REVISION OF REDONDASUCHUS (ARCHOSAURIA: AETOSAURIA) FROM THE UPPER TRIASSIC REDONDA FORMATION, NEW MEXICO, WITH DESCRIPTION OF A NEW SPECIES

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Abstract-We describe a new species of aetosaur, Redondasuchus rineharti, based on isolated scutes and an incomplete femur from a single locality in the Upper Triassic Redonda Formation of east-central New Mexico. R. rineharti is distinguished from R. reseri, the only other species of Redondasuchus, by its scute morphology, specifically by its large size, presence of a boss at the point of flexure and mediolaterally-oriented row of pits immediately posterior to the anterior bar. Various workers have proposed that Redondasuchus should be synonymized with Typothorax coccinarum, but we review their arguments and find no justification for this synonymy.

INTRODUCTION

Aetosaurs are a suborder of archosaurs known from Upper Triassic strata of North and South America, Greenland, Europe, India, North Africa and Madagascar (Heckert and Lucas, 2000). Aetosaurs are principally known from armor scutes that form a carapace around their neck, trunk and tail. Associated and articulated specimens are rare, but individual scutes have taxonomic utility, allowing identification to genus or species level (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 2000).

The aetosaur genus Redondasuchus was named by Hunt and Lucas (1991) based on isolated scutes from two collecting areas, Apache Canyon and Shark Tooth Hill, both in the Upper Triassic Redonda Formation of east-central New Mexico. Recently, new material of a second species of Redondasuchus has been recognized from the Redonda Formation. Here, we rediagnose the genus, describe the new species and address issues concerning the taxonomic validity of Redondasuchus presented by Long and Murry (1995) and Martz (2002). In this paper, NMMNH = New Mexico Museum of Natural History and Science, Albuquerque, and UCMP = University of California Museum of Paleontology, Berkeley.

SYSTEMATIC PALEONTOLOGY **ARCHOSAURIA AETOSAURIA STAGONOLEPIDIDAE** Redondasuchus

Type Species: Redondasuchus reseri Hunt and Lucas.

Revised Diagnosis: Redondasuchus is differentiated from all other aetosaurs by the strong flexure (approximately 45°) of its dorsal paramedian scutes one-third of the distance from the medial to the lateral edge of the scute, and external ornamentation of the scutes, consisting solely of densely packed pits that lack a radial pattern.

Discussion: The interpretation of the orientation of flexure in the diagnosis of the genus Redondasuchus presented here (Fig. 1) differs from that of previous studies (Hunt and Lucas, 1991; Heckert et al., 1996). These studies suggested that, for the mid-dorsal paramedian scutes, the point of flexure was "two-thirds of the lateral distance from the medial to lateral edge of the scute" (Heckert et al., 1996, p. 620). However, we believe that this is incorrect and that the point of flexure instead lies one-third of the lateral distance from the medial to lateral edge of the scute (Fig. 1). This changes the conception of how the scutes are flexed; previous interpretations had the point of flexure between the medial two-thirds of the scute and the lateral third, while our interpretation has the point of flexure between the medial third of the scute and the lateral two-thirds.

The confusion is due to the holotype of Redondasuchus reseri, and thus of the genus Redondasuchus, being identified as a left dorsal paramedian scute. Although both Hunt and Lucas (1991) and Heckert et al. (1996) acknowledge an anterior bar, this is not congruent with the holotype scute being a left dorsal paramedian. In addition, Heckert et al. (1996) mislabeled their figure 5b as a posterior view, even though it is an anterior view of the holotype scute. This confusion is exacerbated by the scute always being figured, in dorsal view, with its anterior margin oriented toward the bottom of the page; this runs counter to typical protocol, which has the anterior margin facing the top of the page in dorsal view. Thus, we revise the orientation of the holotype scute of R. reseri and interpret it as a right dorsal paramedian, which makes the point of flexure one-third of the lateral distance along the scute. Although this is a change in the way Redondasuchus scutes are interpreted, it does little to fundamentally change the reconstruction of Redondasuchus as illustrated by Heckert et al. (1996, fig. 5). In the cross-sections of Heckert et al. (1996, fig. 5), it is clear that all of the dorsal and caudal paramedians are flexed one-third of the way from their medial margin, except for the holotype (Heckert et al., 1996, fig. 5c). This reevaluation of the holotype actually makes the scute flexure more consistent throughout the carapace (Fig. 1).

Redondasuchus reseri Hunt and Lucas, 1991 Figure 1

- 1985 Typothorax sp.: Lucas et al., p. 199, fig. 3f-g. 1991 Redondasuchus reseri: Hunt and Lucas, p. 728, figs. 2-3.
- 1996
- Redondasuchus reseri: Hekcert et al., p. 619, figs. 3-6.
- 2000 Redondasuchus reseri: Heckert and Lucas, p.1558, fig. 5d-e.

Revised Diagnosis: A species of Redondasuchus that is distinguished from *R. rineharti* by the small size (width <10 cm) of its dorsal paramedians, with possession of a ventral keel that extends laterally from the point of flexure and a lack of any raised bosses on the dorsal scute surface.

Redondasuchus rineharti, sp. nov. Figures 2-4

Holotype: NMMNH P-43312, an incomplete right dorsal paramedian scute (Fig. 2).

Type Locality and Horizon: Redonda Formation (Chinle Group) at NMMNH locality 2671 in Apache Canyon, Quay County, New Mexico.

Paratypes: All paratypes are also from NMMNH locality 2671: NMMNH P-25770, an incomplete left paramedian scute (Fig. 3A-C); NMMNH P-43311, an incomplete left paramedian (Fig. 3D-F); NMMNH P-50745, a proximal right femur (Fig. 4).



FIGURE 1. Previous interpretations of the orientation and carapace reconstruction of *Redondasuchus reseri* contrasted with our revised interpretation. The labels on the scutes indicate the margin direction. The specimen figured is NMMNH C-3171, a cast of the holotype (UCMP 6148/65415). The carapace reconstruction is from Heckert et al. (1996, fig. 5).

Etymology: In honor of Larry Rinehart, chief preparator of the New Mexico Museum of Natural History and Science, for his contributions to Late Triassic paleontology in the field, in the museum and as a researcher.

Diagnosis: A species of *Redondasuchus* that differs from *R. reseri* by the large size (width >10cm) of its dorsal paramedian scutes, possession of a circular boss on the posterior edge of the scute at the point of flexure, a ventral keel that extends laterally from the medial margin of the scute to the point of flexure, and a mediolaterally-oriented row of pits immediately posterior to the anterior bar.

Description: The holotype (NMMNH P-43312) is an incomplete dorsal paramedian scute preserving the lateral two-thirds of the scute, with portions of its anterior margin and its medial one-third missing (Fig. 2). The holotype scute, as preserved, is 103 mm long and 221 mm wide. The boss at the point of flexure is incomplete, missing its medial third. The anterior bar is fragmented, but the mediolateral row of pits posterior to the anterior bar can be clearly discerned. The posterior margin of the scute is the only border that is intact. Ventrally, the keel is thickest at the point of flexure and thins laterally. Like *Redondasuchus reseri*, the keel is anterior to the mediolateral midline of the scute.

NMMNH P-25770, also from NMMNH locality 2671, is the lateral fragment of a large paramedian scute (Fig. 3A-C). The fragment is 107 mm long and 172 mm wide. The medial two-thirds of the scute are missing, and a small portion of the prominent anterior bar has been broken off. The bar lies immediately anterior to a mediolaterally-oriented row of small pits; this is the best example of this feature among the referred material. The rest of the pitting on the scute appears fairly random with no discernable radial pattern.

NMMNH P-43311, another dorsal paramedian from the same locality, is incomplete, missing portions of its anterior, posterior and medial margins (Fig. 3D-F). It measures 73 mm long and 226 mm wide, as



FIGURE 2. *Redondasuchus rineharti*, NMMNH P-43311 from locality 2671, holotype left paramedian scute. **A**, Dorsal view. **B**, Ventral view. **C**, Anterior view.

preserved. In anteroposterior view, the scute displays the characteristic flexure of *Redondasuchus*. In addition, there is a boss developed at the point of flexure between the medial one-third and lateral two-thirds of the scute, which makes it referable to *R. rineharti*.

A large proximal right femur (NMMNH P-50745) collected from the same locality is referred to *Redondasuchus rineharti*. The robust nature of the femur and the hypertrophied fourth trochanter are is characteristic of aetosaurs (Fig. 4). Given the association of this femur with osteoderms of *R. rineharti* and lack of other large aetosaurs in the Redonda Formation, it is most parsimonious to refer this specimen to this species. The femur is complete above the level of the fourth trochanter, and is the first to be found in association with *Redondasuchus* scutes. It is of considerable size, measuring 174 mm long, as preserved, with a proximal end that is 50 x 97 mm wide.

Discussion: The holotype of *Redondasuchus rineharti* and all the referred specimens come from a single site, NMMNH locality 2671, and, based on the relative consistency of size these elements, likely belonged to a single individual. The size of this individual requires a revision of previous ideas regarding the size of *Redondasuchus*. Hunt and Lucas (1991, p. 733) stated that "*Redondasuchus* is also appreciably smaller than other described North American aetosaurs." This is true for *R. reseri*, which is known exclusively from small scutes and is thus interpreted as being 1 m or less in overall body length, making it similar in size to *Aetosaurus* and *Coahomasuchus*. However, the size of the scutes and the femur suggest that *R. rineharti* is about the same size as *Typothorax* and most other large North American aetosaurs, approximately 2-3 m in overall body length (e.g., Hunt et al., 1993; Long and Murry, 1995). We note that the two distinct size classes represented by *R. reseri* and *R. rineharti* suggest that the differences in scute morphol-



FIGURE 3. A-C, *Redondasuchus rineharti*, NMMNH P-25770 from locality 2671, lateral fragment of paratype left paramedian scute in A, dorsal, B, ventral and C, anterior views. D-F, *Redondasuchus rineharti*, NMMNH P-43311 from locality 2671, incomplete paratype paramedian scute in D, anterior, E, dorsal and F, ventral views.

ogy are not due to ontogeny and are thus likely due to species-level differences. At the time of its discovery, *Redondasuchus reseri* was the smallest documented aetosaur from the American Southwest. However, it is probably larger than either *Aetosaurus* or *Coahomasuchus*, both of which have been reported form the Chinle (e.g., Heckert and Lucas, 1998, 1999; Small, 1998) since the last revision of *Redondasuchus* (Heckert et al., 1996). As documented by Hunt and Lucas (1991) and Heckert et al. (1996), *Redondasuchus* possesses a more narrow-bodied carapace, unlike *T. coccinarum* and *Paratypothorax*, both of which have dorsal paramedian scutes as much as four times wider than long. The flexed scutes of the carapace resulted in *Redondasuchus* being one of the narrowest-bodied aetosaurs.

THE VALIDITY OF REDONDASUCHUS

The validity of the genus *Redondasuchus* was questioned by Long and Murry (1995) and more recently by Martz (2002). Both sought to synonymize *Redondasuchus* with *Typothorax*. Long and Murry (1995) argued the species-level synonymy of *Redondasuchus reseri* with *Typothorax coccinarum*, while Martz (2002) proposed that *Redondasuchus* should be synonymized with *Typothorax*, but that the specific name should be retained, creating the new binomial "*Typothorax reseri*." We argue for the retention and recognition of *Redondasuchus* as a distinct genus of aetosaur and examine the analyses that lead to the conclusions presented by both Long and Murry (1995) and Martz (2002). Lucas et al. (2002) named a second species of *Typothorax*, *T. antiquum*, but its paramedian scutes are narrower and flatter than those of *T. coccinarum* and, thus, are not relevant to the discussion here, which principally concerns differentiation of *T. coccinarum* from *Redondasuchus*.

Long and Murry (1995, p. 108) claimed synonymy of *Redondasuchus reseri* with *Typothorax coccinarum* by noting three things: (1) that there are "no differences" between the *R. reseri* material and *T. coccinarum* fossils from the Canjilon Quarry in north-central New



FIGURE 4. *Redondasuchus rineharti*, NMMNH P-50745 from locality 2671, paratype proximal right femur. **A**, Anterior view. **B**, Posterior view. **C**, Proximal view.

Mexico; (2) that many of the *T. coccinarum* paramedian scutes exhibit arching (Long and Murry [1995] referred to this as "flaring") and (3) that such flexure was probably the result of post-mortem distortion They also opined that Hunt and Lucas (1991) illustrated a left lateral scute, not a paramedian scute. However, all three of these conclusions are incorrect.

The issue of similarity between *R. reseri* and the Canjilon *T. coccinarum* material will be discussed below, as Martz (2002) expanded on this idea. The conclusion that the arching of the paramedian scute of *Typothorax coccinarum* and the flexure of *Redondasuchus* paramedian scutes are due to post-mortem distortion is demonstrably wrong. The most complete specimen of *T. coccinarum* is NMMNH P-12964 from the Bull Canyon Formation of east-central New Mexico (Hunt et al., 1993). The specimen is approximately 2.5 m long, preserves nearly the entire skeleton, except for portions of the forelimb, and, most importantly for the discussion at hand, includes nearly the entire carapace. The skeleton was buried in a low energy environment, with some minimal scavenging and likely was not transported after death (Hunt et al., 1993). None of the elements exhibit any serious signs of distortion or crushing.

Of the numerous dorsal paramedian scutes, many of the anterior-most dorsal paramedians were preserved on edge, clearly showing an arching of the paramedians. This arching in a nearly complete, undistorted specimen thus refutes Long and Murry's (1995) contention that the arching of *T. coccinarum* scutes is due to post-mortem deformation. We note that *T. coccinarum* scutes thus are broadly arched, whereas the scutes of *Redondasuchus* are abruptly flexed.

Long and Murry (1995) reinterpreted the holotype of Redondasuchus reseri as a lateral scute of Typothorax coccinarum, but did not provide any justification for this reassignment. In their diagnosis of the genus Typothorax, Long and Murry (1995, p. 101) noted that the "lateral scutes [are] dorsoventrally-compressed, acutely folded into a laterally-directed sharp edge." Based on examination of the cast of the nearly complete T. coccinarum (NMMNH P-12964) mentioned above, we concur with this observation. This contrasts with the holotype scute of R. reseri, which is not acutely folded, but has an obtuse angle between the ventral margin of its dorsal side and the medial margin of its lateral side, and does not have a sharp, laterally-directed edge. In addition: (1) lateral scutes of T. coccinarum are triangular in dorsal view, whereas the holotype of R. reseri is rectangular; (2) no ventral bar is present on the lateral scutes of T. coccinarum as it is on the holotype of R. reseri. Thus, there is no basis for considering the holotype of R. reseri to be a lateral scute of T. coccinarum.

Martz (2002), in an unpublished thesis, synonymized *Redondasuchus* with *Typothorax*, while retaining the species name *reseri*, thus forming the new binomial "*Typothorax reseri*." He based this conclusion on the following four ostensible differences: (1) *Redondasuchus* is smaller than, but otherwise similar to, *Typothorax*; (2) both taxa have "arching" of the scutes at the center of ossification, although it is more pronounced in *Redondasuchus*; (3) both have a ventral keel that is reduced abruptly medial to the center of ossification/arching, but it does so more sharply in *Redondasuchus*; and (4) there is no reason to suspect *Redondasuchus* lacked lateral scutes, which are present in all other aetosaurs (Martz, 2002, p. 36).

Martz (2002) also noted the following features as similarities between *Redondasuchus* and *Typothorax*: the scutes of *Redondasuchus reseri* are "arched" to a greater degree than those of *Typothorax* and that the pitting is finer at the "center of ossification," but that this, too, is similar to *Typothorax*.

However, one of the primary problems when reading Martz is a general vagueness of terminology. Thus, Martz consistently used the term "arched" even when discussing *Redondasuchus reseri* scutes. We define arched, as it pertains to aetosaur scute morphology, to mean that the scute is parabolic, or continuously curvilinear, in anteroposterior view. This definition of arched clearly does not pertain to *R. reseri*, which we instead refer to as flexed. We define flexed, as it pertains to aetosaur scute morphology, to mean that the direction of otherwise linear portions of the scute changes abruptly at a distinct, anteroposteriorly-

oriented plane, that we refer to as the point or plane of flexure and that Martz (2002) refers to as the "center of ossification." Thus, as noted above, undistorted *Typothorax* scutes are noticeably arched, whereas *Redondasuchus* scutes are, instead, flexed. Martz (2002, fig. 3.1) illustrates a *Typothorax coccinarum* paramedian scute that is supposedly flexed, and that he maintains appears similar to that of *R. reseri*. However, it is evident from his photograph that there are numerous anteroposteriorly-directed fractures through the scute. Such fractures, when reconstructed incorrectly, can make a paramedian scute appear flexed. The general lack of such fractures on *R. reseri* paramedians, together with the demonstrated arching of *T. coccinarum* paramedian scutes, make the assertion of Long and Murry (1995) that both scute morphologies are due to distortion that much more puzzling. Thus, we interpret the "flexed" paramedian of Martz (2002, fig. 3.1) as incorrectly reconstructed and distorted.

Martz (2002) noted that the scutes of both *Typothorax coccinarum* and *Redondasuchus reseri* have a ventral keel that is reduced abruptly medial to the "center of ossification/arching." This feature is difficult to assess due to the incongruence of *Redondasuchus* and *Typothorax* scute nomenclature as presented above. The apex of the arch in *Typothorax* scutes would likely be equivalent to the "center of arching," as used by Martz (2002). While this feature is an interesting similarity between the two taxa, it is not sufficient to suggest a synonymy.

Martz (2002) contended that there is no reason to believe that *Redondasuchus* lacked lateral scutes, as originally proposed by Hunt and Lucas (1991) and reinforced by Heckert et al. (1996). However, with the reorientation of the holotype and its ramifications for the carapace reconstruction (Fig. 1), the "lateral protection" that the paramedians offered in previous interpretations is nullified. While this does not strengthen the case for the absence of lateral scutes in *Redondasuchus*, neither does it demonstrate that *Redondasuchus* did possess lateral scutes. Because the paramedians of *Redondasuchus* are so unique among aetosaurs, other novel features of the carapace should not be ruled out. Unfortunately, at the present time there is no definitive evidence for or against *Redondasuchus* possessing lateral scutes.

In summation, the arguments against the validity of *Redondasuchus* as a taxon distinct from *Typothorax* result from a misinterpretation of the fossil material or a misunderstanding of aetosaur scute morphology. Thus, we maintain *Redondasuchus* as a genus distinct from *Typothorax*.

ACKNOWLEDGMENTS

The Duke family allowed land access. George Edgerly prepared most of the scutes illustrated here. Pat Holroyd (UCMP) provided us with a cast of the holotype of *Redondasuchus reseri*. The Samuel Welles Fund allowed one of us (ABH) to view comparative material of *Typothorax* at UCMP. Jerry Harris and Robert Sullivan provided reviews that improved the manuscript.

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