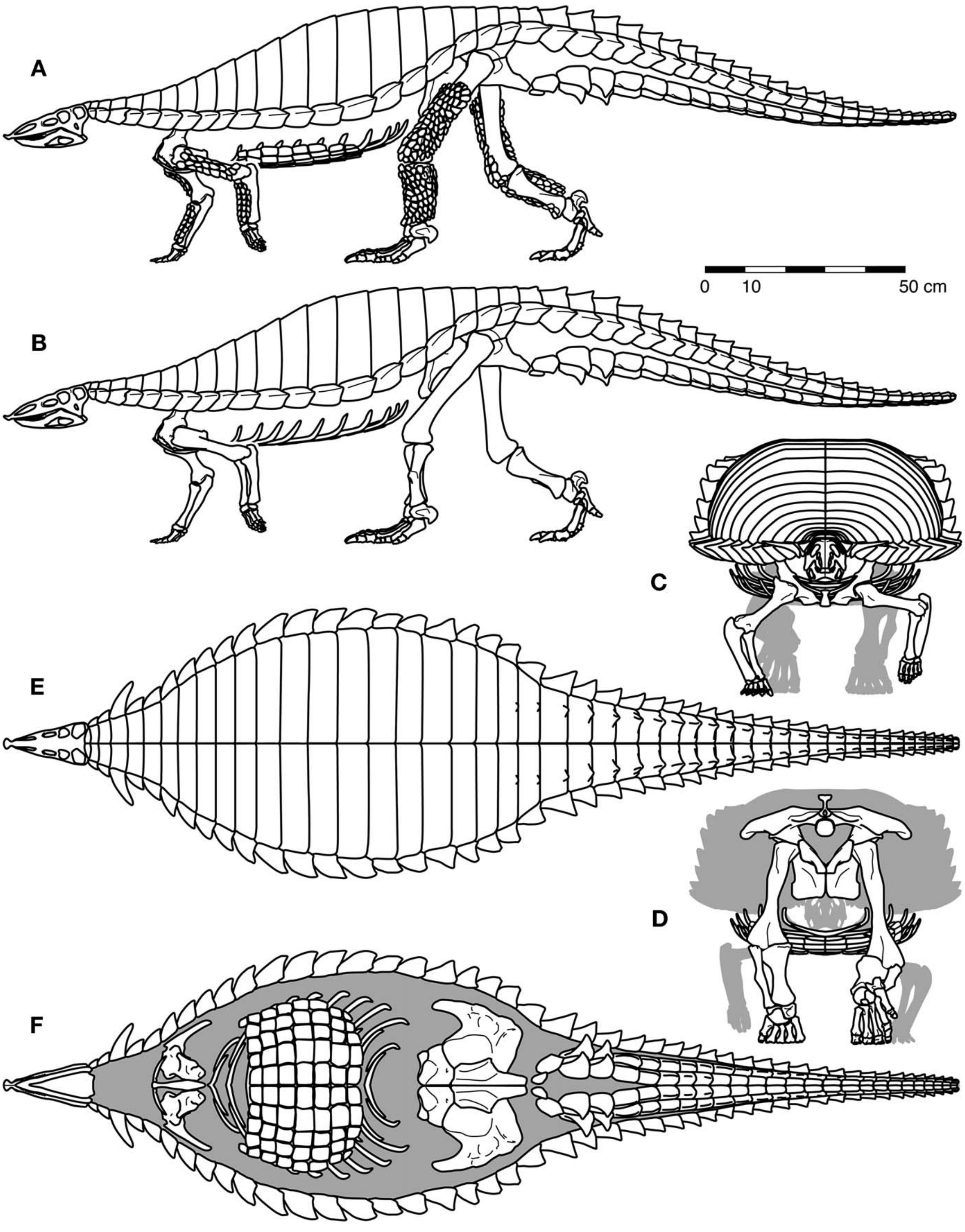

FIGURE 9. Reconstructions of *Typothorax coccinarum* based primarily on the Barranca Creek specimen, NMMNH P-56299, with the skull and some other details from NMMNH P-12964 and manus from MCZ 1488. **A**, lateral view of the skeleton with appendicular and ventral thoracic armor; **B**, lateral view of the skeleton without appendicular or ventral thoracic armor; **C**, anterior view of the skeleton; **D**, posterior view of the skeleton showing pelvic girdle and hindlimbs; **E**, dorsal view of the skeleton; **F**, simplified ventral view showing skull, girdles, gastralia, and lateral and ventral osteoderms.

articular faces of the cervicals are also much wider than tall. The fourth and fifth preserved centra are larger and probably mark the transition to the dorsal portion of the column. These centra are significantly larger, longer, and more robust. The fifth preserved vertebra has a broad transverse ridge connecting the parapophyses, restricting the ventral keel to the posterior half of the centrum. This is the last well-preserved centrum and, based on the abrupt increase in the size of ribs articulating with the following vertebrae, we consider this the last cervical centrum. The preserved centra thus appear to approximate cervicals 5–9 and dorsals 1–2 following Sawin (1947) and Walker (1961), who considered aetosaurs to have nine cervical centra. We have difficulty correlating these vertebrae to the specimens illustrated by Long and Murry (1995:figs. 102–103), because their figure 103 appears to show vertebrae as posterior as centrum 14 with parapophyses on the centra.

Dorsal Vertebrae—Portions of two anterior dorsal centra are visible in ventral view (Fig. 4A), and the last dorsal vertebra is partially visible in anterior view on the dorsal side (Fig. 2). The anterior-most dorsal (sixth preserved centrum) is poorly preserved, but is somewhat larger and longer than the preceding cervical centra. The anteroventral margin of a seventh centrum is barely visible dorsal to the pectoral girdle (Fig. 4A). The exposed, most posterior dorsal vertebra reveals the architecture of the articulation of the neural arch with the overlying dorsal paramedian osteoderms (Fig. 2). The neural arch is low, and the neural spine is transversely broadened to buttress the osteoderms at the midline. The transverse processes diverge and contact the osteoderm more laterally, lateral to the boss (center of ossification of Martz, 2002). From here the corresponding rib then buttresses the osteoderm. Large dorsal ribs are evident in ventral view, one of which articulates with the seventh exposed centrum (second dorsal). Two of these ribs are probably the proximal ends of the two ribs that emerge posterior to the humerus on the left side.

Caudal Vertebrae—The best exposed proximal caudal is probably the second, and is 55 mm long with an even wider (~59 mm) anterior articular surface; it constricts to a waist that is less than 34 mm across (Fig. 6B). The first preserved chevron articulates with this vertebra. Distal caudals exposed in lateral view are typically archosaurian in that they are relatively long with low neural arches and reduced transverse processes (Figs. 2–3).

Ribs—Most of what can be said about the ribs has been mentioned with the corresponding vertebrae. Cervical ribs are exceedingly delicate, appear relatively short, and are preserved projecting laterally to those vertebrae (Fig. 4A). Dorsal ribs project more posteriorly, and indeed the first two begin well anterior to the pectoral girdle yet project significantly posterior to it. Some of this is certainly due to taphonomic effects, but it still implies unusual rib architecture for *Typothorax*. The majority of the dorsal ribs are concealed from view by the armor, but the edges of several are evident along the left side in ventral view (Fig. 3).

Gastralia—As is typical in archosaurs, the gastralia of *Typothorax* are in three columns—an axial column that is convex anteriorly, and two flanking columns of less robust elements (Figs. 3, 4C). In this specimen the lateral elements are preserved posterior to the medial elements, although this is probably at least partly an artifact of crushing. Unlike the condition in phytosaurs (Camp, 1930; Long and Murry, 1995), these gastralia are not closely interlocked. Instead each row is widely spaced at 40–50-mm intervals. In ventral view they are flattened medially and rounder away from the center. The most posterior of the gastralia sets is the best preserved and exposed, and shows the two lateral elements almost completely overlapping the medial element.

Pectoral Girdle and Forelimb

The Badlands Ranch specimen is notable in preserving a relatively intact pectoral girdle (Fig. 4A), the first for a North American aetosaur, as well as one well-preserved and one fragmentary humerus and the most complete ulna and radius known for *Typothorax* (Fig. 4B). Measurements of the major appendicular elements (some following Martz, 2002) are found in the Supplementary Data.

Interclavicle—The interclavicle is an elongate element that is extremely thin anteriorly, widening to a substantial bulge posteriorly before tapering to a rounded point (Figs. 3, 4A). Walker (1961) described this element in *Stagonolepis* and Schoch (2007) in *Aetosaurus*, but it was not known from North American aetosaur taxa until this study. The element is roughly five times longer (121.1 mm as preserved) than the distal bulge is wide (23.7 mm wide at its maximum point). The posteriorly widening blade or bulge occupies more than half the distal length, is rhomboid in ventral view, and thin in lateral view. As preserved, the wide points correspond to the position of the subglenoid pillars on the coracoid (Figs. 3, 4B), although it is somewhat under (dorsal to) the coracoid on the left and above (ventral to) it on the right. This element is gracile relative to that of phytosaurs, and is 11.6 mm wide anteriorly, and only about 8.1 mm wide at its posterior-most point, but is proportionately more robust than that of *Aetosaurus*, which lacks the distal swelling (Schoch, 2007).

Clavicle—The proximal half (66.7 mm long as preserved) of the left clavicle is preserved and is sigmoidal in ventral view (Fig. 4A–B). It appears that it was slightly concave anteromedially and convex posterolaterally. The proximal end is narrow (7 mm wide), blunt, and round in cross-section. Between the interclavicle and the scapula it widens slightly (to 9.4 mm) and becomes more ovoid in cross-section. We note that there is a significant disparity in size and morphology between this clavicle and the incomplete element described by Martz (2002) as a clavicle of *Typothorax*.

Scapula—Neither scapula is easily seen beneath other, more ventral or distal elements (Fig. 3). The right scapula is at least 50 mm across at the glenoid where it presumably contacts the coracoid, although the surface is not preserved. The broken cross-section of the right scapular blade protrudes posterior and dorsal to the right humerus. The blade is robust (>19 mm thick) and ovoid in cross-section. The left scapula must lie directly under the humerus given the proximity of the dorsal ribs to the specimen, but it is not visible.

Coracoid—Both coracoids are visible in ventral view, but only the left is preserved well enough to permit some description and measurements (Fig. 4A–B). The total length, estimated on the left side, is slightly more than 100 mm, and could be as much as 126 mm. This element is more than 50 mm long and 5 mm thick at the glenoid, which is heavily buttressed by the glenoid lip, and 56.6 mm deep at the subglenoid pillar. As Long and Murry (1995) observed, the most striking feature of the coracoid of *Typothorax* is the strong, ventromedially directed subglenoid pillar that is transverse to the animal's long axis in ventral view (Fig. 4A–B). This feature is a prominent proximo-distal (or lateromedial) ridge up to 37 mm long that tapers to ~11 mm wide before expanding again to 19 mm across the ventral margin, where it is strongly thickened (to ~17 mm). The coracoid foramen is more anterior and slightly ventral to the position seen in the specimen illustrated by Long and Murry (1995:fig. 104).

Humerus—The right humerus is crushed, weathered, and missing its distal end, but the left humerus is relatively complete and better preserved (Fig. 4B). Part of the left humeral shaft was lost during recovery of the specimen, but it was reconstructed in situ during preparation (using the impression in the matrix as a guide) so the element accurately represents the original morphology. Proximally the humerus is slightly expanded both anteriorly and posteriorly. The deltopectoral crest is weathered but prominent, thin, and elongate, extending along the anterior 50 mm of the proximal humerus, with a prominent, 12-mm-wide bulge proximally. The humerus tapers to a thin midshaft with an ovoid cross-section, then expands distally. The entepicondyle (ulnar condyle) is smaller and more proximal than the ectepicondyle (radial condyle). The entepicondylar fossa/foramen is hidden by matrix. The ectepicondyle is somewhat buttressed ventrally. The entepicondyle is expanded posteriorly and thickened dorsoventrally.

Ulna—Only the left ulna, lacking part of the distal end, is preserved (Fig. 4B). The element is relatively stout—only three times as long as wide across the olecranon, which is at least 18 mm thick and L-shaped in lateral view, forming one of the sharpest angles seen in the ulnae of aetosaurs. Distally the shaft bears a longitudinal ridge on its dorsomedial surface. The distal end swells slightly and is ovoid in distal view. This is a more robust element than the ulna of *Typothorax antiquum* (Lucas et al., 2002:fig. 7).

Radius—The left radius is displaced dorsally and anteriorly, but otherwise intact (Fig. 4B). The radius is much more gracile than the ulna, but the proximal and distal ends are still roughly equal in size. The proximal end is thinner anterodorsally and thicker posteroventrally. The bone tapers rapidly from this articulation and is ~7 times as long as its minimum width. The distal end is stout, blunt, and slightly expanded anterodorsally.

The radius may be pathological. The dorsal surface appears damaged and the proximal third of the lateral surface bears crushed and pitted bone that is unlike the remainder of the specimen (Fig. 4B). In particular, the middle of the lateral surface bears an unusually rugose, irregular texture and a ventral excavation that is elongate, narrow, and deep (~22 × 4 × 3 mm). This texture may represent a lesion or other response to trauma or infection (cf. Rothschild and Martin, 2006). A more distal pit on the lateral side that is more shallow and subcircular (~13.1 × 8.7 mm) is probably a taphonomic artifact.

Pelvic Girdle and Hind Limb

Presumably all pelvic elements are preserved, but the articulated hind limbs obscure most of the sacrum and pelvis, especially on the right side (Figs. 3, 5A). All that is visible and identifiable is much of the left iliac blade and part of the right, portions of both acetabula, part of the right pubis, and the posterior portions of the paired ischia. Thin, orange, iron-rich concretions cover much of the pelvic girdle, especially the left ilium, more so than the rest of the skeleton. Almost all of both hind limbs are preserved, but articulation obscures many of the elements and some of the pedal phalanges are missing. Measurements of these bones are provided in the Supplementary Data.

Ilium—The ilium of *Typothorax*, especially *T. coccinarum*, is the most derived among aetosaurs. The lateral (actually ventral in life) surface and dorsal (lateral) margin of the ilium are visible on the left side. A similar, but smaller and poorly preserved portion of the ilium is present on the right side.

Upon first examination, the ilium appears much larger and more robust than previously reported in *Typothorax coccinarum* (e.g., Long and Murry, 1995:figs. 106–107). However, this is an artifact of the dorsoventral crushing of the specimen. Normally a 'lateral' view of a *Typothorax* ilium does not show the bulk of the posterior blade, as it is directed dorsomedially out of the plane with the rest of the blade. Thus, when crushed as in P-56299, it gives the appearance of being a much more massive element than do the isolated ilia illustrated by Long and Murry (1995). The anterior blade is difficult to distinguish beneath appendicular armor of the femur and therefore only visible in dorsal (distal) view, but, if identified properly here, then the arc of the entire blade is approximately 30 cm. The anterior supracetabular buttress is visible as a poorly developed ridge that widens slightly toward the top of the ilium. Much more pronounced is the posterior, supracetabular buttress, which forms a broad, gently convex ridge that is also expressed as a strong thickening of the iliac blade from as few as 10 mm to nearly 18 mm. These are the 'iliac blade buttresses' of Martz (2002).

Pubis—A fragment of the right pubic boot is visible between the left pes and the right femur (Fig. 5A), but no morphological details are discernable.

Ischium—The posterior, fused portions of the combined ischia are well preserved, but the anterior portion is hidden beneath the left pes (Figs. 3, 5A). The preserved symphyseal length of the ischia is ~102 mm. Overall, the ischia are strikingly short and somewhat gracile relative to the ilium.

Femur—Both femora are preserved, but the right is more easily studied (Figs. 3, 5A). The femur is elongate, slightly more than 1.5 times as long as the humerus. Previous authors have noted it as 'gracile' or 'delicately constructed' (e.g., Long and Murry, 1995:104), and it is, relative to robust aetosaurs such as *Desmatosuchus*. However, it also corresponds to Benton and Clark's (1988) 'pillar-erect' model (see also Parrish, 1986) and has well-developed proximal condyles, including the additional 'lesser trochanter' on the anterior surface documented by Long and Murry (1995; anterior trochanter of Martz, 2002). The fourth trochanter forms a relatively indistinct, rounded swelling on the posterior surface that is actually fairly substantial on disarticulated comparative specimens. The femur also bears a large, medially developed head as well as thick, well-developed condyles distally.

The femora are twice as long as the tibiae (Figs. 3, 5A, 6–7), and are anteroposteriorly compressed in P-56299. The left femur is largely buried beneath more distal elements, but is at least 291.8 mm long, with a distal end that is at least 97.9 mm wide. There is an extremely prominent lateral condyle on the distal end, which fits into a notch on the proximal tibia. This articulation also effectively pushes the fibula down to the calcaneum and restricts the knee joint to a 'hinge' as described by Parrish (1986).

Tibia—The tibia is particularly short and stout (proximal end half as wide as the element is long), and it articulates with a massively robust ankle (Figs. 5A, 8D–E). The proximal head is broadened and nearly as wide proximally as it is long. The head bears two proximal concavities for articulation with the femur. The distal end is concave, with a distinct medial projection that locks into the astragalus (Figs. 5A, 8F–G). Although the tibia is much less than half the length of the femur, it is still 75% as long as the humerus and almost exactly as long as the ulna and radius. It is also much more massive than any of the forelimb elements, including the humerus.

Fibula—Only the left fibula is visible—the right is completely obscured by matrix and the right pes (Fig. 5A). The fibula is longer than the tibia, with a rounded, subtriangular proximal end and a greatly expanded distal end. A few osteoderms obscure details, but the medial and anterior sides are weakly faceted proximally. The anterior process is exceptionally robust, even for aetosaurs, and projects 15 mm off the surface of the limb. Its surface is rugose, and this rugosity extends onto the fibular shaft both proximally and distally. The bone is sigmoidal in 'side' (anterior) view.

Pes—The exceptional preservation of P-56299 affords the first opportunity to evaluate the articulated pes of *Typothorax* in detail. The left is preserved in dorsal view, and the right in plantar view, with the right somewhat more complete (Fig. 5A). Both preserve the astragali and calcanea, distal tarsals (typically concealed by matrix and other elements), all metatarsals, and many phalanges, including at least two unguals. The Revuelto Creek specimen lacks many of the more distal phalanges but is similarly well preserved (Fig. 8D–G). Measurements of the metatarsals and phalanges of both feet are in Supplementary Data.

Astragalus—Both astragali are visible but difficult to evaluate due to articulations with other elements, with the left somewhat more exposed than the right (Fig. 5A). Both are visible principally in anterior view. The astragalus of *Typothorax* *coccinarum* is a robust element—approximately 30 mm tall anteriorly to 50 mm wide laterally. Preservation is not good but the exposed details well match the astragali illustrated by Lucas et al. (2002:fig. 9) for *T. antiquum* and by Long and Murry (1995:fig. 98) and Parrish (1986:fig. 28) for *T. coccinarum*. As preserved they are closely appressed to the tibiae, with most of the pes' range of motion apparently accommodated at the articulation of the astragalus-calcaneum with the proximal tarsals, as described by Parrish (1986).

Calcanea—Both calcanea are visible, the left partially in anterior view and the right in anterior, distal, and, partially, posterior views (Fig. 5A). They are robust and well match the calcaneum of *Typothorax antiquum* illustrated by Lucas et al. (2002:fig. 9), to the extent that they are visible. Like the astragali, they appear to articulate closely with the more proximal element, in this case the fibula, although this articulation appears looser than that of the astragali with the tibiae.

Distal Tarsals—A few of the more distal tarsals are visible, particularly in plantar view on the right pes (Fig. 5A). Importantly, these compact elements appear to be the primary posterior portion of the pes that was in contact with the ground—functionally, the astragalus and calcaneum appear to be more closely affiliated with the tibia and fibula than the pes.

Metatarsals—The metatarsals, especially the first and fifth, are relatively short and compact, but still possess a distinct shaft that is approximately half the width of the proximal end (Figs. 5A, 8D–G). The distal end is usually no more than 90% as wide as the proximal end. The fifth metatarsal exhibits the typical archosauromorph 'hook,' with a much broader proximal end and distal end that is only half as wide. Proximally, all are laterally compressed and relatively tall (dorsoventrally deep); distally they are much broader and relatively low (mediolaterally wide).

The fourth metatarsal on the right pes appears pathological (Fig. 5A). Unlike its counterpart on the left it is relatively short and stout. There is a taphonomic break that displaced the lateral condyle on the distal end, but even after accounting for this feature the element is ~13 mm shorter than the left, with much thickening of the midshaft. The surface of the thickened area is also somewhat rugose and irregular. It appears likely that this metapodial was fractured and healed at some point in life, with the rugose thickening representing a callus that formed as part of the healing process (cf. Rothschild and Martin, 2006).

Phalanges—The phalangeal formula, including unguals or inferred (= ?) unguals is, minimally, 2-3-3?-4?-3?, although *Stagonolepis* possesses the formula 2-3-4-5-4 (Walker, 1961:fig. 19) and *Aetosaurus* a 2-3-4-5-3? phalangeal formula (Schoch, 2007). All phalanges are much shorter than any metatarsal, and are typically only ~40% as long as the next most proximal element, with their proximal widths being ~10% less than the distal width of their respective metatarsals. Each succeeding phalanx is shorter than the next most proximal, except for the unguals. Not only do the phalanges shorten, but they also narrow rapidly. The most robust digits are I–III, even though IV appears to have the most phalanges. The phalanges of digit V are extremely reduced. Thus, the pes is short and compact, the implications of which are discussed later.

The Badlands Ranch specimen preserves the first unambiguous ungual phalanges reported for *Typothorax*. The preserved pedal unguals are on left phalanges I and II and are striking in that they are strongly laterally compressed. Their proximal articulations are relatively wide, but the blade of each ungual is relatively narrow. Assuming that they were covered with some form of keratinous sheath, they look relatively formidable for an animal that is clearly not a predator. We suspect that they were likely used for scratch-digging (e.g., Benton, 1983) or some similar purpose (see Discussion, below), because it is difficult to imagine a short, squat, heavily armored animal with the majority of its weight on the hind limb using the claws on its pes as weapons.

Osteoderms

Long and Ballew (1985) clearly delineated lateral and paramedian osteoderms and discussed their associated taxonomic characters in aetosaurs. Heckert and Lucas (1999, 2000) began the process of trying to further standardize this nomenclature, utilizing the term 'columns' to describe the longitudinal series of paramedian, lateral, and ventral osteoderms that parallel the vertebral column. 'Rows,' then, are the transverse sets of osteoderms from the most anterior (first row) to the end of the tail (last row). In many aetosaurs the rows are presumed to correspond to vertebrae, but we will show that this is not the case in the presacral column of *Typothorax*. The idealized aetosaur has two axial columns of paramedian osteoderms, each of which is bounded laterally by a column of lateral osteoderms. The number of ventral columns and their coverage (number of rows) is not known in many taxa and varies considerably among the taxa for which it is known (Heckert and Lucas, 1999, 2000). Parker (2007, 2008) attempted to standardize this nomenclature still further, assigning material to anatomical regions with a greater degree of precision.

Only the most posterior thoracic, sacral, and caudal dorsal paramedian armor is preserved on the Badlands Ranch specimen (Fig. 2). These can still be assigned to rows, however, based on the nearly continuous set of left lateral osteoderms (Figs. 2C, 3).

Cervical Paramedians—Definitive cervical paramedian osteoderms are not preserved in the Badlands Ranch specimen, and they are somewhat disarticulated even in the more complete Revuelto Creek specimen (Figs. 6–7, 8C). The first row articulates with the skull and is very small, nearly equant, and lacks lateral osteoderms. The second to sixth rows are also small, although they begin to widen appreciably by row 6, and rows 6–8 each have posterior margins that are wider than the anterior margin as they make the transition from the cervical series to anterior dorsals covering the pectoral girdle (Figs. 2, 8C).

Dorsal Paramedians—Only a few fragments of the anterior dorsal paramedian osteoderms are preserved in the Badlands Ranch specimen, principally their lateral edges where they articulate with the lateral osteoderms. On the Revuelto Creek specimen, many of the osteoderms are only exposed in edge view. On both specimens, osteoderms from the thoracic portion of the carapace are gently arched transversely (Figs. 2, 7A). The very wide, arcuate nature of the mid-dorsal paramedians precludes simple measurement of widths as typically performed in other *Typothorax* specimens (e.g., Heckert and Lucas, 2000; Lucas et al., 2002; Martz, 2002). Apparently, the vast majority of the specimens those authors described are more anterior or posterior to the bulk of the thorax. Measuring around the arc of the osteoderms reveals that both the Bull Canyon Formation specimens described here had osteoderms that were at least 410 mm across their posterior margin and probably as much as 430 mm, indicating that these are the largest *Typothorax* osteoderms yet recovered (see discussion in following section). Hunt et al. (1993) noted that the widest dorsal paramedians of the Revuelto Creek specimen were approximately as wide as the femur was long, and this appears to be the case in the Badlands Ranch specimen as well, but only if the width is measured as a straight-line distance, not along the arc of the osteoderm.

Remnants (lateral edges) of paramedian osteoderms touch laterals in rows 8–13, and possibly 14 and 15 in the Badlands Ranch specimen. Thus, the arched dorsal paramedian visible in dorsal view from the ventral side may be from the 16th row, pushed forwards and inverted (Fig. 3, 4C). If this is the case, the entire carapace was displaced and the viscera accessed between osteoderms 16 and 17. On the left side, dorsal paramedians of rows 17 and 18 are telescoped backwards over row 19, which is the one articulating with the exposed dorsal vertebra. This leaves osteoderm rows 20–21 as the only logical choice for sacrals. The sacral osteoderms are markedly narrower and flatter than the preceding rows, so the armor was probably relatively flat directly above the hips.

The caudal dorsal paramedians narrow rapidly, and by row 27 or 28 (fifth or sixth row of caudals) they are longer than wide (Fig. 5C). As is typical in aetosaurs, the height of the boss increases posteriorly both proportionately and absolutely, eventually developing into a spike. These conical spikes quickly reach the same size as those of the lateral osteoderms, so the distal tail is extremely spinose (Figs. 2–3, 6–7).

Lateral Osteoderms—These specimens are significant in preserving an almost complete series of lateral osteoderms from the cervical region to the end of the tail. Regardless of anatomical region, the lateral osteoderms are all strongly flexed, with a dorsal and a lateral flange that meet at an angle that is typically less than 90° in the presacral series (Fig. 4D) and greater than 90° in the caudal series. All are heavily pitted on the dorsal flange throughout the column, and many possess a faintly radial pattern emanating from the spike anteriorly and medially on the lateral flanges. This radial pattern is always weaker on presacral laterals than it is on proximal caudal lateral and ventral osteoderms.

Cervical Lateral Osteoderms—Martz (2002:147) disputed almost all identifications of cervical osteoderms in *Typothorax* by Long and Murry (1995), and we generally agree with his assessment. Martz (2002), however, did not have bona fide cervical osteoderms at his disposal, so all of the cervical lateral osteoderm anatomy we document here is new.

It appears that there were no more than five rows of osteoderms to cover the entire cervical region, with the first such row consisting solely of dorsal paramedians. This matches well with the shortening of cervical vertebrae noted by Long and Murry (1995) and Martz (2002) as well as the cervical vertebrae/osteoderm count for *Desmatosuchus* proposed by Parker (2008). However, both Long and Murry (1995) and Martz (2002) persisted in reconstructing *Typothorax* as having a 1:1 match between cervical vertebrae and osteoderm rows. Both of the specimens described here instead show that there were no more than five rows of osteoderms covering the cervical region, and indeed perhaps as few as six rows of osteoderms anterior to the pectoral girdle. Disarticulation confuses the relationships of the cervical armor on both specimens, but several apparent lateral osteoderms are evident in ventral view. The most anterior of these, only preserved on the right side of the Badlands Ranch specimen, is folded at a weakly acute angle and is slightly asymmetric. It is badly weathered, and no ornamentation is discernable.

The next most posterior osteoderm is elongate and thin. In ventral view it is a backswept triangle with a prominent ridge on the anteroventral margin (Fig. 3). This spike-like osteoderm is strongly compressed dorsoventrally—if the dorsal and lateral flanges are distinct at all, there is very little space between them. Comparison with the casts of the articulated specimen P-12964 confirms that this is the third cervical lateral osteoderm. This spike-like osteoderm has not been described in *Typothorax* previously.

Posterior to this, the next osteoderm is elongate and more robust (thicker), and lacks a spike. It is relatively gently arched, forming a ~90° angle between distinct dorsal and lateral flanges. Lateral osteoderms from rows 5–7 are poorly preserved, but appear to grade from this 'cervical' morphology into more 'typical' thoracic lateral osteoderms of rows 8–21.

Thoracic Lateral Osteoderms—The well-preserved series of lateral osteoderms on the left side begins with the eighth row, coinciding with the posterior pectoral girdle. In ventral view, the mid-thoracic lateral osteoderms take the shape of one-third of a circle, with a straight border medially and another, gently arched posterior margin, with the strongly arcuate side lateral. The dorsal surface of the lateral flange bears a pattern of subcircular to elongated pits that is faintly radial. Because they are articulated, the anterior bars are usually hidden, rendering precise measurement impossible. Still, typical osteoderms bear a lateral flange that is typically ~50–70 mm wide and 80–110 mm long in this part of the carapace.

The lateral margin bears many fine pits that suggest the presence of additional, keratinous horn-like tissue that was not fossilized. These processes are thin and knife-like from the anterior column through the 12th row, thicken through the 13th row, and broaden from the 14th through 20th rows, and then become sharper again from the sacrum posteriorly. Thus, lateral osteoderms of rows 10–13 taper to sharp points or spikes, whereas rows 14–16 have thicker, rounder/blunter knobs before transitioning back to sharper points again for rows 17–20. Anterior to row 16 all appear to have lateral flanges that are wider than their dorsal counterparts, but by row 20 the two flanges are roughly equal in size. The angle between dorsal and lateral flanges is acute throughout the thoracic series (Fig. 4D), with the possible exception of row 16, where it approximates a right angle, and of row 18, where it is not visible. The angle first opens up (increases) in row 23 and is consistently greater than 90° through the caudal series.

Caudal Lateral Osteoderms—Proximally the caudal lateral osteoderms still possess prominent spike-like projections (Fig. 6B). Overall size and the prominence of these points both decrease markedly after the first few (five to six) rows. Throughout the caudal series the dorsal and lateral flanges are roughly equal in size.

Ventral Thoracic Armor—The Badlands Ranch specimen preserves the first intact, articulated, thoracic ventral armor reported for *Typothorax*. This armor consists of 10 columns of osteoderms arranged in seven rows that are equivalent to rows 10–16 of the lateral and dorsal armor (Figs. 3, 4C). The columns are divided into two medial columns on each side of the midline that are more rectangular, with osteoderms that are generally wider than long, and flanked on each side by three more lateral columns of more equi-dimensional (square) osteoderms. We provide measurements in the Supplementary Data. The only evidence of a row of ventral armor equivalent to row 9 is a single osteoderm on the left side, where it would be in the fifth (most lateral) column. In general, the ventral osteoderms are thinner and less deeply ornamented than their lateral and dorsal counterparts. What patterning is evident is a random to weakly radial arrangement of shallow pits (Fig. 4C). Many of the osteoderms possess weak anterior bars, implying that in life they were probably more imbricated than seen in the specimen, where they typically abut each other laterally and medially but are often separated from each other anteriorly and posteriorly. This may be a taphonomic effect, perhaps due to postmortem bloating of the carcass.

Ventral Caudal Osteoderms—The essentially complete caudal carapace of P-56299 also affords the first detailed view of the ventral armor of the caudal region (Figs. 3, 5B). Unlike *Coahomasuchus* or *Aetosaurus* (Heckert and Lucas, 1999; Schoch, 2007), there is almost no ventral armor over the pelvic area. The first row of ventral osteoderms begins ~70 mm posterior to the ischia and consists of small (~41 × 28 mm; 35 × 23 mm) rounded, flat osteoderms that are longer than wide and that we tentatively associate with the sacral osteoderms of row 21. Posterior to this the osteoderms are arranged in four columns (two medial, two lateral); each row corresponds to a row of lateral and dorsal paramedian osteoderms.

The first true caudal row (row 22 overall) has relatively large osteoderms (60–70 mm long, ~40 mm wide) that are rhomboidal in ventral view. Ventrally, these bear an ornamentation of faintly radial pitting emanating from a longitudinal keel beginning in the middle of the osteoderm. Posteriorly the keel expands laterally and ventrally into a pronounced knob. The following two rows (23, 24) are similar but slightly larger, with pronounced spikes in lieu of a knob in the medial columns. In life position the spikes would have been anteriorly recurved (concave anteroventrally) and ventrally directed. In row 23 this spike is more than 40 mm tall on an osteoderm that is otherwise only 60 mm long. The lateral rows are narrower and more plate-like, with keels or less pronounced spikes. In the 24th row the spike is still present in the median osteoderm, but more in the plane of the osteoderm, projecting ~20 mm posterior to the main body of the osteoderm in the medial columns. These osteoderms' ornamentation is principally a weakly radial pattern of pits that is coarser than that seen on the thoracic ventral osteoderms. This pattern is also seen in the Revuelto Creek specimen as well (Figs. 6–7). Thus, *Typothorax coccinarum* is the only aetosaur known with ventral armor that includes spiked osteoderms. Martz (2002) illustrated similar osteoderms in *T. coccinarum* from the Canjilon quarry (e.g., Martz, 2002:figs. 4.36g–j; 4.38), although, without the benefit of much articulated material, he generally misidentified these as lateral osteoderms.

The ventral caudal armor from the fourth row (25th overall) caudally consists of four columns, with the lateral two columns more rectangular (longer than wide) and the medial columns somewhat more equant. By this point low knobs replace the keels and spikes of the preceding rows. Posteriorly the ornamentation fades (is less incised) from rows 25 to 29, and for the remainder of the column is a relatively shallow series of pits with a weakly radial pattern. The lateral columns bear a faint longitudinal keel that extends more or less down the middle of the osteoderm and ends in a slight posterior projection. The more medial columns are narrower, less ornamented rectangles that are equally long. The principal feature distinguishing these osteoderms from ventral thoracic osteoderms is that they are longer than wide, whereas the thoracic osteoderms tend to be wider than long. Curiously, these columns are folded so that the ventral (outer) surfaces of the medial sides are facing each other in P-56299.

DISCUSSION

The high degree of articulation and completeness of these *Typothorax* skeletons, as well as the relatively undeformed skeleton of the Badlands Ranch specimen, permit us to make observations and interpretations of *T. coccinarum* that were not possible previously. In the following sections we discuss the taxonomic implications of these specimens, and present a new reconstruction of *T. coccinarum* (Fig. 9). This allows us to consider the size and overall body shape of *T. coccinarum*, examine the limb proportions and their apparent locomotor implications, investigate possibility of digging behavior in *Typothorax*, comment on the apparent match between the hind foot anatomy of this relatively large aetosaur and the pes impressions of the Upper Triassic ichnogenus *Brachychirotherium*, and note the unique cloacal morphology preserved in these specimens.

Taxonomic Implications

Osteoderms of *Typothorax coccinarum* are among the most frequently recovered fossils in the Chinle Group (Long and Ballew, 1985; Long and Murry, 1995; Lucas et al., 2002), whether they are isolated occurrences such as the type (Lucas and Hunt, 1992; Lucas et al., 2007b) or abundant disarticulated material in quarries (Long and Murry, 1995; Martz, 2002; Heckert et al., 2003). These osteoderms are highly distinctive and thus form a significant basis for the development of an aetosaur taxonomy based on osteoderm characters that is now widely accepted (e.g., Long and Ballew, 1985; Long and Murry, 1995; Heckert et al., 1996; Heckert and Lucas, 1999, 2000; Martz, 2002; Parker, 2007).

As part of this development, Hunt and Lucas (1991) first described a relatively small aetosaur from the Redonda Formation of east-central New Mexico as *Redondasuchus reseri*. Long and Murry (1995:108) compared the type material of *Redondasuchus reseri* to the UCMP Canjilon *Typothorax coccinarum* specimens and synonymized *R. reseri* with *T. coccinarum*, suggesting that the *R. reseri* type material might be osteoderms from the "anterior portion of the body" of *T. coccinarum*. Heckert et al. (1996) redescribed the available specimens and reiterated its distinctiveness from *Typothorax*, a position maintained by Heckert and Lucas (1999, 2000). Martz (2002) considered *Redondasuchus reseri* congeneric with *Typothorax* but a distinct species, *T. reseri*, based on incomplete *T. coccinarum* material from western Texas and eastern New Mexico and the aforementioned Canjilon quarry specimens. Lucas et al. (2002) named a second species of *Typothorax*, *T. antiquum*. Spielmann et al. (2006) described a second species of *Redondasuchus, R. rineharti*, and reiterated the distinctiveness of *Redondasuchus* from *Typothorax*. Although both species of *Redondasuchus* are known solely from osteoderms, the relatively complete carapaces of *T. coccinarum* described here afford an additional opportunity to test the distinctiveness of *Redondasuchus* relative to *Typothorax* and to compare the two species of *Typothorax*, *T. antiquum* and *T. coccinarum*.

Comparisons of the holotype and referred specimens of both species of *Redondasuchus* based on casts and actual specimens housed at the NMMNH reveal that the type series of both *R. reseri* and *R. rineharti* are distinct from any osteoderm of *T. coccinarum*. None of the cervical paramedian and lateral osteoderms of either the Revuelto Creek or the Badlands Ranch specimens exhibit flexing of the osteoderm as seen in *R. reseri*, falsifying Long and Murry's (1995) hypothesis. None of the paramedian osteoderms assigned to either species of *Redondasuchus* is an exact match for osteoderms on either of the Bull Canyon Formation *T. coccinarum* specimens described here. Importantly, *Redondasuchus* specimens are strongly flexed, consisting of two flat surfaces connected at an obtuse angle (Hunt and Lucas, 1991; Heckert et al., 1996; Spielmann et al., 2006). This abrupt flexure is distinct from the gently arcuate curvature seen in the thoracic paramedians of *T. coccinarum* readily seen in the Revuelto Creek specimen (Figs. 6, 7). The more complete Revuelto Creek and Badlands Ranch specimens therefore confirm the observations of Spielmann et al. (2006) that *Typothorax* is distinct from *Redondasuchus*, contra Long and Murry (1995) and Martz (2002).

The other taxonomic issue associated with *Typothorax* is the distinctiveness of *T. coccinarum* from *T. antiquum*. As first noted by Lucas et al. (2002), the extremely wide and short dorsal paramedians of the Revuelto Creek specimen (maximum width:length > 3.5:1) are readily distinguished from the narrower (width:length ~2–3) osteoderms of *Typothorax antiquum*. The relatively denser and smaller pitting on the dorsal paramedians, the less prominent radial ridges on the lateral osteoderms, and the less robust ilium of the Badlands Ranch *T. coccinarum* also distinguish it from *T. antiquum*. These are all diagnostic features that distinguish *T. coccinarum* from *T. antiquum* according to Lucas et al. (2002). As described previously, the more robust ulna is another feature that distinguishes *T. coccinarum* from *T. antiquum*.

Reconstruction of *Typothorax coccinarum*

Reconstructions of *Typothorax coccinarum* in the scientific literature include Long et al. (1989:fig. 3a), Long and Murry (1995:fig. 99; see also Irmis, 2005:fig. 6f), Martz (2002:fig. 4.41), and a common popular reconstruction by Doug Henderson based on Long and Ballew's (1985) understanding and first published in Long et al. (1988). Insight from the articulated specimens documented here allows us to present a much more accurate reconstruction than was previously possible (Fig. 9). In particular, we note that this reconstruction features the first accurate depiction of the skull and cervical series (based on the Revuelto Creek specimen), has only slightly more than half as many rows of osteoderms as previous reconstructions, displays a dramatically different body shape, much more accurate limb proportions and posture, and the first understanding of the ventral armor.

Both Long and Murry (1995) and Martz (2002) followed Hunt et al. (1993) in noting the reduced length of the cervical vertebral series of *Typothorax*, but both still reconstructed the carapace as having the 1:1 relationship between osteoderms and vertebrae considered typical of aetosaurs (Walker, 1961) and, possibly, characteristic of Crurotarsi generally (e.g., Sereno, 1991). The specimens we describe here instead show that although the cervical vertebrae are reduced, there is no concomitant shrinkage of the length of the dorsal paramedian osteoderms. Thus, perhaps as few as five rows of osteoderms covered the first 10 presacral vertebrae. As a consequence, *T. coccinarum* has only ~20 rows of presacral osteoderms, counting the dorsal paramedian that articulates with the skull but lacks a corresponding lateral osteoderm, even though disarticulated specimens retain ~26 presacral vertebrae (Long and Murry, 1995; Lucas et al., 2007b).

Similarly, neither Long and Murry (1995) nor Martz (2002) properly illustrate the tail of *Typothorax coccinarum*, in spite of specimens and information available to them. Although Hunt et al. (1993:209; reiterated by Sealey et al., 1995) stated that "the tail actually accounts for half the length of the animal, and the carapace narrows rapidly in the shoulder region," Long and Murry (1995) and Martz (2002) failed to show the increasing length of caudal rows of armor, and therefore consistently show far too many rows of osteoderms that are each too short, effectively repeating errors of the older Henderson reconstruction in Long et al. (1988) based on incomplete material. Thus, although Long and Murry's (1995) reconstruction shows 25 presacral and more than 30 caudal rows, and Martz (2002) shows at least 29 and 36, respectively, the Bull Canyon Formation specimens demonstrate that there are in fact no more than ~46 rows of osteoderms total, relatively evenly split between the presacral-sacral (~22) and caudal (24) series.

Martz's (2002:fig. 4.41) reconstruction was based in large part on TTUP 9214, a specimen he interpreted as belonging to a juvenile *Typothorax coccinarum*, but which is, throughout his narrative and illustrations, always distinct from other specimens of the species. We strongly suspect that this specimen represents a different taxon that Martz (2002) has mistakenly included in his concept of *Typothorax coccinarum*. We also note that the number of presacral osteoderm rows (28–30) is not consistent in his lateral and dorsal (Martz, 2002:fig. 4.41c and b, respectively) reconstructions, and neither agrees with the apparent number of presacral vertebrae in his (4.41a) lateral reconstruction of the skeleton without armor.

The mechanism by which the armor was reduced in *T. coccinarum* is intriguing because the vertebral column shortened by reduction of the length of the individual vertebrae, particularly the cervicals, but the osteoderms are reduced in number, while retaining a relatively uniform length. Indeed, the caudal paramedians, which do match 1:1 with underlying vertebrae, are not noticeably longer than are the presacral osteoderms. An additional hypothesis supporting the reduction in total number of osteoderm rows is the third cervical spike. Among the aetosaurs known well enough to produce realistic reconstructions, *Desmatosuchus haplocerus* is the best known with lateral spikes, and it is well known for the large, posteriorly recurved spike on its fifth lateral osteoderm (Case, 1922; Long and Ballew, 1985; Long and Murry, 1995; Parker, 2008). If this spike is homologous with the third cervical spike shown here on *T. coccinarum*, then this suggests that shortening of the carapace occurred in part by removing two rows anterior to the fifth. This reduction or substitution strongly hints that different genetic mechanisms accommodated the reduction of the presacral column. One genetic mechanism shortened the individual centra, whereas a second (HOX?) reduced the number of rows of armor, perhaps by essentially removing some of the 'even' rows (second, fourth). If this is the case, then the large fifth lateral osteoderm of *Desmatosuchus* (Case, 1922) may actually be homologous with the third lateral spike of *T. coccinarum*. Obviously, additional work with extant taxa will be necessary to determine the genetic basis for this observation, but the fact that the number of osteoderm rows and vertebrae is decoupled in the cervical series of *T. coccinarum* is significant.

Body Size and Overall Proportions

Both skeletons of *Typothorax coccinarum* described here are almost exactly the same size—approximately 2.5 m long. The appendicular elements associated with these specimens are also universally larger than those of the Canjilon quarry specimens from north-central New Mexico (A.B.H., pers. observ.; Martz, 2002; Nesbitt and Stocker, 2008) and within 5 mm of the maximum length for *T. coccinarum* measured by Martz (2002) in AMNH 2713. Furthermore, the dorsal paramedian armor of these specimens, although often incomplete, is as wide or wider than any others of which we are aware, and the lateral osteoderms are also comparable in size to any that we have seen. The largest published *Typothorax* osteoderm is the right dorsal paramedian PEFO 23388 from the Painted Desert Member of the Petrified Forest Formation, with a width of 432 mm (Parker and Irmis, 2005:fig. 10b), which is comparable to osteoderms preserved in the Revuelto Creek specimen. Hunt et al.'s (1993) observation that maximum paramedian width is similar to femoral length is informative, and we are not aware of any osteoderms larger than those of the specimens described here in spite of numerous quarry samples (e.g., Long and Murry, 1995; Martz, 2002; Heckert et al., 2003; Nesbitt and Stocker, 2008). Therefore, we hypothesize that these specimens represent adult individuals and thus approximate the upper limit of *T. coccinarum* body size. Consequently, *T. coccinarum* probably did not reach, let alone exceed, 3 m in body length, *contra* the 2–4-m estimates of Long and Murry (1995). Importantly, as documented by Hunt et al. (1993; Sealey et al., 1995), the tail represents nearly half the length of *T. coccinarum*, so the snout-vent length of *T. coccinarum* was probably only 1.25 m.

The exceptionally complete nature of these fossils also allows us to estimate their mass. We calculated the mass of P-56299 using the empirically derived formula of Anderson et al. (1985). This formula predicts the mass of quadrupeds based on the midshaft humerus and femur circumferences:

$$\text{Mass} = 0.078 \times (\text{Circumference}_{\text{Humerus+Femur}})^{2.73}$$

The Badlands Ranch specimen yielded circumference measurements of $C_{\text{Humerus}} = 68$ mm and $C_{\text{Femur}} = 107$ mm, for a $C_{\text{Humerus+Femur}}$ of 175 mm. Applying Anderson et al.'s (1985) formula yielded a mass of ~104 kg. We approximated C_{Humerus} in the Revuelto Creek specimen by using the combined cross-sectional area (336 mm^2) of the ulna (196 mm^2) and radius (140 mm^2), because no humerus is available but the combined strength of the ulna and radius should be similar to that of the humerus (McGowan, 1999). The measured femoral midshaft circumference C_{Femur} of 108 mm and the approximated humeral midshaft circumference of 65 mm yield an estimate for $C_{\text{Humerus+Femur}}$ of 173 mm and thus an estimated mass of 100 kg for the animal. We describe our measurement process and protocols in the Supplementary Data, noting the sensitivity of the Anderson et al. (1985) equation to errors in measurement, or in this case, errors in estimates of circumference. Still, it is informative that these two similar-sized specimens yielded essentially indistinguishable results, and we suspect that ~100–110 kg is therefore a reasonable estimate for the upper limit of *T. coccinarum* body mass.

Limb Proportions and Posture

The skeletons described here, especially the Badlands Ranch specimen, afford some insight into the posture of *Typothorax coccinarum* (Fig. 9). The Badlands Ranch skeleton is clearly dorsoventrally compressed, but because the pectoral girdle is comparatively small and lacks evidence of significant dislocation (e.g., imbrication or disarticulation of elements) we suspect that it approximates life position, because the coracoids simply cannot be moved much farther apart without losing contact with the interclavicle. The pelvis likewise appears to have only minimal displacement of elements, primarily the pubes, and thus appears to represent its approximate life position. As preserved, the medial edges of the glenoids are ~130 mm apart, and those of the acetabula are only ~100 mm apart. Even accounting for some dorsoventral crushing, *T. coccinarum* clearly had a relatively narrow gauge. If the 'flexed' nature of the hind limbs is still lifelike, the hind feet are ~250 mm apart, measured at the medial side of the respective ankle hinges. The preserved humerus is rolled out of the glenoid, but it still appears that the forelimbs probably were less upright and instead had a more sprawling posture than the hind limbs. This combination of 'sprawling' forelimbs and 'upright' hind limbs is uncommon, but has been hypothesized to occur convergently to some extent in both ankylosaurs and ceratopsians (Coombs, 1978; Johnson and Ostrom, 1995; Dodson et al. 2004) as well as the Permian therapsid *Procynosuchus* (Kemp, 1980).

Parrish (1986, 1987, 1989) discussed the evolution of erect posture in archosaurs at length, and *Typothorax* was one of the aetosaurs he focused on in his analyses. The *Typothorax* specimens examined here confirm his observations (based largely on MCZ 1487 and MCZ 1488, also examined here—see Supplementary Data). Specifically, the femur is straight (not significantly twisted), the crus 'hinges' on the tarsus, the calcaneal tuber projects posteriorly and perpendicular to the axis of this hinge, and the pes is anteriorly directed with digit V not markedly divergent from the rest of the pes (Parrish, 1986:31). These are in addition to classically recognized features of his 'upright paradigm,' of which *Typothorax* possesses a deep acetabulum, tight articulations on the surface of the knee and well-developed flexor and extensor musculature (as inferred from the femoral trochanters and the expanded anterior and medially deflected posterior processes of the ilium) enabling parasagittal movement of limbs. This specimen also confirms the near-ventral orientation of what is normally considered the lateral side of the ilium (Fig. 9D), which has been commented on by many authors regarding upright posture in crurotarsans (e.g., Bonaparte, 1984; Benton and Clark, 1988) but which is seldom seen in actual reconstructions of aetosaurs (Long and Murry, 1995).

Our reconstruction places the pes forward of the sacrum and under the heaviest part of the body, even though the proximal femur articulates with the sacrum at a point posterior to the knee joint. This posture matches well with the better-developed anterior processes, including the 'lesser trochanter' on the femur and the elongate anterior process on the ilium. This may explain the broadened, knob-like fourth trochanter and the deflected posterior iliac blade, which would provide for more muscle mass to retract the femur and/or pull on the tibia, as numerous muscles propelling the hind limb, such as the *M. ilio-femoralis*, *M. coccygeo-femoralis brevis*, and, in part, *M. ilio-tibialis,* among others, originate on the posterior side of the ilium (Romer, 1923).

It is important to recognize that Kubo and Benton's (2007) recent work on limb posture in extinct archosauromorphs relies on the skeleton of *Longosuchus* (= "*Typothorax*") *meadei* for its analysis of "*Typothorax*," contradicting all published literature on aetosaurs since Hunt and Lucas (1990). Because the femora of actual *Typothorax* specimens are dramatically different from those of *Longosuchus*, and much more similar to those of *Desmatosuchus* in having an elliptical cross-section (Long and Murry, 1995; Martz, 2002), it is likely that the biomechanical performance of *Typothorax* within the context of the Kubo and Benton (2007) model is much more like *Desmatosuchus*.

Functionally, the limbs appear convergent with diverse upright taxa such as dinosaurs in that the hind limb is functionally mesotarsal and divided into the femur, tibia/fibula + astragalus/calcaneum, and distal pes, with the hinge at the contact between the astragalus and the more distal tarsals. On the right leg this yields proportions of ~311/215/184 mm for these three functional units. Not surprisingly, the high femur: tibia ratio (even with the astragalus included) of 1.4–1.5 indicates a slow-moving animal.

Typothorax as a Possible Digger

Although these specimens confirm the upright posture of aetosaurs, it remains unclear exactly what their mode of life was. Traditionally interpreted as terrestrial herbivores, aetosaurs' oddly-shaped skulls have led some to consider the possibility that they were capable of using their snouts to grub or dig (Walker, 1961; Parrish, 1994), but no worker has examined other skeletal features to consider this. We use the morphology and proportions of the limbs and girdles of the two specimens described here to examine whether *T. coccinarum* was well suited to digging.

Relatively few workers have examined the functional morphology of digging (Hildebrand, 1974, 1983), and even fewer as it pertains to fossil taxa (Benton, 1983; Coombs, 1983). Hildebrand (1974, 1983) examined digging in generalized terms, looking at advantageous limb and girdle features. Benton (1983) discussed the possibility of scratch-digging behavior in rhynchosaurs (following Huene, 1939), and Coombs (1983) looked specifically at large, clawed mammals.

Hildebrand (1974) listed 11 characteristics common in digging tetrapods: (1) radius shorter than humerus (low brachial index); (2) manus shorter than radius (exclusive of terminal phalanges); (3) metacarpals short and wide; (4) proximal phalanges short and wide; (5) prominent deltopectoral crest continuing well distal on the humerus; (6) large acromion process on scapula (origin of deltoid musculature); (7) wide entepicondyle on humerus (origin of forearm pronators and manual flexors); (8) proximal extension on humerus of supinator crest from ectepicondyle (origin of supinator and manual extensor musculature); (9) long pisiform (insertion of *M. flexor carpi ulnaris*); (10) long olecranon process compared to the length of the entire ulna (insertion of *M. triceps*); and (11) large posterior angle on scapula (origin of *M. teres major*). Of these and other features Coombs (1983:fig. 1) interpreted the following as the most indicative of digging: low intermembral index; long olecranon process; short, wide metacarpals; and short or absent pubic symphysis. We examine each of Hildebrand's (1974) features as they apply to *T. coccinarum*.

Typothorax possesses a relatively low (120:193, or 62.2) brachial index (Coombs, 1983:fig. 1), because the radius is significantly shorter than the humerus. Hildebrand's criteria 2–4 cannot be evaluated in these specimens because they lack mani, although a manus preserved with MCZ 1488 is compact, probably shorter than the radius, with short and wide metacarpals and proximal phalanges. The Badlands Ranch specimen has a prominent deltopectoral crest that is approximately one-fourth the length of the entire humerus, a condition that is typical among aetosaurs. Although neither specimen described above possesses a scapula that is visible, based on other examples of scapulae (e.g., Long and Murry, 1995:figs. 104, 105a–b), *T. coccinarum* lacks a large acromion process. Although the distal humerus of *T. coccinarum* expands with wide ent- and ectepicondyles, the supinator crest only extends along approximately the distal fifth of the humerus. The olecranon process in the Badlands Ranch specimen is 28 mm long and is 19% the length of the ulna. Coombs (1983:fig. 1) makes the distinction of long olecranon processes at 20% or 30% the length of the ulna. Based on the illustrations in Hildebrand (1974:fig. 21–25), *T. coccinarum* lacks a prominent posterior expansion of the dorsal scapular blade equivalent to Hildebrand's (1974) large posterior angle on the scapular blade.

Thus, five of Hildebrand's (1974) features of digging taxa are present in *T. coccinarum* (features 1, 3–5, 7), with one additional feature (10) being only slightly underdeveloped compared to diggers, and four features could not be assessed definitively (2, 6, 8–9). This suggests that although *T. coccinarum* was not specifically adapted to digging, it was likely able to dig better than its Triassic contemporaries. The ability to dig, however well, along with the upturned snout of *T. coccinarum* may indeed indicate that it was rooting around in soil for food.

Benton's (1983) exhaustive study of the Upper Triassic rhynchosaur *Hyperodapedon* included a review of the hypothesis that rhynchosaurs may have utilized their hind limbs in scratch-digging. Huene (1939) had proposed that the robust hind limb with large claws, prominent hind limb retractors, strong foot flexors, and rolling tarsus were all adaptations that facilitated digging. To Huene's (1939) list Benton (1983:683) added the long posterior projection of the ischia, laterally inflexible sacral vertebral column, and strong caudifemoral origins of the tail as additional possible adaptations. All of these characteristics are also evident in the *Tyopthorax coccinarum* specimens described here. Further, he (Benton, 1983:684) considered rhynchosaurs similar to scratch-digging mammals described by Hildebrand (1974) in having (1) a larger, primary digging digit; (2), large, curved, laterally compressed claws; and (3) interlocking phalangeal articular surfaces that inhibit hyperflexion and hyperextension but that (4) allow for a wide arc of motion and (5) may include a proximal metatarsal digit that is expanded proximally with curved lateral processes. Of these, *T. coccinarum* has at least two pes digits (I–II) with large, curved, laterally compressed unguals, fulfilling criterion (2) and possibly (1), and has a pes with a very similar structure of short, strongly articulated phalanges similar to rhynchosaurs (compare Figure 5A to Benton, 1983:fig. 39). The long femur and proportionately shorter distal elements combined with the functionally mesotarsal ankle also suggest that *Typothorax* may have engaged in scratch-digging. We note that the anteroposteriorly compressed femur, although allowing for prominent muscle attachments facilitating parasagittal motion, would not have maximized strength in this plane, because the elliptical cross-section would actually be stronger (see also Kubo and Benton, 2007).

Typothorax and the *Brachychirotherium* Trackmaker

The Triassic ichnogenus *Brachychirotherium* is often attributed to an aetosaurian trackmaker, but no large, complete aetosaur pes has been available for comparison before now. *Brachychirotherium* represents a quadruped in which the pes and manus are pentadactyl and plantigrade or semiplantigrade (Karl and Haubold, 1998; Fig. 10A–C). The manus is about one-fourth the size of the pes and typically positioned equally as far from the midline as the outer half of the pes impression. The pes is semiplantigrade and has digit V set apart from the other digits, all of which face forward and are thick (spatulate) and terminate in fine, curved claws. Digit III is longest, and thick digital pads are often present. Each of digits I–IV is about as broad as long. The manus is nearly overstepped by the pes, and the manus is often represented by a tridactyl, digitigrade undertrack.

Brachychirotherium is the most common Late Triassic chirotherian ichnogenus, and its stratigraphically highest occurrence is Late Triassic with reliable records confined to Europe and North America (e.g., Haubold, 1971; Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Klein and Haubold, 2003, 2004; Szajna and Hartline, 2003; Demathieu and Demathieu, 2004; Lucas et al., 2006a, 2006b; Lucas, 2007; Lucas and Tanner, 2007). Chirothere tracks assigned to *Brachychirotherium* have been attributed to derived crurotarsans such as rauisuchians (e.g., Olsen et al., 2002) or to aetosaurs (Haubold, 1971, 1986; Lockley and Hunt, 1995; Hunt and Lucas, 2007). The abundance of *Brachychirotherium* relative to traces of presumed predators and its prevalence in a range of sedimentary environments suggests that it represents an herbivore. Additionally, based on their body fossil record, rauisuchians are rare components of Late Triassic faunas (e.g., Long and Murry, 1995; Hunt, 2001), whereas aetosaurs are much more abundant. Therefore, Hunt and Lucas (2007) argued that most Late Triassic *Brachychirotherium* represent aetosaurs.

Brachychirotherium is a relatively common track in Late Triassic ichnofaunas of the Chinle Group of western North America. Hunt and Lucas (2007) tentatively assigned the majority of Chinle Group specimens to *Brachychirotherium parvum.* The presence of articulated hind feet in the specimens described here affords an opportunity to test the hypothesis that *Brachychirotherium* represents the track of an aetosaur. This is significant because *Brachychirotherium* tracks are often moderately large, and considerably larger than the best-articulated pes of *Aetosaurus*, the most complete known aetosaur (Walker, 1961; Schoch, 2007).

The pes of NMMNH P-56299 has five digits, digit V being much smaller than the others (Fig. 10E). Indeed, digit V has very small phalanges and articulates with a large, trapezoidal metatarsal. Digits I–IV are longer and relatively slender; this is also the first relatively large aetosaur fossil to show that pedal digits have unguals that are curved, laterally compressed claws. Digit lengths (in mm)/phalangeal formulas are: V = 100/3, IV = 115/4, III = 160/3?, II = 158/3, I = 130/2. Total pes length (including the tarsals) = 215 mm, and width across the distal digits = 180 mm, but proximal width only 85 mm. Digits I–IV are fairly close together, and digit V is laterally divergent. The total digit divarication = 110°, with interdigital divarications of V–IV = 40°, IV–III = 20°, III–II = 20°, and II–I = 30°. Without a preserved manus, we can only infer that the size of the manus was much smaller than the pes based on comparing the distal width of the tibia-fibula (100 mm) with the distal width of the radius-ulna (56 mm), although we have scaled the manus of MCZ 1488 to match the pes of the Badlands Ranch specimen in Figure 9. Distal tarsals and the metatarsals take up approximately two-thirds of the pes length on the right side. This is more difficult to measure on the left side, but still yields estimates of a plantar surface 160 mm long by 80 mm wide. Incorporating the astragalus and/or calcaneum into the footprint would add approximately 35 mm to the length. Digit V terminates in the vicinity of the first phalanx of IV on the right side, but would probably be even shorter on a normal specimen, given the apparent pathological shortening of MT IV in this specimen. As preserved, the foot of P-12964 is broadly comparable although the left foot is splayed out to approximately 140 mm wide.

The pes of *Typothorax coccinarum* represented by NMMNH P-56299 is compatible with the pes of the trackmaker of *Brachychirotherium.* Key similarities include relative digit lengths (III > II > IV > I > V), relatively short digits with clawed tips, digits I–IV approximately as wide as long, and digit V pad impression (imprint of the proximal metatarsal) posterior or slightly lateral to digit IV (Hunt and Lucas, 2007). The sprawling forelimb and upright hind limb described in NMMNH P-56299 support this assessment by showing that the posture of *Typothorax* could easily leave a *Brachychirotherium* track with the manus as far from the midline as the pes, even though the glenoids are much closer to the midline than are the acetabula (Fig. 9E, F). We conclude that *T. coccinarum*, and probably other large aetosaurs, are suitable models for the *Brachychirotherium* trackmaker.

Cloacal Vent

To date, well-preserved cloacal regions are known from the aetosaurs *Aetosaurus* (Walker, 1961) and *Coahomasuchus*

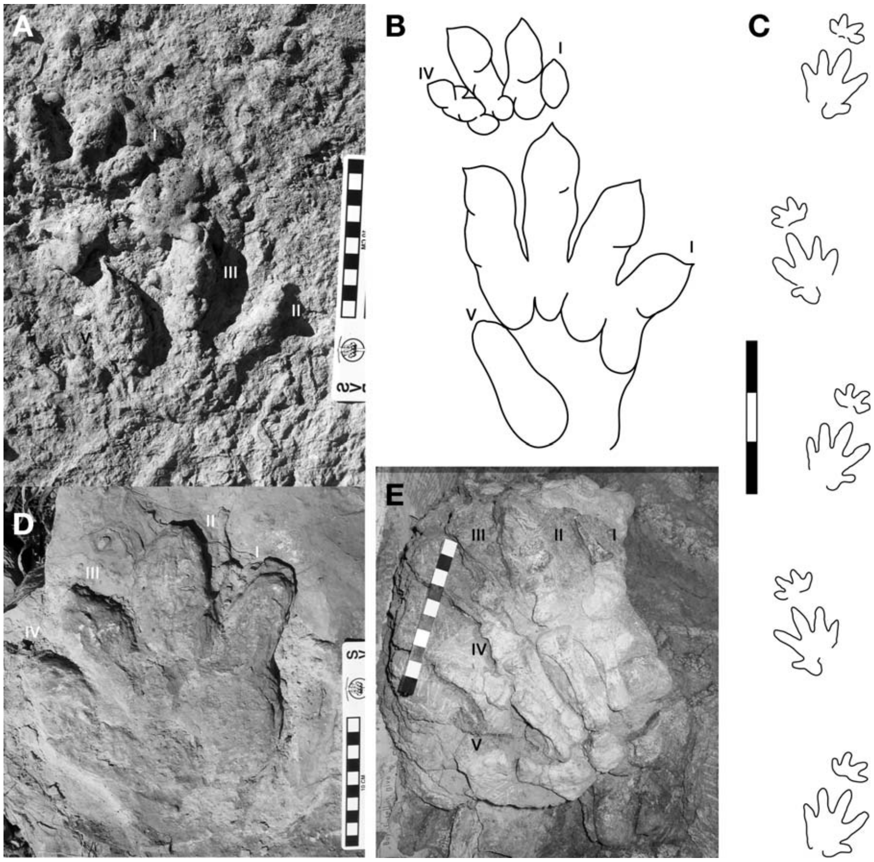

FIGURE 10. Comparison of *Brachychirotherium* tracks (**A**–**D**) to the pes of *Typothorax coccinarum* (**E**). **A**, *Brachychirotherium* manus and pes impression (NMMNH P-45215) from the Redonda Formation, east-central New Mexico; **B**, *Brachychirotherium parvum* sketch after Conrad et al. (1987:fig. 5a); **C**, *Brachychirotherium* trackway in Utah (after Lockley and Hunt, 1995:fig. 3.9); **D**, *Brachychirotherium* right pes impression (NMMNH P-45207) from the Redonda Formation, east-central New Mexico; **E**, Right pes of NMMNH P-56299 in plantar view. Scale bars in A, D–E equal 1 cm; B–C equal 10 cm.

(Heckert and Lucas, 1999). Walker (1961:fig. 23c) also provided a tentative restoration of the armor surrounding the cloacal vent of *Stagonolepis*, although he stated (p. 159) that this interpretation was based largely on that seen in *Aetosaurus*. Osteoderms surrounding the cloacal vent are articulated and well preserved in both specimens described here and are dramatically different from any previously described for an aetosaur. Walker (1961:pl. 16, fig. 44) provides the best information on the distribution of armor surrounding the cloacal vent in *Aetosaurus*, describing two ventral osteoderms followed by two rows of eight ventral osteoderms anterior to the cloacal opening in specimen XXII (S. 22 of Schoch, 2007). Posterior to this, the osteoderms are much wider and the number of osteoderm columns is reduced to four, with the medial pair of the first three rows of these larger osteoderms modified for the cloacal opening. A fourth row is modified in a second, smaller individual (XXI), a difference Walker (1961:172) took to be a possible marker of sexual dimorphism. The cloacal region of *Coahomasuchus* has three rows of ventral caudal osteoderms that were in some way modified to accommodate the vent—the first pair with medioposteriorly angled posterior borders, a second pair that was narrower, and a third row with latero-posteriorly angled anterior borders to close the gap again. These modifications effectively created a hexagonal-shaped hole in the armor for the cloacal vent (Heckert and Lucas, 1999:fig. 4).

As described previously, the first caudal ventral osteoderms of *Typothorax* are posterior to the ischia. This is somewhat unusual in archosaurs, especially crurotarsans, where the distal end of the fused ischia is a good approximation of the anterior limit of the cloacal vent (Hurlburt et al., 2003). These osteoderms are probably associated with the first and second rows of dorsal and lateral osteoderms posterior to the sacrum. The pattern of ventral osteoderms around the vent includes a first row with only two rounded osteoderms (the medial two columns), followed by multiple rows with four columns (two medial, two lateral) (Fig. 9F). Displacement of individual osteoderms renders it difficult to ascertain the actual shape and position of the cloaca, but it apparently lay between the medial osteoderms in these anterior rows. None of these osteoderms are as closely articulated as typically seen in the smaller aetosaurs described previously.

The vent of *Typothorax coccinarum* is thus more open than that of *Coahomasuchus* or *Aetosaurus*, which coincides with a general reduction in thoracic ventral armor (fewer rows and columns) in *Typothorax* relative to these taxa. In particular, the proximal caudal series and sacrum of *T. coccinarum* lack the anterior armor covering the same region in the smaller taxa, perhaps reflecting the greater mass and protection of spiked lateral osteoderms in *T. coccinarum*. However, the spiked osteoderms in close proximity to the cloacal opening are a feature previously undescribed in aetosaurs.

Given the rarity of articulated specimens, the possibility exists that the spiked ventral osteoderms observed in the two specimens described here are gender-related, and that the few other aetosaurs with known cloacal armor represent the opposite gender. We reject this hypothesis on both fossil and recent morphological evidence. Because two different specimens of *Aetosaurus* show distinct modifications of the ventral armor to accommodate the cloaca (Walker, 1961), this hypothesis already appears weak. Furthermore, it is not surprising that *Aetosaurus*, *Stagonolepis robertsoni*, and *Coahomasuchus* all lack ventral spikes, because their skeletons lack spikes altogether (Heckert and Lucas, 2000). Thus, we suspect that the presence of ventral spikes near the cloaca is at least partially of taxonomic significance in *Typothorax coccinarum*.

Modern crocodilians lack ventral osteoderms, but not ventral scutes. Extant species have a single copulatory organ (Gadow, 1887), but identifying the sex of modern crocodilians by external analysis is all but impossible because the cloacal opening in both genders is typically surrounded by two or more rings of small scutes that disrupt the normal pattern of transverse rows of polygonal ventral scutes (Ziegler and Olbort, 2007:figs. 11–13). Thus, without additional articulated specimens the cloacal morphology described here cannot be reliably attributed to gender differences.

Walker (1961:139) tentatively advanced a sexual dimorphism hypothesis for *Stagonolepis robertsoni* based on size and the lack of chevrons for caudals 1–5 on females (smaller), as opposed to only the first caudal on the larger males. According to this hypothesis, both NMMNH skeletons would be male, because chevrons or the remnants thereof are present by the second caudal vertebra, but we note that chevron-based arguments for sexual dimorphism in other archosaurian taxa such as tyrannosaurs have not fared well upon critical evaluation (e.g., Brochu, 2002).

The function of these osteoderms remains more speculative. It is possible that there is gender-based variation within *Typothorax coccinarum* as to the number, degree, size, and extent of spiked osteoderms, and that both the Badlands Ranch and Revuelto Creek specimens happen to represent the same gender. We can envision evolutionary scenarios in which the females, the males, or both evolved more spiked ventral osteoderms for reproductive, defensive, or other purposes, but in all cases testing these hypotheses remains problematic.

CONCLUSIONS

Aetosaurs are commonly recovered fossils in Upper Triassic deposits, but most specimens are fragmentary skeletons or isolated elements represented primarily by osteoderms that can only tentatively be identified to skeletal region. Thus, articulated, largely complete specimens provide important opportunities to document not only previously undescribed elements such as the ulna, radius, and pes described here, but also further our understanding of the posture, proportions, and biology of aetosaurs.

The Bull Canyon Formation specimens support taxonomic hypotheses asserting the distinctiveness of *T. coccinarum* from *Redondasuchus* at the genus level and *T. antiquum* at the species level, and thus affirm the taxonomic significance of isolated aetosaur osteoderms. They also document that many presacral *T. coccinarum* paramedian osteoderms are naturally gently curved across the transverse width so the body was probably more dorsoventrally tall and less wide than in previous reconstructions.

The cervical vertebral series is greatly reduced in size, so much so that isolated cervicals of these (adult specimens) would likely be mistaken for juveniles if found in isolation. Importantly, the osteoderms of the cervical armor are not similarly reduced in size, but instead in number of rows, so that no more than five rows of osteoderms cover the entire cervical series. The third row possesses an elongate, dorsoventrally thin spike that extends much farther laterally than the spikes on other lateral osteoderms. Posteriorly, there is a 1:1 correspondence of vertebrae to osteoderm rows, and this also applies to the ventral osteoderms, which have six well-preserved thoracic rows and portions of two more in 10 columns between the pectoral and pelvic girdles. This is a reduction in the number of osteoderm columns relative to more primitive aetosaurs such as *Aetosaurus*, *Stagonolepis*, and *Coahomasuchus* (Heckert and Lucas, 1999, 2000), in spite of the fact that *T. coccinarum* is wider both relatively and absolutely.

The limb proportions and articulations in these specimens argue for a 'hybrid' posture, with short, sprawling or semi-erect forelimbs and dramatically longer, 'pillar-erect' hind limbs. The anatomy of the latter well-match pes impressions attributed to the footprint ichnogenus *Brachychirotherium*, and thus supports assignment of an aetosaurian trackmaker to that ichnogenus (e.g., Hunt and Lucas, 2007). Both limbs possess some adaptations for digging, and so *Typothorax* probably could have engaged in digging behaviors as well or better than many contemporaneous taxa, although its skeleton is clearly not optimized for such as lifestyle.

Importantly, these fossils appear to represent adult *Typothorax* specimens and are at least as large as any other known specimen. Thus, their restored skeletal length of 2.5 m and calculated mass estimates of ~100–104 kg demonstrate that *T. coccinarum* was actually only a medium-sized aetosaur, much smaller than the geologically older taxa *Desmatosuchus* and *Stagonolepis wellesi*. The reconstruction presented here, based on substantially complete and articulated specimens, fixes many errors of previous reconstructions by better documenting the limb position, the small number of presacral osteoderm rows (20), and a much smaller number of caudal osteoderm rows (24), and generally presenting a more accurate shape for the body.

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