

REDESCRIPTION OF *REDONDASUCHUS RESERI*, A LATE TRIASSIC AETOSAUR (REPTILIA : ARCHOSAURIA) FROM NEW MEXICO (U.S.A.), AND THE BIOCHRONOLOGY AND PHYLOGENY OF AETOSAURS

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HECKERT A.B., HUNT A.P. & LUCAS S.G. 1996. Redescription of *Redondasuchus reseri*, a Late Triassic aetosaur (Reptilia : Archosauria) from New Mexico (U.S.A.), and the biochronology and phylogeny of aetosaurs. [Nouvelle description de *Redondasuchus reseri*, un aetosaure (Reptilia : Archosauria) du Trias supérieur du Nouveau Mexique (Etats-Unis) et biochronologie, phylogénie des aetosaures]. GEOBIOS, **29**, **5** : 619-632. Villeurbanne, le 31.10.1996.

Manuscrit déposé le 03.11.1994 ; accepté définitivement le 08.06.1995.

ABSTRACT - The Late Triassic (Rhaetian) aetosaur *Redondasuchus reseri* from the Redonda Formation of eastern New Mexico, U.S.A. is distinguished from all other aetosaurs except *Typothorax* by its paramedian scutes with ventral keels, and from *Typothorax* by its paramedian scutes with discontinuous ventral keels. *Redondasuchus* can be further distinguished from other aetosaurs by its paramedian scutes in which the lateral third is flexed downward approximately 45° . It is the only Rhaetian aetosaur currently known from the United States and is an index taxon for the Apachean land-vertebrate faunachron. A cladistic analysis of the aetosaurs, utilizing both characters derived from armor and other skeletal information, indicates that two distinct grades of aetosaurs exist. There is a basal grade consisting of the paraphyletic assemblage of *Aetosaurus* and (*Stagonolepis + Aetosauroides*), and an advanced grade consisting of the clade Neoaetosauroides + Redondasuchus + ((Longosuchus + Desmatosuchus) + (*Paratypothorax + Typothorax*)). Integration of the existing aetosaur biochronology with operating cladistic definitions of aetosaur taxa produces a useful biostratigraphy of Upper Triassic strata in the western United States.

KEY-WORDS : AETOSAURS, *REDONDASUCHUS RESERI*, BIOCHRONOLOGY, TRIASSIC, RHAETIAN, LAND-VERTEBRATE FAUNACHRON, APACHEAN

RÉSUMÉ - L'aetosaure Redondasuchus reseri du Trias supérieur (Rhétien) de la Formation de Redonda du Nouveau Mexique oriental (Etat-Unis) est distingué de tous les autres aetosaures sauf Typothorax par ses plaques paramédianes avec carènes ventrales et de Typothorax par ses plaques paramédianes avec carènes ventrales discontinues. Redondasuchus peut être, de plus, distingué des autres aetosaures par ses plaques paramédianes dont le tiers latéral est plié vers le bas à environ 45° . C'est le seul aetosaure rhétien actuellement connu aux Etats-Unis et il est un taxon index pour le faunachron des vertébrés terrestres de l'Apachéen. Une analyse cladistique des aetosaures, utilisant à la fois les caractères dérivés de l'armure et d'autres informations squelettiques, indique qu'il y a deux grades d'aetosaures. Un grade basal correspond au groupement paraphylétique de Aetosaurus et (Stagonolepis + Aetosauroides) et un grade évolué correspond au clade Neoaetosauroides + Redondasuchus + ((Longosuchus + Desmatosuchus) + (Paratypothorax + Typothorax)). L'utilisation conjointe de la biochronologie des aetosaures et la définition cladistique des taxons d'aetosaures fournit une biostratigraphie utilisable pour le Trias supérieur de l'Ouest des Etats-Unis.

MOTS-CLÉS : AETOSAURES, *REDONDASUCHUS RESERI*, BIOCHRONOLOGIE, RHÉTIEN, FAUNACHRON DE VERTÉBRÉS TERRESTRES, APACHÉEN.

INTRODUCTION

Aetosaurs are a suborder of armored, quadrupedal, herbivorous archosaurs whose fossils are well known from sediments of Late Triassic age in Europe, North America, and South America. Additional material is incompletely known from India and North Africa. Fossilized aetosaur scutes are among the most commonly recovered fossils in the Chinle Group in western North America, and are generically determinate (Long & Ballew 1985). As such they make ideal index fossils, because a single incomplete scute from, for example, a channel lag deposit, can provide an age determination for otherwise unfossiliferous strata (e.g. Lucas & Hunt 1992; Lucas & Heckert 1994). Recently, Lucas (1993, 1997) and Lucas & Hunt (1993) have demonstrated that four distinct land-vertebrate faunachrons (lvf) can be distinguished in the nonmarine upper Triassic strata of the western United

	str	stratigraphic intervals				
tetrapod taxa	A	В	C' C	D		
Metoposauridae :						
Metoposaurus bakeri		•				
Buettneria perfecta						
Apachesaurus gregorii						
Parasuchidae :						
Paleorhinus spp.		_				
Angistorhinus spp.						
Rutiodon sp.			•			
Pseudopalatus spp.						
Redondasaurus spp.						
Aetosauria :						
Longosuchus meadei -						
Desmatosuchus haplocer	us .					
Stagonolepis wellesi						
Paratypothorax and ress	i	—				
Typothorax coccinarum						
Redondasuchus reseri						
dinosaurs :						
Placeria hesternus						
rhynchosaurs -		•				
						
	្អ	a l	d			
	ĮĮ.	uia.	iaı	an		
tetrapod-based land-vertebrate	nal	lar	elt	pe		
faunachrons	sch	an	n n	ba(
);	Ad	Re			
	CAR	NIAN	NORIAN	RHAETIAN		

FIGURE 1 - Stratigraphic ranges of Chinle tetrapods and the four land vertebrate faunachrons. *Extensions stratigraphiques des tétrapodes de Chinle et les quatre faunachrons de vertébrés terrestres.*

States (Fig. 1). *Redondasuchus* has been found in the Redonda Formation of east-central New Mexico (Fig. 2), and serves as an index fossil for the youngest (Apachean) of these faunachrons. The purposes of this paper are : (1) to redescribe the existing material of *Redondasuchus*; (2) to discuss the biochronologic utility of aetosaurs in general and *Redondasuchus* in particular; and (3) to analyze the phylogenetic utility of aetosaur dermal armor. In this article, NMMNH = New Mexico Museum of Natural History and Science, Albuquerque; UCMP = University of California Museum of Paleontology, Berkeley; and YPM = Yale Peabody Museum, New Haven.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA Laurenti, 1768 Order CROCODYLOTARSI Benton & Clark, 1988 Suborder AETOSAURIA von Huene, 1908 Family STAGONOLEPIDAE Lydekker, 1887



FIGURE 2 - Map showing east-central New Mexico, U.S.A., and approximate locations of Shark Tooth Hill and Apache Canyon. Inset shows location of New Mexico within the United States. Carte montrant la partie cene-est du Nouveau Mexique, USA, et localisations approximatives de Shark Tooth Hill et d'Apache Canyon. L'encart montre la localisation du Nouveau Mexique dans les Etats-Unis.

Genus Redondasuchus HUNT & LUCAS, 1991a

Type Species - Redondasuchus reseri HUNT & LUCAS, 1991a.

Revised Diagnosis - *Redondasuchus* is differentiated from other aetosaurs by its dorsal paramedian scutes which are strongly flexed (approximately 45°) two-thirds of the lateral distance from the medial to lateral edge of the scute, possess a discontinuous ventral keel, lack either raised bosses or a radial pattern on the dorsal surface, and have a pitted, not ridged ornamentation.

Redondasuchus reseri HUNT & LUCAS, 1991A

Diagnosis - Same as for genus.

Type specimen - UCMP 64515, a left, dorsal paramedian scute (Hunt & Lucas 1991a, fig. 2 A-C ; Fig. 3 A-C).

Material - Material pertaining to Redondasuchus was collected in east-central New Mexico by parties working for J.T. Gregory in the 1950's (YPM and UCMP specimens), and subsequently by one of us (APH) in the same area from 1986 through 1990 (NMMNH specimens). Gregory's collections include a variety of scutes from the cervical to caudal regions. The specimens at YPM include two dorsal paramedian scutes, YPM 4256 and 4257 (Lucas et al. 1985, fig. 3F-G ; Hunt & Lucas 1991a, fig. 3A-B ; Figs. 4B,A) and a variety of previously undescribed material. This undescribed material includes YPM 55715, a dorsal cervical paramedian scute (Fig. 3D-F), 55716 (Fig. 4I) and 55717 (Fig. 3J), partial dorsal paramedian scutes, 55718, a partial dorsal paramedian from either the sacral or proximal caudal series (Fig. 4H), 55719, a complete dorsal mid-caudal paramedian scute (Fig. 4C-E), 55720, two distal caudal paramedian scutes (Fig. 4 F,G), 55723 three ribs (Fig. 4 I,J), two of which are complete, and



FIGURE 3 - Scutes of *Redondasuchus*: **A-C** Holotype scute UCMP 65415 in (A) dorsal (B) posterior and (C) ventral views; **D-F** cervical paramedian scute YPM 55715 in (D) dorsal (E) ventral and (F) posterior views; **G-I** cervical paramedian scute UCMP 65258 in (G) dorsal (H) ventral and (I) posterior views; **J** dorsal view of YPM 55717, dorsal paramedian scute. All scale bars are 2 cm. *Plaques de* Redondasuchus: **A-C** plaque holotype en vues dorsale (A), postérieure (B) et ventrale (C); **D-F** plaque paramédiane cervicale en vues dorsale (D), ventrale (E) et postérieure (F); **G-I** plaque paramédiane cervicale en vues dorsale (G), ventrale (H) et postérieure (I); **J** vue dorsale de YPM 55717, plaque paramédiane dorsale. Toutes les échelles graphiques sont de 2 cm.



FIGURE 4 - Scutes of *Redondasuchus* : A dorsal view of YPM 4257, dorsal paramedian scute ; B dorsal view of YPM 4256, dorsal paramedian scute ; C-E YPM 55719, mid-caudal paramedian scute in (C) posterior (D) dorsal and (E) ventral views ; F-G dorsal views of caudal paramedian scutes catalogued as YPM 55720 ; H dorsal view of YPM 55718, a possible sacral paramedian scute ; I dorsal view of YPM 55716, dorsal paramedian scute ; J-K ribs of 55723 in (J) anterior and (K) lateral views. All scale bars are 1 cm. *Plaques de* Redondasuchus : A vue dorsale de YPM 4257, plaque paramédiane dorsale ; B vue dorsale de YPM 4256, plaque paramédiane ; C-E YPM 55719, plaque paramédiane mi-caudale en vues postérieure (C), dorsale (D) et ventrale (E) ; F-G vues dorsales de plaques paramédianes caudales répertoriées YPM 55720 ; H vue dorsale de YPM 55718, une plaque paramédiane peut-être sacrée ; I vue dorsale de YPM 55716, plaque paramédiane dorsale ; J-K côtes de 55723 en vues antérieure (J) et latérale (K).

55724, two incomplete scutes, one of which is a possible distal caudal paramedian. Collections at UCMP include, in addition to the holotype specimen, UCMP 65258 (Hunt & Lucas, 1991a; Fig. 3C,D,E; Fig. 3 G-I), a cervical scute referred to *Redondasuchus*, and 65314 and 65331, assorted scute fragments. NMMNH specimens include NMMNH 17064 (incorrectly listed as NMMNH 17084 in Hunt & Lucas, 1991a), seven scute fragments, 17091, an additional pair of scute fragments, and 25003, six scute frag-

ments. Most of the material was collected at Apache Canyon quarry # 2 (NMMNH locality 485) with the exception of YPM 4256 and NMMNH 17091, collected at Shark Tooth Hill (NMMNH locality 487) (Fig. 2).

Discussion - The holotype of *Redondasuchus reseri*, the almost complete left dorsal paramedian scute (UCMP 65415), is pitted, with no evidence of

grooves or ridges, and lacks any radial pattern, effectively distinguishing it from the aetosaurs Desmatosuchus (CASE 1922; see also Long & Ballew, 1985), Longosuchus (HUNT & LUCAS, 1990), Stagonolepis (WALKER, 1961; including Calyptosuchus of Long & Ballew, 1985), Aetosaurus, (WALKER, 1961), Paratypothorax (LONG & BALLEW, 1985), Aetosauroides (CASAMIQUELA, 1960), and Neoaetosauroides (BONAPARTE, 1969; 1970). The presence of a ventral keel and the lack of a prominent central eminence or raised boss further separates Redondasuchus from the above taxa, although it provides a superficial resemblance to Typothorax. Indeed, specimens of Redondasuchus, particularly YPM 4256 and 4257, have occasionally been referred to Typothorax (e.g. Lucas et al. 1985; museum labels on YPM and UCMP specimens). However, the discontinuous ventral keel of Redondasuchus terminates at the flexure, as opposed to the continuous keels and unflexed scutes that typify Typothorax. Thus, Redondasuchus is easily diagnosed from all aetosaurs, including Typothorax, by its marked ventral flexure of the dorsal paramedian scutes two-thirds of the width of the scute from the midline and discontinuous ventral keel.

Some clarification of the original description of the holotype of *Redondasuchus reseri* is presented here. The holotype has a width (not length, as stated by Hunt & Lucas [1991a]) of 90 mm in dorsal aspect. The length of the scute is approximately 45 mm. As noted by Hunt & Lucas (1991a), the anterior bar on UCMP 65415 is approximately 10 mm wide, flaring out somewhat along the medial edge. The ventral keel varies slightly in width from 16 mm near its termination to 20 mm near the midline. The keel is located so that slightly more than half of the keel lies on the anterior portion of the scute, with the anterior margin of the keel typically positioned approximately 10 mm from the anterior edge of the scute.

Referred material - YPM 4256 and 4257 (Fig 4B,A) exhibit the non-radial pitting, ventral keel, and, particularly in the case of 4257, marked flexure, that typifies Redondasuchus. YPM 4257, if it were complete, might be slightly larger than the holotype scute of *Redondasuchus*, as is one scute fragment from NMMNH 25003, and all other scutes are roughly subequal to or smaller than the holotype. All scute fragments listed above from the YPM collection, with the exception of 55715, can be demonstrated to belong to Redondasuchus on the basis of having at least two of the following features: (1) marked flexure; (2) pitted ornamentation lacking both a radial pattern or prominent eminences; and (3) presence of a discontinuous ventral keel. UCMP 65314 and 65331 can be assigned to *Redondasuchus* for the same reasons.

YPM 55715 is a likely candidate for first cervical dorsal paramedian scute (Fig. 3D-F). There is a discontinuous ventral keel, but the scute is not flexed. The pitting on the dorsal surface is randomly distributed, and both the anterior and posterior margins are curved in an irregular fashion, indicating that YPM 55715 articulated with other oddly shaped scutes or bones. Another unusual scute, UCMP 65258, the "problematic scute" of Hunt & Lucas (1991a, p. 733), also possesses Redondasuchus-like pitting and some degree of flexure, but is more equant than the holotype and other referred specimens that are complete enough to estimate overall shape (Fig. 3G-I). It lacks a prominent ventral keel, but the sinuous anterior margin of the scute precludes assignment of this scute to any other known aetosaur, and its association with other scutes of *Redondasuchus* is strong evidence that it belongs to this taxon. Hunt & Lucas (1991a, p. 733) considered it likely that UCMP 65258 represents an anterior cervical scute, noting that the sinuous anterior edge was not repeated on the posterior side, and thus may represent the articulation of this scute with a scute directly behind the skull. With our interpretation of YPM 55715 as the first cervical scute this seems less likely, as YPM 55715 and UCMP 65258 do not articulate, but nonetheless UCMP 65258 appears to represent an anterior cervical paramedian scute of Redondasuchus. Among the other known North American aetosaurs, only Paraty*pothorax* is not currently represented by cervical scutes. However, no aetosaur other than Redondasuchus and another undescribed aetosaur (Hunt 1994, unpub.) is known from the Redonda Formation or any correlative horizons, and the association of YPM 55715 and UCMP 65258 with other scutes of Redondasuchus in Gregory's Apache Canyon Quarry #2 suggests that these specimens pertain to Redondasuchus.

YPM 55716 is a partial dorsal paramedian scute which is identified as Redondasuchus because of its keel and random pitting (Fig. 4I). It apparently broke in the immediate vicinity of the flexure. YPM 55717 is essentially a mirror image of 4257, indicating that it is a partial left dorsal paramedian scute (Fig. 3J). YPM 55718 is either a posterior sacral or anterior caudal paramedian. It is incomplete, but what is present lacks strong flexure. However, it has an anterior bar, randomly distributed pitting, and a ventral keel. The posterior margin is oddly shaped, essentially tapering anteriorly toward the lateral margin, suggesting that the next scute posterior to YPM 55718 was significantly narrower (Fig. 4H). For these reasons, we suggest that YPM 55718 may represent a sacral paramedian scute, marking the transition from relatively wide paramedians covering the sacrum to a narrower series of paramedian scutes protecting the tail. YPM



FIGURE 5 - Cross sections through the carapace of *Redondasuchus* reseri in anterior view. (A) YPM 55715 (B) UCMP 65258 (C) Holotype scute UCMP 65415 (D) YPM 4257 (E) YPM 55718 (F) YPM 5519 (G) YPM 55720 Scale bar is 2 cm. *Coupes transversales* dans la carapace de Redondasuchus reseri en vue antérieure.

55719 is a mid-caudal paramedian scute, and is interesting because it demonstrates that the flexure, and with it the termination of the ventral keel, migrates medially in the caudal series (Fig. 4 C-E). Both of the caudal paramedians catalogued as YPM 55720 (Fig. 4 F-G) demonstrate this feature as well.

Additional YPM specimens not originally assigned to *Redondasuchus* present some difficulties, but can nonetheless be assigned to *Redondasuchus*. The ribs, YPM 55723, exhibit a ventrally recurved morphology that closely matches that of the paramedian scutes (Fig. 4-J), suggesting that these ribs belonged to *Redondasuchus* and provided an underlying framework for supporting the dorsal carapace. Interestingly, these ribs have a "T'-shaped cross-section in lateral view, with the head of the "T' on the dorsal side, perhaps providing further support for the paramedian scutes (Fig. 4-J).

RECONSTRUCTION OF REDONDASUCHUS

Hunt & Lucas (1991a, p. 733) stated that *Redonda*suchus possessed "an anomalously narrow body for an aetosaur". This is in part due to the low width to length ratio (2.2:1) exhibited by *Redondasuchus* paramedian scutes, but is also a result of the ventral flexure of the paramedian scutes and lack of lateral scutes. The strong downward bowing of paramedian scutes, as exemplified by the holotype UCMP 65415, results in an apparent width to length ratio of 2:1, in contrast to ratios in excess of 4:1 for wide-bodied genera such as *Paratypothorax* and *Typothorax* (LONG & BALLEW, 1985). Furthermore, the absence of lateral scutes, combined with the close fit of paramedian scutes to dorsal ribs (see above), suggests that the lateral end of the paramedian scutes marked the lateral edge of the thorax. When these factors are taken into account, doubling the apparent width of the holotype scute gives *Redondasuchus* a width, when viewed dorsally, that may have been as low as 18 cm. Only *Aetosaurus*, as redescribed by Walker (1961), was narrower, but its width to length ratio is higher, and so its narrowness is due principally to small size, averaging about 86 cm in total length (Walker 1961 p. 165).

In spite of the limited amount of material, the available scutes of *Redondasuchus* actually represent paramedian scutes from most portions of the body. As such, it is possible to present some conclusions regarding the overall shape of the carapace and cross-sections through the body (Fig. 5) and present a possible restoration of Redondasuchus (Fig. 6). Anteriorly, the cervical scutes, represented by YPM 55715 and UCMP 65258, are more equant and not nearly as flexed as the holotype scute, resulting in a narrow, flat dorsal surface. UCMP 65258 has a broken surface on the anterior lateral edge which may have been a lateral spike or other projection (Fig. 3G). If it was a lateral spike it differs from other aetosaurs bearing lateral spikes in that the spike on Redondasuchus branches off of the lateral surface of a paramedian scute. The dorsal paramedian holotype scute UCMP 65415 indicates a narrow-bodied aetosaur with a series of flexed paramedian scutes providing the lateral margins of the carapace, an idea further borne out by YPM 4257. YPM 55718 apparently marks the transition from the posterior dorsal scutes to the anterior caudals. As such it lacks strong flexure but tapers anteriorly along the posterior margin to suggest articulation with narrower scutes behind it. A complete mid-caudal scute, YPM 55719, demonstrates that as the tail tapered posteriorly the flexure of the paramedian scute migrated medially, producing a narrow, dorsoventrally deep tail (Fig. 5 E). The distal caudal paramedians (YPM 55720) further demonstrate this process near the end of the tail (Fig. 5 F,G).

BIOCHRONOLOGY

Redondasuchus is the only described aetosaur from the Apachean lvf of Lucas (1993, 1997). The Apachean lvf is characterized by the phytosaur Redondasaurus (HUNT & LUCAS, 1993b; Hunt 1994, unpub.), the theropod dinosaur Rioarribasaurus (HUNT & LUCAS, 1991b), the small metoposaurid Apachesaurus (HUNT, 1993), and the vertebrate ichnotaxa Grallator, Brachychirotherium, Pseudotetra-



sauropus and Tetrasauropus (HUNT et al. 1993a). Huber et al. (1993) demonstrated that a fossil fish assemblage consisting of Turseodus dolorensis, Tanaocrossus kalliokoski, Cionichtys dunklei, Synorichthys stewarti, Lasalichthys hillsi, indeterminate perleidids, Semionotus sp., Hemicalypterus weiri, Chinlea sorenseni, Arganodus sp. and a new species of Lissodus is characteristic of strata of Apachean age. Of these fish, only Cinoichthys dunklei and the new species of *Lissodus* are unique to the Apachean lvf (Huber et al. 1993). In addition to the Redonda Formation, fossiliferous Apachean strata in the western U.S.A. include the Travesser, Sloan Canyon, and Sheep Pen Formations of northeastern New Mexico, southeastern Colorado, and northwestern Oklahoma, the Rock Point Formation of north-central New Mexico and east-central Utah, and the Bell Springs Formation of northeastern Utah, northwestern Colorado, and central Wyoming. These can be correlated on the basis of tetrapods, fish, and tetrapod ichnofossils (Lucas 1993,1997; Lucas & Hunt 1993).

Recent work has shown that aetosaurs can be used to construct a reliable biochronology of the Chinle Group (e.g. Lucas 1993, 1997; Lucas & Hunt 1993). These authors have defined four lvfs largely on the basis of aetosaurs and phytosaurs (Fig. 1). The oldest Chinle faunachron, the Otischalkian, is typified by the North American aetosaur Longosuchus, although in some places it co-occurs with Desmatosuchus (SMALL, 1989). Strata immediately younger than the Otischalkian fall into the Adamanian lvf, which is characterized by Stagonolepis, with overlap of the longer-lived aetosaurs Desmatosuchus and Paratypothorax. Above strata of Adamanian age are rocks bearing a fauna indicative of the Revueltian lvf, including the first appearance of the aetosaur *Typothorax*. The Revueltian can be subdivided on the basis of the presence or absence of the aetosaurs *Desmatosuchus* and *Paratypothorax* (HUNT, 1994, unpub.; Lucas, 1995). In the oldest Revueltian (Interval C in Fig. 1), *Paratypothorax* and *Desmatosuchus* co-occur with *Typothorax*. However, in the later Revueltian (C' in Fig. 1) only *Typothorax* is known (Hunt 1994, unpub. ; Lucas 1997). As discussed previously, *Redondasuchus* is the only formally described aetosaur in the Apachean faunachron, the youngest of the four faunachrons.

In spite of this reliable biochronology of aetosaurs. *Redondasuchus* is of little biochronological utility because it is known only from the Redonda Formation. Instead, the phytosaur Redondasaurus is the most biochronologically important body fossil derived from strata of Apachean age. The Ghost Ranch guarry, in the Rock Point Formation (Lucas & Hunt 1991b ; Lucas & Hunt 1993) has vielded dozens of skeletons of Rioarribasaurus (formerly referred to Coelophysis), but dinosaur fossils are rare in the Chinle Group, and are of little utility for correlation. The utility of Rioarribasaurus for biochronologic purposes is also limited by the tendency of earlier authors to refer any small theropod from the Chinle Group to "Coelophysis" (e.g., Case, 1932b). The labyrinthodont amphibian Apachesaurus (HUNT, 1993, 1994 unpub.) has an extensive stratigraphic range, and is only useful in terms of its relative abundance compared to the larger metoposaurid amphibians (Hunt 1993 ; Hunt & Lucas 1993a ; Lucas 1993, 1995). Other, as-yet undescribed body fossils that occur in the Apachean lvf include another aetosaur, a new

genus of phytosaur, a therapsid, a sphenosuchian, and a large carnivorous reptile of unknown affinities (Hunt 1994, unpub.).

Although definition of these faunachrons relies heavily on the stratigraphic ranges of phytosaurs, the utility of aetosaurs is unmistakable, despite the limited distribution of *Redondasuchus*. This is in part because the only postcranial phytosaur material which is particularly diagnostic is the ilium, and even then generic assignments are difficult (Hunt 1994, unpub.). In contrast, aetosaur scutes are remarkably diagnostic, and we anticipate that the cladistic analysis provided below will further facilitate efforts to assign aetosaur scutes to a given genus. In order to better demonstrate this we present here several examples of the utility of aetosaur scutes for correlation.

Recently, Lucas & Hunt (1992) demonstrated that the Salitral Formation of north-central New Mexico is early late Carnian in age on the basis of a single paramedian scute of Longosuchus. In addition, they noted that the presence of both Paratypothorax and Typothorax scutes indicated an early to mid-Norian age for the overlying Petrified Forest Formation in the same area. As a further example of the utility of using aetosaur scutes for biostratigraphy, Lucas and Heckert (1994) recently reaffirmed the late Carnian-early Norian age of the San Pedro Arroyo Formation (Lucas 1991) in central New Mexico by identification of a single scute of Desmatosuchus from a conglomeratic channel lag in otherwise unfossiliferous strata.

In addition to the easy recognition of aetosaur genera on the basis of their scutes, some of the genera that occur in the Chinle are also represented elsewhere. For example, Stagonolepis, described in detail by Walker (1961) from the Lossiemouth Sandstones in Scotland, is also known from West Texas (Case 1932a, this is the holotype of Calyptosuchus wellesi LONG & BALLEW, 1985), the Petrified Forest National Park, and Apache County in eastern Arizona (Long & Ballew 1985; Murry & Long 1989). Furthermore, Hunt & Lucas (1992) noted that Paratypothorax andressi occurs in strata of Late Triassic age in both Germany and the western United States, and Jalil et al. (1995) have identified specimens of Paratypothorax from the Zarzaïtine Series in eastern Algeria. Although P. andressi is a relatively long-lived taxon, ranging form latest Carnian to the middle Norian in the United States, it still possesses some value in biostratigraphic terms by facilitating correlations between the Chinle Group, the Newark Supergroup, the Keuper, and now, North Africa (Hunt & Lucas 1992; Jalil et al. 1995). In light of these examples from the recent literature we advocate that parties working in the Upper Triassic, particularly in the western United States.

make use of aetosaur fossils for biochronological purposes whenever possible.

PHYLOGENY

The history of the study of aetosaur taxonomy and phylogeny is replete with misinterpretations, from Camp's (1922) assignment of *Desmatosuchus* as a representative of a new suborder of the Phytosauria to Sawin's (1947) misidentification of *Longosuchus* as *Typothorax* and Long and Ballew's (1985) misdiagnosis of North American specimens of *Stagonolepis* as the new genus *Calyptosuchus*. Recent work has moved toward generating a new synthesis regarding aetosaur distribution (Long & Ballew 1985), biochronology (Hunt & Lucas 1990, 1991a, 1992; Lucas 1993, 1995; Hunt 1994, unpub.), and, most recently, phylogeny (Parrish 1994). This last work resulted in what is the first testable cladogram for the Aetosauria.

Parrish (1994, p. 206) distinguished a monophyletic Aetosauria from the rauisuchians based on the following synapomorphies : (1) edentulous anterior portion of premaxilla consisting of an anteroventrally projecting, mediolaterally expanded "shovel" with an "upturned, anteriorly flattened dentary that lacks teeth anteriorly"; (2) teeth that are reduced in size and nearly conical; (3) a complete dorsal and ventral carapace; (4) paramedian scutes that are markedly wider than long, sculptured, and lack anterior or posterior projections; and (5) limb bones that are disproportionately robust with "hypertrophied trochanters" on the humerus, femur, tibia, and fibula. Of these characters, Redondasuchus remains unknown for all but (3) and (4). Because of the numerous characteristics Redondasuchus shares with other aetosaurs (see below), we consider it likely that Redondasuchus' apparent lack of lateral or ventral scutes, and thus a complete carapace, is a secondary reversal of the general aetosaur plan. Redondasuchus paramedians do correspond to Parrish's (1994) definition of aetosaur scutes. Thus, we are completely confident in assigning Redondasuchus to the Aetosauria and the Stagonolepidae.

Unfortunately, due to the relatively small number of characters utilized (15 characters for 10 taxa), several branches of Parrish's cladogram remain unresolved trichotomies. We have already noted that aetosaur scutes are among the most common fossils recovered from strata in the Chinle Group, so we build upon Parrish's work by adding numerous characters derived from dermal ossifications. To do this we first recognize Parrish's definition of a monophyletic Aetosauria, and use *Aetosaurus* as an outgroup to all other aetosaurs. Beyond those assumptions we have gathered information on the various genera of aetosaurs from numerous sources, including not only Parrish (1994), but also Case (1922, 1932a), Sawin (1947), Casamiquela (1960, 1961, 1981), Walker (1961), Bonaparte (1969, 1971a,b, 1978), Long & Ballew (1985), Small (1989), Hunt & Lucas (1990, 1991a, 1992), Hunt *et al.* (1993a,b), and personal observations.

Doing this, we have determined an additional 15 characters that can be used to diagnose the various aetosaurs. These were incorporated into a data matrix with those characters of Parrish that were informative within the Aetosauria. Given that Redondasuchus is unknown except for isolated scute and rib material, it necessarily remained unknown in the bulk of Parrish's characters. However, we were able to characterize accurately Typothorax as having maxillary teeth extending forward from the posterior margin of the naris, based on personal observation of NMMNH P-12964, a complete skeleton of Typothorax coccinarum under preparation at NMMNH (Hunt et al. 1993b). This allowed us to slightly update the information contained in Parrish (1994).

The following is a brief description of the characters we developed based on aetosaur armor. For a complete description of both these characters and those we utilized from Parrish (1994), as well as a data matrix, see the Appendix. Of the 22 characters evaluated in this analysis, 17 related to the morphology of the armor. Three of those characters regarding the armor and all non-armor related characters were defined and used by Parrish (1994) in his phylogeny of aetosaurs. Specific armor characters utilized by Parrish include the presence or absence of raised bosses on the paramedian scutes (the median excresences of Parrish 1994), the presence or absence of lateral spikes, and whether or not the length : width ratio of dorsal paramedian scutes exceeds 4:1.

Beyond this, we evaluated cervical paramedian scutes as to their overall shape, either rectangular, with the width representing the long axis, or equant, and their dorsal-ventral thickness. Dorsal paramedian scutes were further characterized by the presence or absence of the following features : anterior bars; radial patterning on the dorsal surfaces of paramedian scutes ; raised bosses contacting the posterior margin; flexure; and presence or absence of ventral keels. Presence or absence of lateral scutes was marked, in addition to the presence or absence of lateral spikes noted above. Two characters describing the flanges of lateral scutes were used, namely whether they were (1) symmetrical on the dorsal and ventral sides ; and (2) met at an obtuse or narrower angle. Caudal paramedians were coded as either transversely arched or not, following Long & Ballew (1985). Finally, the overall shape of the carapace was coded in two different characters. The first of these was for the presence of a "waist" or narrow spot in the carapace anterior to the sacrum as typified by *Aetosaurus* and *Stagonolepis* (Walker 1961). The second carapace character noted the presence or absence of a discoidal or "wide-bodied" carapace, as evidenced by *Typothorax* and *Paratypothorax* (Long & Ballew 1985; Hunt *et al.* 1993b).

After coding of characters and designation of Aetosaurus as an outgroup the branch and bound and exhaustive search algorithms of PAUP 3.1.1 were employed, and in all cases gave identical results. Our combination of Parrish's characters and our own produced five most parsimonious trees, the strict consensus of which is shown in Figure 7A. Figure 7B shows the 50% majority rule tree, which corresponds to the third of the five most parsimonious trees. The strict consensus tree, which was not represented by any of the five trees, was of length 26 and possessed a consistency index (CI) of .85, while the majority-rule tree possessed a length of 27 and a CI of .81. Although these consistency indices are somewhat lower than the .938 reported by Parrish (1994, p. 205), we feel this simply reflects that characteristics of dermal armor are more likely to be convergent than other traits.

The strict consensus tree recognizes a basal unresolved multichotomy between Aetosaurus, Neoaetosauroides, Redondasuchus, a relatively unspecialized clade consisting of Stagonolepis + Aetosauroides, and a more derived clade made up of ((Longosuchus + Desmatosuchus) + (Paratypothorax + Typothorax)). The synapomorphies that diagnose the clades Stagonolepis + Aetosauroides, Longosuchus + Desmatosuchus, Paratypothorax + Typothorax, and ((Longosuchus + Desmatosuchus) + (Paratypothorax + Typothorax)) are described after a brief discussion of characters that separate other aetosaurs from Aetosaurus.

Relative to *Aetosaurus* all other aetosaurs except *Redondasuchus* are advanced in possessing raised bosses on the paramedian scutes. Other characters that demonstrate the derived nature of all other aetosaurs relative to *Aetosaurus* include possession of conical, as opposed to recurved, teeth (unknown in *Paratypothorax* and *Redondasuchus*) and the loss of teeth in the anterior portion of the dentary (unknown in *Aetosauroides, Paratypothorax*, and *Redondasuchus*).

Parrish (1994) recognized the unnamed clade consisting of Aetosauroides + Stagonolepis by their shortening of the maxillary tooth row such that it does not extend anteriorly under the external nares (unknown in Paratypothorax and Redondasuchus). Our analysis does not contradict this assessment, but neither does it offer additional support for his hypothesis.



FIGURE 7 - Cladograms showing the relationships of the Aetosauria: (A) Strict consensus tree derived from five most parsimonious trees resulting from analysis of twenty two characters for the nine terminal taxa; (B) 50% majority rule tree. This tree corresponds with the third of five trees derived from the first analysis. (C) Single most parsimonious tree that results from inclusion of a character concerning overall tail morphology.

The strict consensus tree prohibits assignment of either Neoaetosauroides or Redondasuchus to a more derived clade, although for very different reasons. In the case of *Neoaetosauroides* this is in large part due to our inability to characterize either its cervical armor, which is currently unknown, or its dorsal ornamentation, which is not preserved except on the tail where it is apparently similar to that of Aetosauroides (BONAPARTE, 1971a, p. 99). Redondasuchus, on the other hand, cannot be placed in any of the more derived clades because it is so autapomorphic. For instance, the clade of ((Longosuchus + Desmatosuchus) + (Paratypothorax + Typothorax)) is defined below on a suite of characters involving advances in lateral scute morphology, effectively excluding Redondasuchus from consideration as it has apparently lost all traces of its lateral scutes.

The clade consisting of ((Longosuchus + Desmatosuchus) + (Paratypothorax + Typothorax)) is well defined on the strict consensus tree by five synapomorphies. The first of these is the loss of transverse arching on the caudal paramedians (undetermined in Longosuchus, unknown in Paratypothorax and paralleled in Redondasuchus). The clade is also defined by the presence of lateral spikes on dorsal lateral scutes, reduction of the angle at which the dorsal and lateral flanges of the lateral scutes articulate, loss of the "waist" in the carapace anterior to the sacrum (unknown in Redondasuchus), and loss of posterior premaxillary teeth (unknown in Paratypothorax and Redondasuchus).

Longosuchus and Desmatosuchus were tentatively linked together by Parrish (1994) by the presence of a "deep hemispherical fontanelle in the bottom of the basisphenoid between the basal tubera and basiopterygoid process" (p. 207). This character is unknown in Paratypothorax, Aetosauroides, Neoaetosauroides, and Redondasuchus, but we present an additional synapomorphy, namely a change in shape of cervical paramedians from wide and short to nearly equant, a character state thus far unknown in Neoaetosauroides and Paratypothorax, and paralleled in Redondasuchus.

Paratypothorax and *Typothorax* are united by their strap-like paramedian scutes that are up to four times as wide as long, asymmetrical dorsal and ventral flanges on the lateral scutes, and discoidal carapace. This third character is admittedly somewhat linked to the width : length ratio of the dorsal para-

Cladogrammes montrant les relations des Aetosauria : (A) arbre de consensus strict dérivé des cinq arbres les plus parcimonieux résultant de l'analyse de trente deux caractères pour les neuf taxons terminaux ; (B) arbre de la règle de majorité à 50 %. Cet arbre correspond au troisième des cinq arbres dérivés de la première analyse ; (C) seul arbre le plus parcimonieux résultant de l'inclusion d'un caractère concernant l'ensemble de la morphologie caudale.

median scutes. However, we consider it independently because : (1) it represents a dramatically different body plan among the aetosaurs, and (2) it is possible to imagine aetosaurs with narrower paramedians still obtaining a discoidal carapace, or aetosaurs with wide paramedians retaining a more primitive body plan.

Interestingly, addition of a single character regarding the morphology of the tail of aetosaurs reduces the data matrix to a single most parsimonious tree (Fig. 7c) which is almost identical to the majority rule tree of the first analysis. This character concerns the degree to which the proximal third of the tail is reduced or tapers. This is shown in its most extreme form by *Longosuchus*, in which there are only a handful of caudal paramedians, but is also shown in varying degrees by *Neoaetosauroides* (Bonaparte 1971a), *Redondasuchus*, and *Typothorax* (personal observation). *Desmatosuchus* appears to have undergone a reversal (Case 1922), and *Paratypothorax* remains unknown but almost certainly resembles *Typothorax* in this character.

If this character is utilized, and we exercise caution in doing so as it is not at all clear that reduction of the tail has a single, uniform cause, then tail reduction becomes a synapomorphy of Neoaetosauroides + (Redondasuchus + ((Longosuchus + Desmatosuchus) + (Paratypothorax + Typothorax))), subject to the qualifying statements noted above. The clade Redondasuchus + ((Longosuchus + Desmatosuchus) + (Paratypothorax + Typothorax)) is then diagnosed by two synapomorphies. The first of these is the loss of transverse arching in the caudal paramedians (treated as undetermined, but we consider it likely, in Longosuchus [Sawin 1947, fig. 12] and Paraty-pothorax [Hunt & Lucas 1992, fig. 3C,D]). A second synapomorphy of this unnamed clade is the development of equant cervical paramedian scutes, a character state that is apparently reversed in Typothorax and unknown in Paratypothorax.

The resulting tree (Fig. 7C) has a length of 29 and a CI of .793. Although this consistency index is rather low, we note that this is in large part due to convergences in characters that could be expected to be prone to parallel evolution, namely features involving the type and pattern of ornamentation on the dorsal scutes. Removal of characters regarding the pattern and pitting of the dorsal armor reduces the tree length to 25 and raises the CI to .84. If the parallel development of ventral keels is ignored as well, and we have already distinguished some differences between the ventral keels above, the CI rises to .87, while length falls to 23.

Because we chose to include *Redondasuchus* in our evaluations, we differed from Parrish's approach in using characters which were autapomorphic for some terminal taxa. Although the purpose of this paper is not to diagnose all the aetosaurs, abbreviated diagnosis are offered below.

Among basal aetosaurs, *Aetosaurus* retains an entirely primitive suite of characters. *Aetosauroides* and *Stagonolepis* are not diagnosed in our cladogram, although differences certainly exist, particularly in the ventral scutes and appendicular skeleton (see Casamiquela 1961; Walker 1961). If our character utilizing the apparent reduction of the tail is utilized, *Neoaetosauroides* is the only aetosaur with a rapidly tapering tail and raised bosses that possesses transversely arched caudals.

Redondasuchus has been diagnosed exhaustively above, but we reiterate here the distinct separation of Redondasuchus from Typothorax. Although the two taxa convergently share the derived characters of entirely pitted ornamentation, ventral keels, and random pitting, the numerous synapomorphies listed above linking Typothorax to advanced clades of aetosaurs prohibit any connection between the two taxa. Among the spiked aetosaurs, Longosuchus is noteworthy for its faceted lateral spikes and extremely short caudal paramedian scute series. Desmatosuchus is autapomorphic in having dorsoventrally thick cervical paramedian scutes (unknown in Neoaetosauroides), anterior laminae as opposed to bars, and the forward placement of the raised boss off of the posterior margin of the paramedian scutes, a character for which neither Aetosauroides nor Neoaetosauroides can be evaluated from the literature. Desmatosuchus shares convergently with Typothorax lowered or less prominent bosses relative to other aetosaurs. Within the clade formed by Typothorax + Paratypothorax the former can be diagnosed by its lack of ridges on the paramedian scutes, random pitting, and ventral keels, all of which are convergent with Redondasuchus, while the latter is not diagnosed on our cladogram.

CONCLUSIONS

Redondasuchus is a derived aetosaur known from an incomplete series of scutes and three ribs found in the Rhaetian Redonda Formation of east-central New Mexico. It is easily recognized from isolated material by the presence of random pitting, discontinuous ventral keels, and lateral flexure on the paramedian scutes and by the lack of articular surfaces for lateral scutes, which we consider indicative of a lack of lateral scutes. In life, *Redondasuchus* would have been a narrow-bodied aetosaur, larger than but perhaps as narrow as the primitive *Aetosaurus. Redondasuchus* is the only aetosaur thus far described from the Apachean land-vertebrate faunachron, and the same characteristics that make it readily recognizable among the aetosaurs also provide a means of easily dating strata of Rhaetian age. Furthermore, characters obtained from scutes also facilitate a cladistic analysis of the aetosaurs. Within the Aetosauria, Redondasuchus represents the basal yet highly autapomorphic taxon inside the clade Redondasuchus + ((Desmatosuchus + Longosuchus) + (Typothorax + Paratypothorax)). We hope that the extreme wealth of morphological, biochronological, and phylogenetic information derived from seemingly isolated aetosaur fossils will motivate future workers to collect and thoroughly describe these specimens whenever possible.

Acknowledgments - We thank P. Porter and J. Duke for access to their land, J.H. Hutchison (UCMP) and J.H. Ostrom (YPM) for access to specimens under their care and for loaning us critical specimens, P.L. Sealey for assistance in collecting specimens of *Redondasuchus*, and J.T. Gregory for sharing crucial information about his work in eastern New Mexico. E. Buffetaut reviewed an earlier version of this manuscript and provided helpful comments.

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APPENDIX

DESCRIPTION OF CHARACTERS

The following characters were utilized in our analysis. Of these, characters number 4, 7, 13, and 18-22 correspond to characters 15, 10, 13, 8, 9, 11, 12, and 14 of Parrish (1994).

1. Shape of cervical paramedians : Short and wide (0) or approximately as long as wide (1).

2. Dorsal-ventral thickness of cervical paramedians : Thin (0) or thick (1).

3. Anterior bars on dorsal paramedian scutes : Present (0) or absent (1)

4. Width to length ratio of dorsal paramedian scutes : Less than 4:1(0) or greater than (4:1).

5. Patterning on dorsal paramedian scutes : Radial (0) or random (1).

6. Ornamentation on dorsal paramedian scutes : Pits and ridges (0) or pits alone (1).

7. Raised bosses on dorsal paramedian scutes : Absent (0) or present (1).

8. Position of bosses on dorsal paramedian scutes : On posterior margin (0) or anterior to posterior margin of scute (1).

9. Transverse arching of anterior caudal paramedian scutes : Transversely arched (0) or flattened (1).

10. Flexure of paramedian scutes : None or minimal (0) or strongly flexed ventrally (1).

11. Presence of a mediolateral ventral keel on paramedian scutes : Absent (0) or present (1).

12. Presence of lateral scutes : Present (0) or absent (1).

13. Presence of lateral spikes on lateral scutes : Absent (0) or present (1).

14. Angle of articulation between dorsal and ventral flanges of lateral scutes : Obtuse (0) or approximately 90° or less (1).

15. Symmetry of dorsal and ventral flanges of lateral scutes : Symmetrical (0) or asymmetrical, with the ventral flange larger than the dorsal flange (1).

16. Presence or absence of a discoidal carapace : Absent (0) or present (1).

17. Presence of a narrow region ("waist") in the carapace anterior to the sacrum : Present (0) or absent (1).

18. Tooth morphology : Recurved (0) or conical (1).

19. Anterior dentary : Possesses teeth (0) or edentulous (1).

20. Forward limit of maxillary tooth row : Underneath external nares (0) or posterior to external nares (1).

21. Presence of posterior premaxillary teeth : Present (0) or absent (1).

22. Presence of a "deep, hemispherical fontanelle in the bottom of the basisphenoid between the basal tubera and basiopterygoid process" (Parrish 1994, p. 204): Absent (0) or present (1).

DATA MATRIX

	100/5	070010	1110101415	1017101000	100				
	12345	678910	1112131415	1617181920	122				
Aetosaurus	00000	00000	00000	00100	00				
Aetosauroides	??000	01?00	00000	$0\ 0\ 1\ ?\ 1$	0?				
Stagonolepis	00000	01000	00000	00111	00				
Neoaetos auroides	???0?	?1?00	00000	00110	0?				
Redondasuchus	10001	10011	11000	0????	??				
Longosuchus	10000	010?0	00110	01110	11				
Desmatosuchus	11100	01110	00110	01110	11				
Paratypothorax	?0010	010?0	00111	111??	??				
Typothorax	00011	11010	10111	11110	10				
When considering tail morphology as a character, the									
column of this matrix would read : 0 0 0 1 1 1 1 1 1									

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