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THE POSTCRANIAL SKELETON OF *REVUELTOSAURUS CALLENDERI* (ARCHOSAURIA: CRUROTARSI) FROM THE UPPER TRIASSIC OF ARIZONA AND NEW MEXICO, USA

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Abstract—*Revueltosaurus callenderi* is an armored crurotarsan that is widely distributed in early Norian (Reveultian: Barrancan) vertebrate fossil assemblages in Arizona and New Mexico. It is a highly distinctive taxon that has apomoprhic postcranial features including: (1) rectangular paramedian osteoderms with an irregular pattern of deep pits with an anterior bar that extends onto the lateral margin: and (2) wide tarsus (because of wide astragalus) that has a small astragalar medial process and corresponding medial calcaneal concavity. *R. callenderi* is a crurotarsan that may be a sister taxon of Stagonolepididae.

Key words: *Revueltosaurus*, dinosaur, aetosaur, Late Triassic, Chinle Group, Arizona, New Mexico

INTRODUCTION

Hunt (1989) described *Revueltosaurus callenderi* for teeth from the Uper Triassic of eastern New Mexico which he interpreted as an ?ornithischian. Other teeth were subsequently referred to this taxon (e. g., Padian, 1990). *Revueltosaurus callenderi* teeth are associated with obviously non-dinosaurian cranial and postcranial material and it is clear that this taxon is not dinosaurian as previously supposed (Hunt and Lucas, 2005; Parker et al., 2005a,b). The purpose of this paper is to give a preliminary description of the postcranial anatomy of *Revueltosaurus callenderi* and to utilize this to initially assess its taxonomic relationships. NMMNH refers to New Mexico Museum of Natural History and Science, Albuquerque. PEFO refers to Petrified Forest National Park, Ariona.

HISTORY OF STUDY

In 1912, E. C. Case of the University of Michigan found vertebrate fossils five miles (8 km) west of San Jon, Quay County in eastern New Mexico (Case, 1914; Hunt, 1997). Case made a small collection here that he catalogued as UMMP (University of Michigan Museum of Paleontology) 7441. UMMP 7441 is a collection of fragmentary specimens that Case identified as "fragments, limb bones, vertebrae, etc. of small phytosaurs" but that actually encompasses at least seven taxa, including *Vancleavea* (Hunt et al., 2002). UMMP 7441 also includes the proximal left femur of a crurotarsan.

In 1986, field parties from the NMMNH began to collect an extensive vertebrate fossil assemblage from the Late Triassic (Revueltian land-vertebrate faunachron (lvf): early Norian) Bull Canyon Formation of east-central New Mexico (Hunt, 1994, 2001). These specimens included teeth from NMMNH locality 1 that Hunt (1989) named *Revueltosaurus callenderi* as an ?ornithischian dinosaur. NMMNH locality 1 is the locality from which Case collected UMMP 7441 (Hunt, 1997). Other localities that yielded *Revueltosaurus callenderi* also included diverse skeletal remains. These specimens include a partial skeleton (NMMNH P-16932), and numerous more incomplete remains, of an armored crurotarsan that Hunt (1994, 2001) assigned to an undescribed new genus.

Just a few months after the initial publication of *Revueltosaurus callenderi*, three teeth of this taxon were identified from a locality at Petrified Forest National Park (PEFO) in Arizona (Padian, 1990). These teeth derive from the Painted Desert Member of the Petrified Forest Formation. In 1996, APH started the "Dawn of the Dinosaurs" project at PEFO. This ongoing project greatly increased the number of localities that yielded small terrestrial tetrapods, including dinosaurs (Hunt and Wright, 1999). As part of the project, in January 2000, Jeremiah Wright found dentulous specimens of *Revueltosaurus callenderi* at two localities (Zuni Well Mound and *Revueltosaurus* site). The Zuni Well Mound specimen consists of a partial dentary (Fig. 4A-B). The *Revueltosaurus* site specimens encompass cranial and postcranial specimens, including osteoderms (Fig. 4C-I). In 2004, a new site (PFV 297) was found at PEFO that yielded fossils consisting almost entirely of skeletal and cranial material of *Revueltosaurus callenderi* (Stocker et al., 2004; Parker and Irmis, 2005; Parker et al., 2005a,b).

Heckert (2002) named a second species of *Revueltosaurus, R. hunti,* based on teeth collected in the 1980s by Phil Bircheff from the Los Esteros Member of the Santa Rosa Formation in Santa Fe County, New Mexico. In the 1930s, C. L. Camp of the University of California found about 30 teeth of this taxon in the Blue Hills, northeast of St. Johns, Arizona (Blue Mesa Member of Petrified Forest Formation). Subsequently, Heckert (2005) erected the new genus *Kzryzanowskisaurus* for this species.

The association of *Revueltosaurus callenderi* teeth with obviously non-dinosaurian cranial and postcranial material indicates that this taxon is not an ornithischian (Hunt and Lucas, 2005; Parker et al., 2005a,b) as previously supposed.

SKELETON OF *REVUELTOSAURUS*

Referred Material

The incisiform holotype tooth (NMMNH P-4957) and paratype teeth (NMMNH P-4958, dentary/maxillary tooth; NMMNH P-4959, premaxillary tooth) of *Revueltosaurus callenderi* are from NMMNH locality 1 in the Revuelto Creek badlands of east-central New Mexico (Hunt, 1994, 2001). This locality is part of a pedogenically-modified channel-fill deposit. This bed extends laterally and encompasses other NMMNH localities, including locality 467, which yields NMMNH P-16932, a partial skeleton of *R. callenderi* that was collected in 1986 (Figs. 1- 5). We thus consider NMMNH P-16932 to be a topotype of *Revueltosaurus callenderi*. The Bull Canyon Formation also yields numerous other specimens of *Revueltosaurus* (Table 1).

NMMNH P-16932 is the most complete specimen known of *Revueltosaurus callenderi* and consists of an articulated series of dorsal osteoderms with associated osteoderms and two ribs, many other elements of comparable size and a proximal femur and right astragalus and calcaneum of a larger individual. The

articulated block consists of seven dorsal vertebrae. The anterior three vertebrae have associated paramedian osteoderms, one pair for each vertebra. The osteoderms are thick and have a deep ornamentation of rounded, irregularly placed pits. The posterior dorsal vertebra is heavily grooved, and a laterally compressed, serrated tooth (?rauisuchian) is preserved on this vertebra. Several skull fragments are present, one of which is a portion of a maxilla that preserves the tip of a replacement tooth. This tooth has large, dorsally-directed denticles. A fragment of a larger isolated tooth has a 5-mm-wide root that flares to a 6-mm-wide crown that has longitudinal striations.

Skull

The skull of *Revueltosaurus* is best represented by specimens from PEFO from the sites mentioned above and awaits complete description (Parker et al., 2005b, fig. 4A-I). Parker et al., (2005b) noted several significant aspect of the skull including: (1) ventral process of postorbital articulates with jugal medially; (2) mediolaterally expnded anterior end of squamosal; (3) posterior process of maxilla fits into slot in nasal; (4) jugal articulates with groove in quadratojugal; and (5) nasals, frontals and parietals covered by distinct sculpturing of pits and grooves. The sculpturing consists of very small pits and groves (e. g., Fig. 4D-E, F-G).

Parker et al. (2005b) note the following features of the mandible of *Revueltosaurus*: (1) dentary covered by distinct sculpturing of pits and grooves (fine pits are visible in Fig. 4A-B); (2) lack of mandibular fenestra; and (3) articular foramen completely pierces medial flange of articular. We concur with Parker et al., (2005b) there is no evidence of the presence of a predentary bone on the anterior termination of the dentary (Fig. 4H).

Axial Skeleton

The atlas (Fig. 4K-M) is approximately bow-tie shaped. Other cervical vertebra are platycoelus with ovoid articular surfaces (Fig. 1F-G). They are relatively short craniocaudally and moderately constricted mediolaterally. The caudal articular surface extends more ventrally than does the cranial surface. In anterior view, the diapophyses are pendant. The neural spine is craniocaudally long and robust. In ventral view the cervical centra have sharp ventral keels (Fig. 5F).

The dorsal vertebrae are more elongate craniocaudally than the cervical vertebrae (Fig. 1A-C). They are platycoelous and constricted mediolaterally. The neural spine is craniocaudally long, dorsoventrally tall, robust and has a prominent mediolateral expansion at the dorsal extremity (Fig. 1C).

Sacral vertebrae are slightly shorter craniocaudally than dorsal vertebrae and have prominent lateral processes for attachment to the ilium.

Pectoral Girdle

NMMNH P-16932 includes the dorsal portion of a left ?scapula (Fig. 2A-B), which is broadly triangular in shape.

Pelvic Girdle

Pelvic specimens of *Revueltosaurus* from the Bull Canyon Formation include a partial articulated pelvis (Fig. 2C-D) and proximal extremities of the pubes and ischia (Fig. 5B). The majority of the acetabulum is on the ilium. These specimens will be described in more detail elsewhere.

Hindlimb

The Bull Canyon Formation specimens encompass four proximal femora (Fig. 2E-H), including the specimen collected by Case (Fig. 3E-F) and a distal femur. The proximal femur has a rounded head reminiscent of *Alligator* and a poorly-developed fourth trochanter. The femora represent two size morphs that characterize the New Mexico collections (compare Figs. 2E-F and G-H). The Bull Canyon sample also includes a distal tibia that has a "screw joint" morphology (*sensu* Gauthier, 1984).

The ankle is represented by an associated right astragalus and calacaneum. The calcaneum has a hemicylindrical condyle for articulation with the fibula and a robust calcaneal tuber (Fig. 2I-K; Fig. 5J-K). The tuber is flattened dorsoventrally, and the transverse width is greater than its height. The calcaneal tuber has a flared end but, as noted by Parker et al. (2005), it is only expanded dorsally (Fig. 5K).

The astragalus is mediolaterally wide in cranial or caudal view. The ventral astragalo-calcaneal articulation is larger than the

TABLE 1. Specimens of *Revueltosaurus callenderi* from the Bull Canyon Formation of eastern New Mexico.

NMMNH Locality	NMMNH Spec.	Taxon	Element
1	4664	*R. callenderi*	(4) neural arches
1	4680	*R. callenderi*	(1) distal femur fragment
1	4691	*R. callenderi*	(1) left proximal femur
1	4700	*R. callenderi*	(1) distal femur
1	4869	*R. callenderi*	(1) scapula blade?
1	4888	*R. callenderi*	(1) right proximal femur (large)
1	4902	*R. callenderi*	(1) partial dorsal vertebra
1	4955	*R. callenderi*	(3) caudal vertebrae
1	4957	*R. callenderi*	incisiform tooth-isolated
1	4958	*R. callenderi*	dentary/maxillary tooth-isolated
1	4959	*R. callenderi*	premaxillary tooth-isolated
1	4960	*R. callenderi*	(28) premaxillary & dentary/maxillary teeth
1	16573	*R. callenderi*	teeth-isolated
1	16685	*R. callenderi*	(1) scute
1	16687	*R. callenderi*	(1) scute fragment
1	16919	*R. callenderi*	partial skeleton fragments
1	16920	*R. callenderi*	(1) proximal ischium
1	16922	*R. callenderi*	(36) scute fragments
1	16923	*R. callenderi*	partial carapace
1	16924	*R. callenderi*	(1) proximal ischium
1	16925	*R. callenderi*	part of a carapace
1	16928	*R. callenderi*	(1) proximal pubis fragment
1	16929	*R. callenderi*	(1) sacral vertebra
1	16930	*R. callenderi*	(1) cervical vertebra
1	16931	*R. callenderi*	(1) quadrate
1	33783	*R. callenderi*	(1) premaxillary tooth
1	33784	*R. callenderi*	(1) premaxillary tooth
1	33785	*R. callenderi*	(1) premaxillary tooth
1	33786	*R. callenderi*	(1) premaxillary tooth
1	33787	*R. callenderi*	(1) premaxillary tooth
1	33788	*R. callenderi*	(1) premaxillary tooth
1	33789	*R. callenderi*	(1) premaxillary tooth
1	33790	*R. callenderi*	(1) premaxillary tooth
1	33791	*R. callenderi*	(1) premaxillary tooth
1	33792	*R. callenderi*	(1) maxillary/dentary tooth
1	33793	*R. callenderi*	(1) maxillary/dentary tooth
1	33794	*R. callenderi*	(1) maxillary/dentary tooth
1	33795	*R. callenderi*	(1) maxillary/dentary tooth
1	33796	*R. callenderi*	(1) maxillary/dentary tooth
1	33797	*R. callenderi*	(1) maxillary/dentary tooth
1	33798	*R. callenderi*	(1) premaxillary tooth
1	45559	*R.* sp.	(1) small maxillary/dentary tooth (incomplete)
132	4426	*R. callenderi*	(1) tooth-isolated
162	4665	*R. callenderi*	1-cervical,7-dorsal,2-dorso-sacral,ant.caudal
171	16637	*R. callenderi*	(1) tooth fragment-isolated
171	16730	*R. callenderi*	(1) neural spine
182	16912	*R. callenderi*	(1) iliac blade
467	16932	*R. callenderi*	partial skeleton
498	17187	*R. callenderi*	tooth-isolated
523	17455	*R. callenderi*	scute fragments
523	17459	*R. callenderi*	(5) dorsal vertebrae fragments
526	17362	*R. callenderi*	teeth
526	17382	*R. callenderi*	(1) tooth fragment-isolated
527	17474	*R. callenderi*	(2) scute fragments
534	17384	*R. callenderi*	(1) scute fragment
535	17352	*R. callenderi*	(1) distal tibia fragment

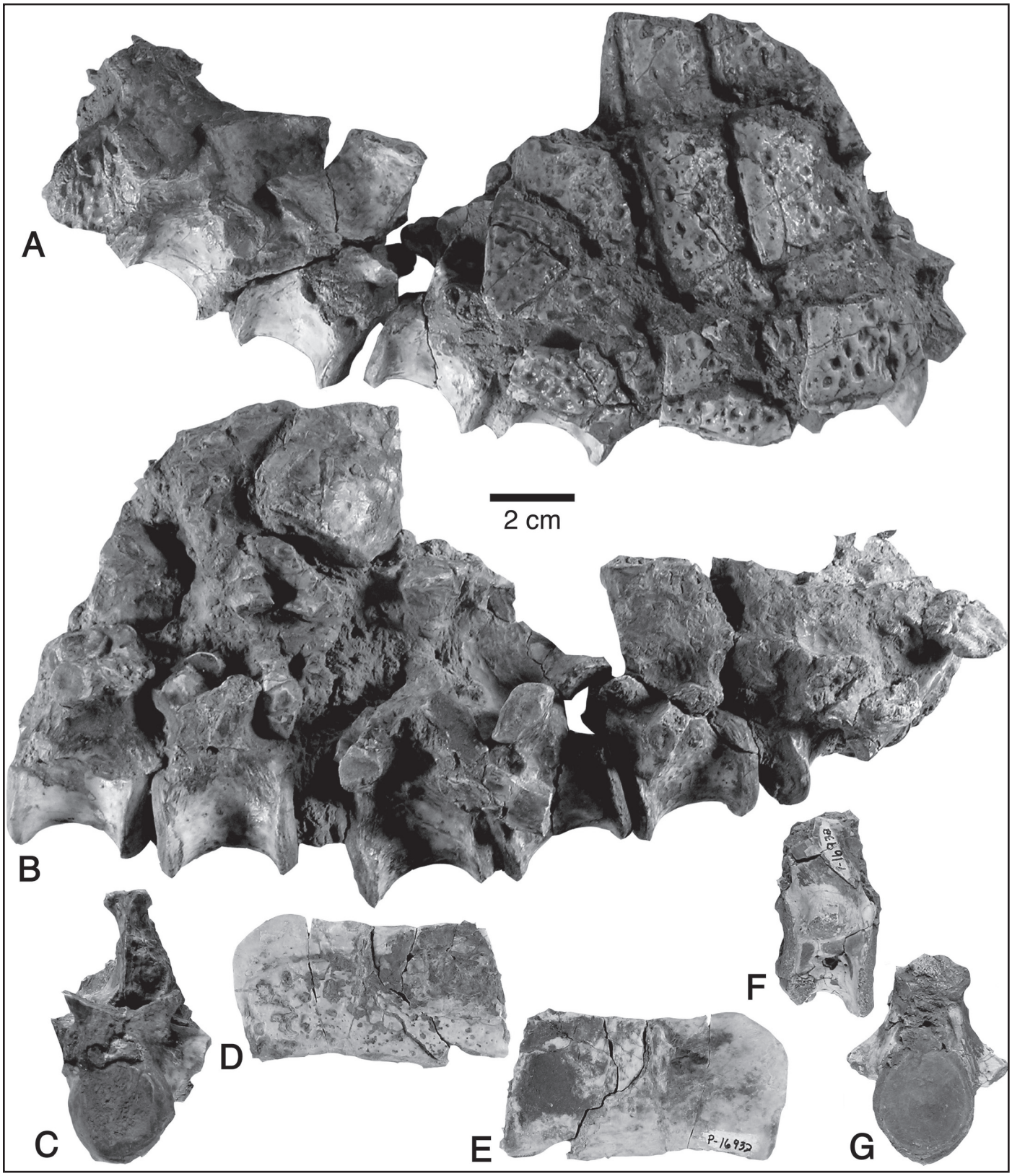

FIGURE 1. Skeleton of *Revueltosaurus callenderi* (NMMNH P-16932) from the Bull Canyon Formation of east-central New Mexico. **A-B**, Dorsal vertebral series with associated osteoderms in right (A) and left (B) lateral views. **C**, Dorsal centrum in cranial view. **D-E**, Paramedian osteoderm in dorsal (D) and ventral (E) views. **F-G**, Partial cervical vertebra in right lateral (F) and cranial (G) views. All scale bars = 2 cm.

dorsal articulation. The peg-and-socket articulation between the astragalus and calcaneum is well-developed, but is not as deep as in derived crurotarsans such as stagonolepidids.

Osteoderms

Numerous osteoderms are in the NMMNH collection. There

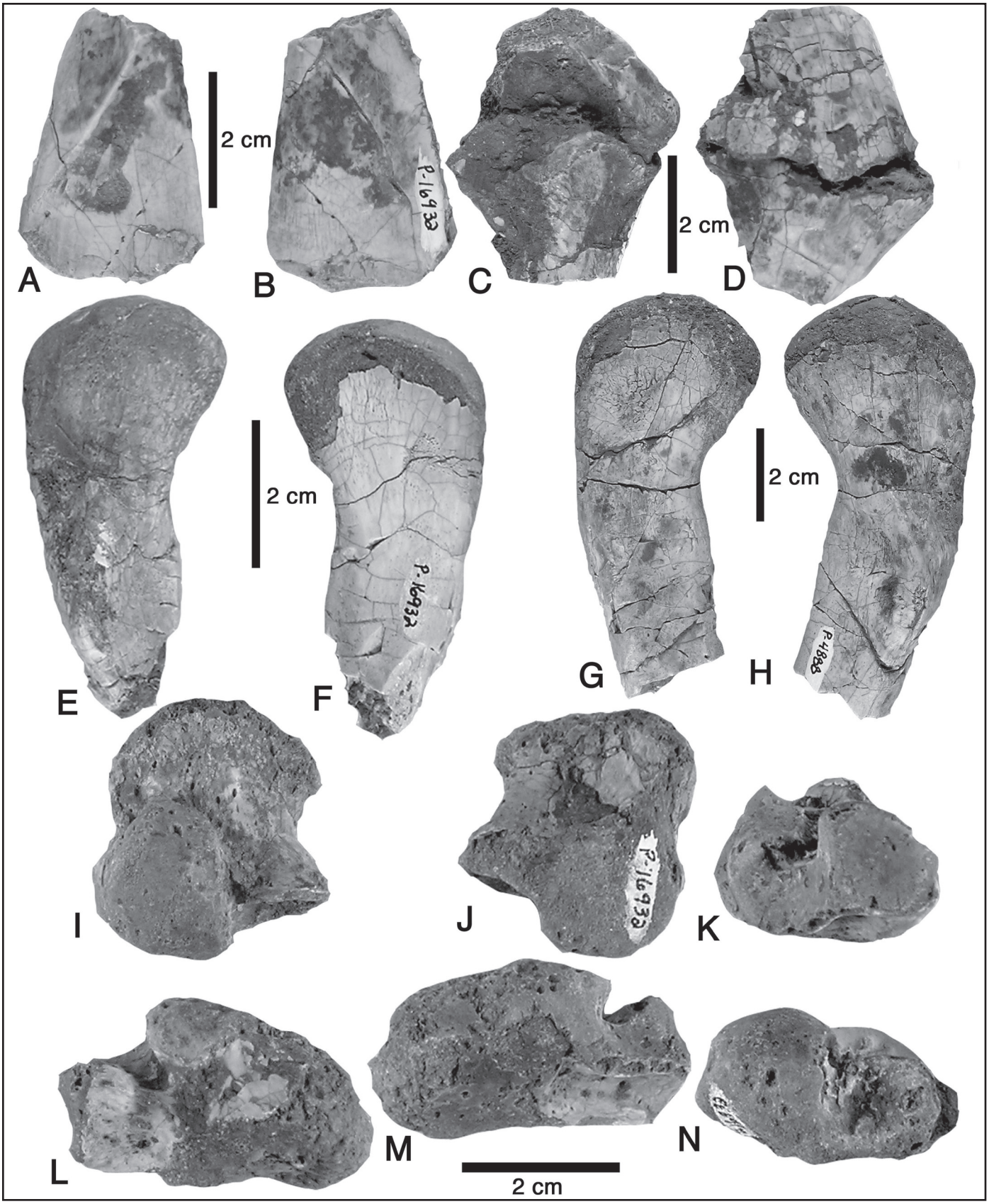

FIGURE 2. Topotype postcranial elements of *Revueltosaurus callenderi* from the Bull Canyon Formation of east-central New Mexico. **A-B**, NMMNH P-16932, ?Dorsal extremity of left scapula in lateral (A) and medial (B) views. **C-D**, NMMNH P-16932, Partial articulated pelvis (ilium and pubis) in lateral (C) and medial (D) views. **E-F**, NMMNH P-16932, proximal left femur in caudal (E) and cranial (F) views. **G-H**, NMMNH P-4888 proximal right femur in cranial (G) and caudal (H) views. **I-J, N**, NMMNH P-16932, right calcaneum in dorsal (I), ventral (J) and cranial (N) views. **K-M**, NMMNH P-16932, Right astragalus in medial (K), dorsal (L), and ventral (M) views. All scale bars = 2 cm.

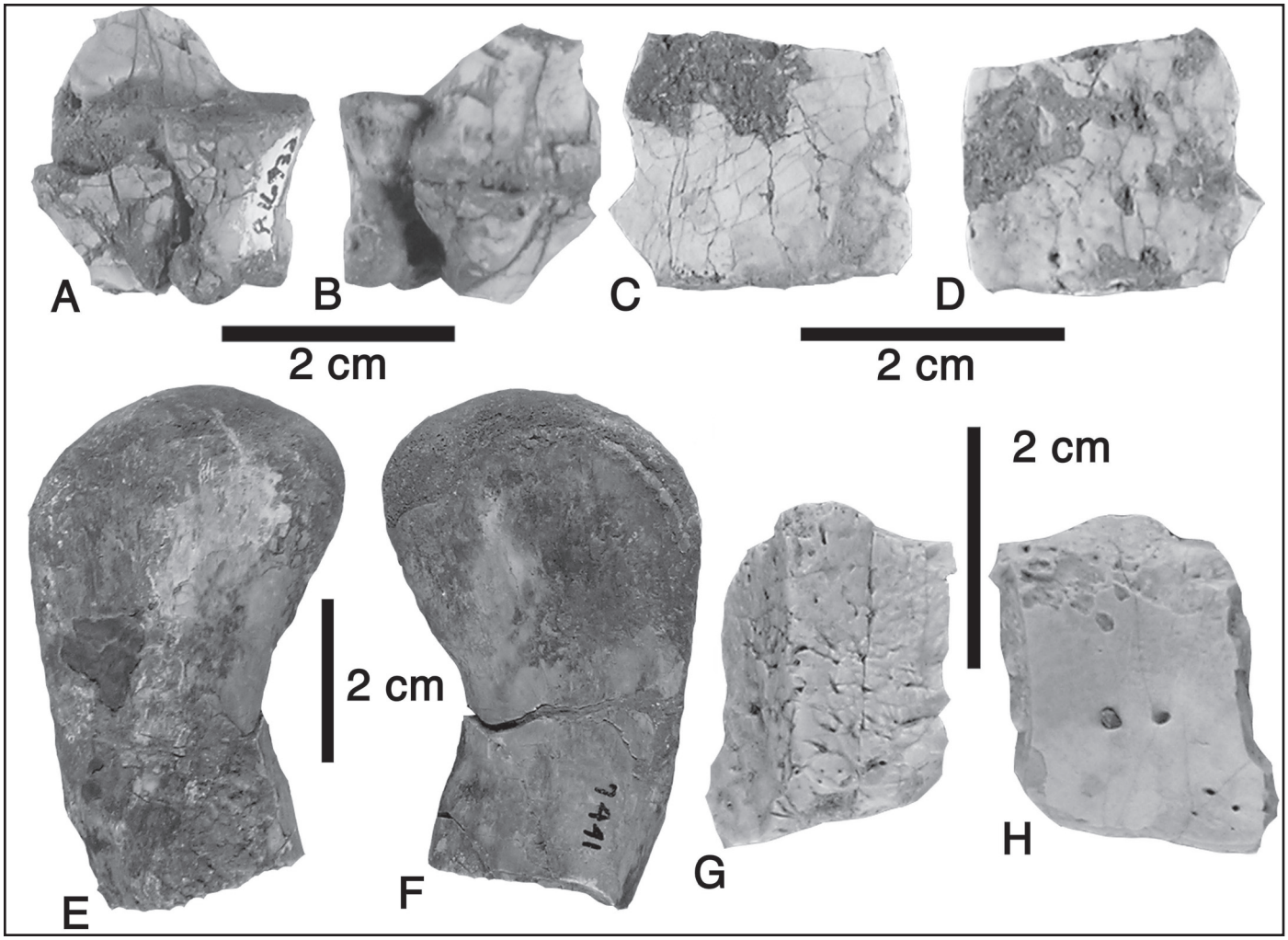

FIGURE 3. Postcranial elements of *Revueltosaurus callenderi* from the Bull Canyon Formation of east-central New Mexico and the Painted Desert Formation at Petrified Forest National Park. **A-B**, NMMNH P-16932, topotype articulated partial pes? **C-D**, PEFO unnumbered, caudal osteoderm in ventral (C) and dorsal (D) views from Dinosaur Hill. **E-F**, UMMP 7441, topotype proximal left femur in caudal (E) and cranial (F) views. **G-H**, NMMNH P-16932, topotype caudal osteoderm in dorsal (G) and ventral (H) views. All scale bars = 2 cm.

is a single osteoderm pair per vertebra. A complete paramedian osteoderm (NMMNH P-16932) is rectangular and is 64 mm long, 33 mm wide and 5 mm thick (Figs. 1D-E, 5C). The dorsal surface is covered by an irregular pattern of deep, rounded pits. The medial end of the osteoderm is thickened. The osteoderm thins at its lateral and anterior margins. An anterior (unraised) bar extends along the anterior edge of the osteoderm and the cranial half of the lateral margin. This suggests the presence of lateral osteoderms that have not yet been recognized. Ventrally there is a craniocaudal-oriented ridge at about the midpoint of the osteoderm (Fig. 1E). Caudal osteoderms include sub-rectangular forms that are arched around a sharp midline keel (Fig. 4G).

RELATIONSHIPS OF *REVUELTOSAURUS CALLENDERI*

Revueltosaurus callenderi represents a crurotarsan (*sensu* Sereno, 1991) because it possesses: (1) a hemicylindrical calcaneal condyle for the fibula; (2) a flexed tibial facet on the astragalus; (3) a single articulation between astragalus and calcaneum; and (4) a single paramedian osteoderm pair per vertebra (Benton and Clark, 1988; Sereno, 1991). Further, it is assignable to a clade containing derived crurotarsans (= Suchia of Sereno, 1991) on the basis of an advanced "crocodile-normal" tarsus (Benton and Clark, 1988). However, the pit in the calcaneum to receive the astragalar process is shallower than in other members of this clade and thus is arguably less derived. The heavy dorsal armor is reminiscent of the aetosaurs, but there are no lateral osteoderms preserved. There is currently little consensus about the interrelationships of crurotarsans, so we hesitate to offer definite conclusions on the relationships of *Revueltosaurus*. However, based on the tarsal configuration, this taxon appears to be more derived than Phytosauria, but less derived than Stagonolepididae. Indeed, Hunt (1994, 2001) considered that it might be a sister taxon of the latter.

LIFESTYLE

The orientation of the large denticles and wear facets indicates that *Revueltosaurus callenderi* was herbivorous (Hunt, 1989; Hunt and Lucas, 1994; Heckert, 2002, 2004). This is consistent with the heavy dorsal armor, which is rare in carnivores that are not semiaquatic. The articulated specimen represents an animal about 1.5 m long. Other specimens indicate individuals about twice as large. The taphonomy and faunal associations of *Revueltosaurus* sites (e. g., NMMNH locality 1; Dinosaur Hill) indicate a terrestrial ecology.

BIOSTRATIGRAPHY OF *REVUELTOSAURUS*

There are two fossil assemblages present within the Bull

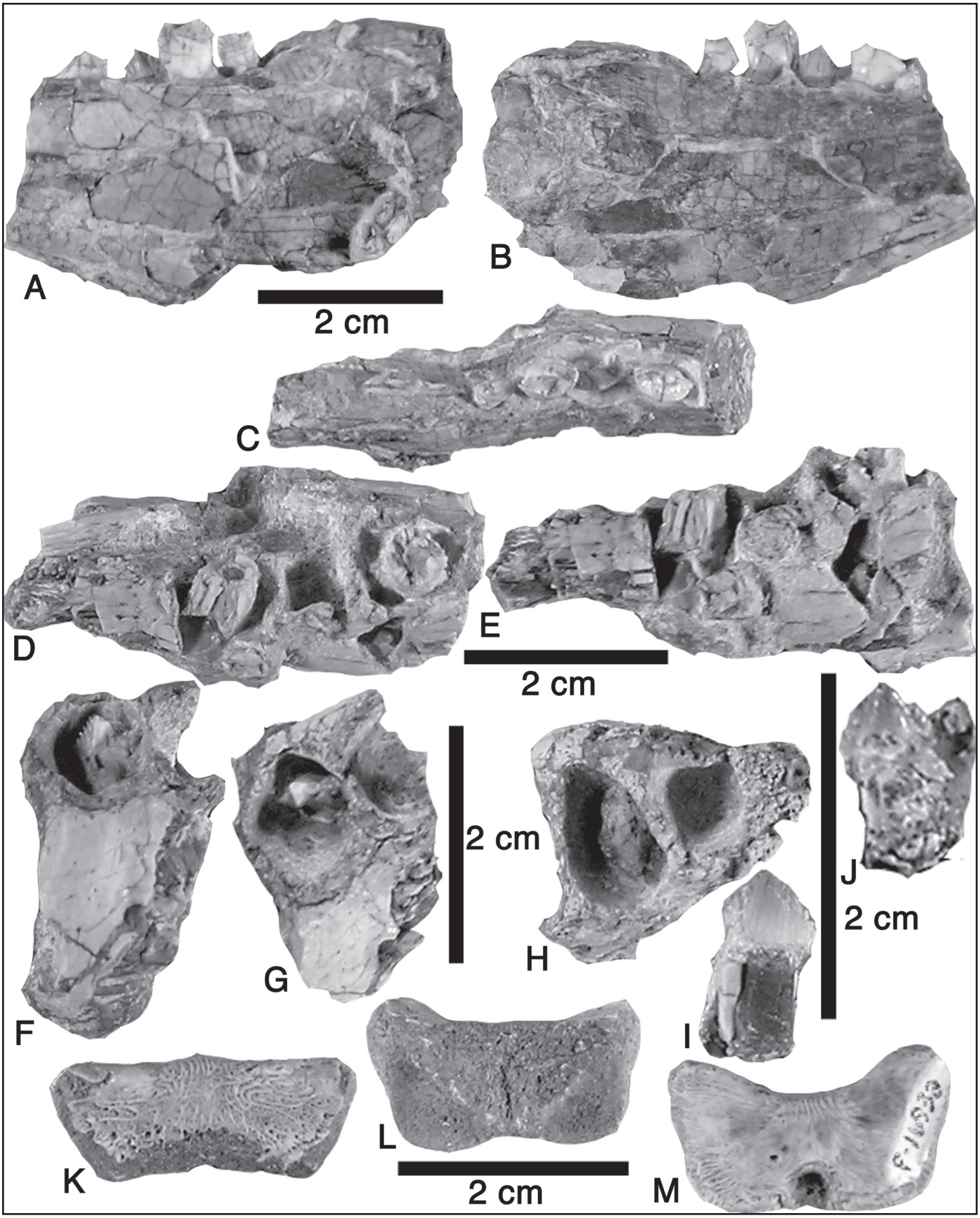

FIGURE 4. Cranial, mandibular and vertebral specimens of *Revueltosaurus callenderi* from the Bull Canyon Formation of east-central New Mexico and the Painted Desert Formation at Petrified Forest National Park. **A-C**, PEFO unnumbered, partial dentary from Zuni Well Mound in medial (A), lateral (B) and dorsal (C) views. **D-E**, PEFO unnumbered, partial maxilla from *Revueltosaurus* site in occlusal view. **F**, PEFO unnumbered, partial dentary from *Revueltosaurus* site. **G**, PEFO unnumbered, partial dentary from *Revueltosaurus* site. **H**, PEFO unnumbered, partial dentary from *Revueltosaurus* site. **I**, PEFO unnumbered, maxillary/dentary tooth in lingual view from *Revueltosaurus* site. **J**, PEFO unnumbered partial dentary from *Revueltosaurus* site in lateral view. **K-M**, NMMNH P-16932, Atlas in caudal (K), dorsal (L), and ventral (M) views. All scale bars = 2 cm.

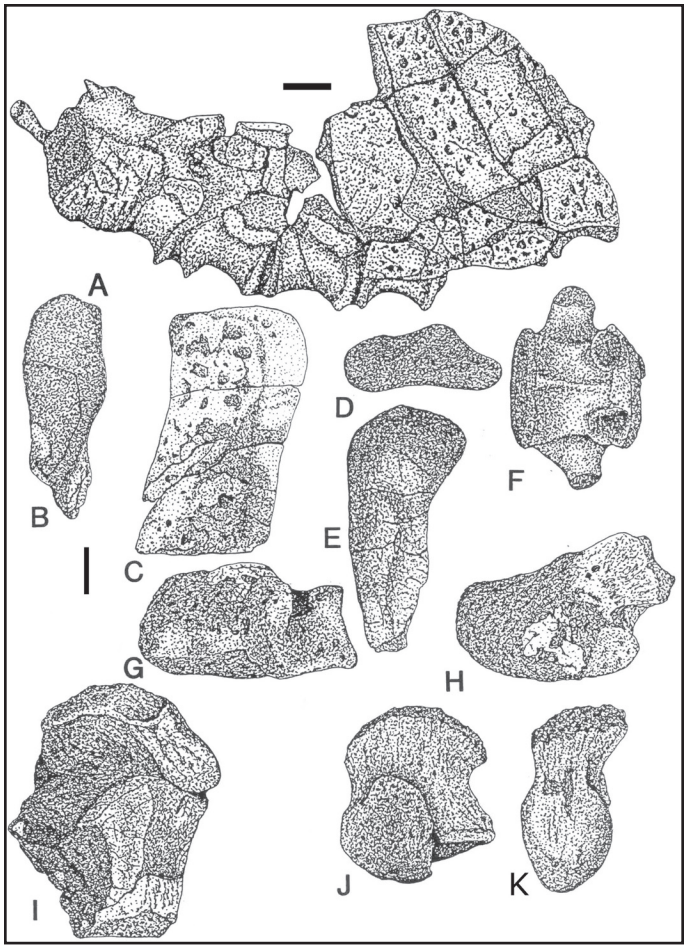

FIGURE 5. Topotype skeleton of *Revueltosaurus callenderi* (NMMNH P-16932) from the Bull Canyon Formation of east-central New Mexico. **A**, Dorsal vertebral series with associated osteoderms in right views. **B**, Proximal ischium in dorsal view. **C**, Paramedian osteoderm in dorsal views. **D-E**, Proximal left femur in proximal (D) and caudal (E) views. F, Cervical vertebra in ventral view. **G-H**, Right astragalus in ventral (G) and cranial (H) views. **I**, Partial articulated pelvis (ilium and pubis) in medial view. **J-K**, Right calcaneum in dorsal (J) and lateral (K) views. Scale bar = 1 cm.

Canyon Formation of east-central New Mexico (Hunt, 1994, 2001). The lower assemblage occurs in the basal 50 m of the formation in the Revuelto and Barranca badlands and in the lower part of Bull Canyon. The upper assemblage is restricted to the upper part of the formation in Bull Canyon. Taxa in common between the faunas include "Colobontidae", Redfieldiidae, *Apachesaurus*, Squamata, *Pseudopalatus*, *Typothorax*, *Shuvosaurus*, Rauisuchidae and Herrerasauridae (small).

Taxa restricted to the lower assemblage include *Semionotus*, ?*Tanaocrossus*, *Quayia*, Metoposauridae (large), *Pseudopalatus* n. sp., *Aetosaurus*, Stagonolepididae gen. et sp. nov., *Paratypothorax*, *Desmatosuchus*, *Postosuchus*, Sphenosuchidae, Herrerasauridae gen. et sp. nov. 1 , Theropoda *incertae sedis* gen. et sp. nov. and *Revueltosaurus*. Taxa restricted to the upper assemblage are Herrerasauridae gen. et sp. nov. 2, *Lucianosaurus* and *Pseudotriconodon*.

Petrified Forest National Park (PEFO) preserves the most fossiliferous nonmarine sequence across the Carnian-Norian boundary. This rock sequence encompasses, in ascending order, the Blue Mesa (late Carnian), Sonsela Sandstone (Norian) and Painted Desert (early-middle Norian) members of the Petrified Forest Formation and the Owl Rock Formation (middle Norian).

Revueltosaurus is found at 12 localities at PEFO in a narrow stratigraphic interval near the base of the Norian Painted Desert Member between the Sonsela Sandstone and Black Forest Bed of the Painted Desert Member (e.g., Dinosaur Hill, Dinosaur Hollow, RAP Hill, Zuni Well Mound). Localities that are higher in the Painted Desert Member, and above the Black Forest Bed, lack *Revueltosaurus* (Howard's End, Judy's Luck and Ted's Tip)(Beuhler et al., 2001; Hunt, 2003).

In conclusion, *Revueltosaurus* is restricted the lower portion of the Painted Desert Member of the Petrified Forest Formation at Petrified Forest National Park and the lower portion of the Bull Canyon Formation in eastern New Mexico.

BIOCHRONOLOGY OF *REVUELTOSAURUS*

Lucas and Hunt (1993) named a series of land-vertebrate faunachrons (lvf) for the Late Triassic of western North America. The Revueltian lvf was based on the assemblage of the Bull Canyon and Trujillo formations in the Revuelto Creek area (Barranca and Revuelto badlands of this report). Lucas (1998) provided a formal definition of the Revueltian lvf and identified its characteristic assemblage as that of the Bull Canyon Formation in east-central New Mexico (Quay and Guadalupe counties). Lucas and Hunt (1993) listed the index taxa of the Revueltian to be *Pseudopalatus* and *Typothorax,* and Lucas (1998) added *Aetosaurus* to this list. Lucas (1998) defined the base of the Revueltian as the First Appearance Datum (FAD) of *Pseudopalatus*. Diverse vertebrate, pollen, magnetostratigraphic and sequence stratigraphic data indicate that the Revueltian is equivalent to most, if not all, of Norian time (e. g., Litwin, 1986; Litwin et al., 1991; Ash, 1987; Good, 1993; Hunt, 1994; Lucas, 1991, 1993, 1998).

Hunt (2001) divided the Revueltian into two sub-land-vertebrate-faunachrons (sub-lvfs). The Barrancan sub-lvf is based on the vertebrate fauna from Barranca Creek and it begins with the FAD of the phytosaur *Pseudopalatus* spp. Among the index taxa of the Barrancan are the coelacanth *Quayia zideki*, *Revueltosaurus callenderi* and a new species of the phytosaur, *Pseudopalatus* sp. nov. The principal correlatives are the Post quarry and associated faunas of the lower Bull Canyon Formation, Garza County, Texas and the lower fauna of the Painted Desert Member of the Petrified Forest Formation (below the Black Forest Bed), Petrified Forest National Park and environs, Apache County, Arizona.

The Lucianoan sub-lvf is based on the fauna of the upper Bull Canyon Formation at Bull Canyon and Luciano Mesa, and it begins with the FAD of *Lucianosaurus*. Index taxa include the mammal-like reptile *Pseudotriconodon*. The principal correlatives are the Canjilon quarry and other localities from the upper Petrified Forest Formation, Rio Arriba County, New Mexico and the Owl Rock Formation of Arizona (Kirby, 1989, 1991). This sub-lvf is also easy to recognize on the basis of an aetosaur fauna that includes *Typothorax coccinarum*, but not *Aetosaurus arcuatus*, or *Paratypothorax* sp. But, the FAD of *Lucianosaurus* is weak because of its restricted distribution and low abundance. Thus, *Revueltosaurus callenderi* is an index taxon of a robust biochronologic unit, the Barrancan sub-lvf of the Revueltian lvf.

HERBIVOROUS ARCHOSAURS DURING THE LATE TRIASSIC

As noted by Parker et al. (2005b), the assignment of *Revueltosaurus callenderi* to the Crurotarsi calls into question the assignment of Late Triassic isolated teeth to the Ornithischia. Dental characters have been featured in all cladistic definitions and discussions of the Ornithischia (Table 2). *Revueltosaurus callenderi* appeared to be the most believable ornithischian based on isolated teeth because it includes both forms of teeth found in basal ornithischians (premaxillary and dentary/maxillary). Other putative Triassic ornithischians include only one form of tooth morphology (Hunt and Lucas, 1994). The only features that appear tenable to define

TABLE 2. Dental definitions of Ornithischia

	Gauthier (1986)	*Sereno (1986)*	*Sereno et al. (1993)*	*Hunt and Lucas (1994)*	*Heckert (2002, 2004)*	*Weishampel (2004)*	*Norman et al. (2004)*
Overall	Cheek teeth with distinct crown and root. Crown of cheek teeth low, bulbous basally, subtriangular in profile.	Low, triangular-shaped tooth crowns in lateral view. Recurvature absent in maxillary and dentary teeth. Well-developed neck separating crown from root.	Subtriangular maxillary/ dentary crowns.	Low, triangular tooth crown in lateral view. Recurvature absent from maxillary and dentary teeth. Well developed neck separating crown from root. Premaxillary teeth distinct from dentary/maxillary teeth. Maxillary and dentary teeth asymmetrical in mesial and distal views.	Tooth crowns expanded basally and asymmetrical in dorsal view. Six premaxillary teeth. Low, triangular tooth crowns in lateral view. Recurvature absent in maxillary and dentary teeth. Well developed neck separating crown from root. Premaxillary teeth distinct from dentary/maxillary teeth. Maxillary and dentary teeth asymmetrical in mesial and distal views.		Six slightly bulbous, conically pointed premaxillary teeth. Maxillary and dentary teeth with cylindrical roots separated from the crown by a constriction; the base of the crown expanded to form a cingulum. The maxillary and dental crowns laterally compressed and broadly triangular in lateral profile, with a thick central portion. The crowns of the teeth wider at the base than at the roots and consequently.
Denticles	Cheek teeth bear enlarged accessory denticles on margins.			Prominent large denticles arranged at 45° or greater to the mesial and distal edges.	Coarse denticles oblique to the tooth margin.	Maxillary & dental crowns have denticulated mesial & distal margins.	Mesial and distal edges of the maxillary and dentary crowns bearing a fringe of five to nine simple, pointed denticles.
Placement		Overlap of adjacent crowns in maxillary and dentary teeth.					Maxillary and dentary teeth arranged in an *en echelon* fashion; the long axis of the crown offset from the long axis of the root in mesial or distal view.
Maximum size		Maximum tooth size attained near the central, or posterior central, portion of the maxillary & dentary rows.	Largest maxillary/ dentary tooth in centre of tooth row.				

Ornithischia in the face of the surprising occurrence of both forms of "ornithichiaform" teeth in a non-dinosaur are (Table 2): (1) largest maxillary / dentary tooth in center of tooth row; (2) maxillary and dentary teeth with cylindrical roots separated from the crown by a constriction *and the base of the crown expanded to form a cingulum* (Sereno, 1986; Norman et al., 2004) and (3) maxillary and dentary teeth arranged in an *en echelon* fashion; the long axis of the crown offset from the long axis of the root in mesial or distal view (Norman et al., 2004).

There are several Late Triassic reptiles from North America, known solely, or principally, from teeth (e.g., Hunt and Lucas, 1994; Heckert, 2004, 2005). Several of these have "ornithichiaform" teeth which resemble *Revueltosaurus* (Table 3). *Technosaurus* and *Krzyzanowskisaurus* (Chatterjee, 1984; Heckert, 200, 2005) are the most likely to represent ornithischians (Table 3). The other taxa (*Galtonia, Tecovasaurus, Protecovasaurus, Pekinosaurus, Tecovasaurus, Lucianosaurus*) may represent revueltosaurs. Ornithischians appear not to have been as numerous in the Late Triassic as previously considered (Hunt and Lucas, 1994).

Clearly, there were several lineages of herbivorous archosaurs in the Late Triassic: prosauropods (many taxa), revueltosaurs, ornithischians (*Pisanosaurus*, unnamed heterodontosaur of Báez and Marsicano, 2001), possible ornithischians (*Technosaurus*), *Krzyzanowskisaurus*), aetosaurs, and *Silesaurus* (Dzik, 2003). This abundance of forms is not surprising considering the explosive radiation of archosaur lineages in the latter half of the Triassic. Aetosaurs are generally considered to be the principal herbivores in the Late Triassic but they are extremely specialized cranially and underived dentally. These features suggest that there might have been ecological niches available for exploitation by other herbivores.

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TABLE 3. Affinities of putative ornithischian taxa from North America.

Genus	Material	Ornithischian?	References
Technosaurus	Dentary	Probably ornithischian because: (1) imbication of tooth crowns; (2) increase in tooth size to posterior center of tooth row; (3) tooth row not marginal.	Chatterjee (1984); Sereno (1991); Hunt and Lucas (1994)
Galtonia	Premaxillary teeth	Equivocal: could be premaxillary teeth of an ornithischian or a revueltosaur.	Hunt and Lucas (1994)
Pekinosaurus	Dentary/maxillary teeth	Equivocal: possibly ornithischian because the crowns are more elongate than *Revueltosaurus* which may have required imbrication, but no cingulum.	Hunt and Lucas (1994)
Tecovasaurus	Dentary/maxillary teeth	Equivocal: but probably not ornithischian as no cingulum.	Hunt and Lucas (1994)
Lucianosaurus	Dentary/maxillary teeth	Equivocal: but probably not ornithischian as no cingulum.	Hunt and Lucas (1994)
Protecovasaurus	Dentary/maxillary teeth	Equivocal: but probably not ornithischian as no cingulum.	Heckert (2004)
Crosbysaurus	Dentary/maxillary teeth	Equivocal: but probably not ornithischian as no cingulum.	Heckert (2004)
Krzyzanowskisaurus	?Dentary/maxillary teeth	Equivocal: but probably an ornithischian as some teeth bear a cingulum.	Heckert (2002, 2005)

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