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# **Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi)**



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with 9 figures and 1 appendix

**Abstract:** The Aetosauria are a monophyletic group of quadrupedal, armored, primarily herbivorous reptiles ranging from 1 to 6 m in body length that are known from Upper Triassic strata in North and South America, Greenland, Europe, Africa, and India. To date, 17 genera and 20 species of aetosaurs have been named, and several new forms are currently under study. Of these, we recognize ten valid genera: *Aetosaurus*, *Coahomasuchus*, *Desmatosuchus*, *Longosuchus*, *Neoaetosauroides*, *Paratypothorax*, *Redondasuchus*, *Stagonolepis*, *Typothorax*, and one other unpublished genus. Most of these genera are monospecific, with the exception of *Aetosaurus* (*A. ferratus*, *A. crassicauda*, *A. arcuatus*) and, possibly, *Stagonolepis* (*S. robertsoni*, *S. wellsi*). Most footprints assigned to the ichnogenus *Brachychirotherium* are probably of aetosaurs.

A phylogenetic analysis using 60 characters and utilizing the rauisuchians as an out-group produces the following phylogenetic hypothesis: *Aetosaurus* is the sistergroup to all other aetosaurs, which are divided into two clades – a more primitive clade consisting of *Stagonolepis* + one of the unnamed new taxa, and a more advanced clade consisting of (*Neoaetosauroides* + ((*Desmatosuchus* + (*Typothorax* + *Redondasuchus*)) + (*Longosuchus* + *Paratypothorax*))). We refer *Aetosaurus* to the Aetosaurinae, n. subfam., the more primitive clade to the Stagonolepininae and the more advanced clade to the Desmatosuchinae, both preexisting names. Of the other genera, *Stegomus* is a junior subjective synonym of *Aetosaurus*; *Aetosauroides*, *Argentinisuchus*, *Calyptosuchus*, and, *Ebrachosaurus* (in part) are junior subjective synonyms of *Stagonolepis*; *Lucasuchus* is a junior subjective synonym of *Longosuchus*; *Acaenasuchus* is based on juvenile specimens of *Desmatosuchus* and thus is a junior subjective synonym of that taxon; *Fukangolepis* is based on fragmentary dicynodont skull material and thus is not an aetosaur; and *Chilenosuchus* from the El Bordo Formation in Chile is neither from Triassic rocks nor is it an aetosaur. The holotype of *Acompsosaurus wingatensis* is lost, and probably represents an individual of *Stagonolepis*. The German Schilfsandstein reptile *Dyoplax* is a sphenosuchian, not an aetosaur.

Based on the stratigraphic succession of aetosaurs in the upper Carnian-Rhaetian Chinle Group of the western U.S.A., we identify seven aetosaur biochrons: (1) *Longosuchus* biochron of early to late Carnian (late Julian to Tuvanian) age; (2) *Desmatosuchus* biochron that straddles the Carnian-Norian boundary; (3) *Stagonolepis* biochron of latest Tuvanian age; (4) *Paratypothorax* biochron straddling the Carnian-Norian boundary; (5) *Typothorax* biochron of Norian age; (6) *Aetosaurus* biochron of Norian-Rhaetian age; and (7) *Redondasuchus* biochron of Rhaetian age. Many of these biochrons correlate strata

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across much of Pangea. Additionally, a marine occurrence of *Aetosaurus* from the Calcare di Zorzino in Italy (middle-late Norian = younger portion of the *Himavatites columbianus* Zone) directly correlates the *Aetosaurus* biochron, including strata in the U.S.A., Greenland, and Germany, to the global marine timescale. An eighth biochron, the *Neoetosauroides* biochron of late Norian-Rhaetian age, can only be identified in the Los Colorados Formation in Argentina.

Aetosaur genera were relatively cosmopolitan during the late Carnian, as evidenced by intercontinental correlations based on *Longosuchus* (from the U.S.A., Morocco, and possibly India) and *Stagonolepis* (from Scotland, the U.S.A., Argentina, and Brazil). However, with the exception of *Aetosaurus*, aetosaurs became increasingly provincial in the Norian-Rhaetian, as evidenced by endemic taxa such as *Typhothorax* (North American Norian), *Neoetosauroides* (South American late Norian-Rhaetian), and *Redondasuchus* (North American Rhaetian). *Aetosaurus* is known from Germany, Italy, Greenland, the United Kingdom, and both the eastern and western United States.

## 1. Introduction

The purpose of this paper is to summarize the taxonomy, phylogeny, biochronology, paleobiogeography, and evolution of the Aetosauria. The Aetosauria are an extinct suborder of quadrupedal, primarily herbivorous, heavily armored archosaurs known from Upper Triassic strata in North and South America, Greenland, Scotland, Germany, Italy, Africa, and India (Fig. 1). Although there is significant disagreement regarding the phylogenetic relationships of Triassic archosaurs, all recent authors consider the Aetosauria to be a monophyletic group within the Archosauria (e.g., Gauthier 1984, 1994, Benton and Clark 1988, Sereno 1991, Parrish 1993, 1994, Juul 1994). They are either pseudosuchians (Gauthier 1984, Benton and Clark 1988) or suchians (Benton and Clark 1988, Sereno 1991, Parrish 1993) based primarily on their crocodile-normal tarsus. Adult body lengths of individual genera range from 0.8 m (*A. ferratus*) to 5–6 m (*Desmatosuchus*).

One of the most distinctive features of the Aetosauria is their armored carapace that extends from the back of the skull to the tip of the tail. This carapace consists of multiple columns of articulated dermal osteoderms (scutes), with each row of scutes approximately corresponding to a vertebra. Two columns of paramedian scutes parallel the vertebral column and are usually bordered by corresponding lateral scutes. All dorsal and lateral scutes are reticulated, with the posterior margin of each scute overlapping the anterior margin of the scute behind it. The ventral carapace is less well-known but typically consists of 8–12 columns of ventral scutes. The paramedian and lateral scutes that comprise the dorsal carapace of aetosaurs are generally identifiable at least to the genus level (Long and Ballew 1985, Heckert et al. 1996). These animals are among the most commonly recovered fossils in the Chinle Group of western North America (Long and Ballew 1985) and have been used extensively for correlation, biostratigraphy, and biochronology in the Chinle and elsewhere (e.g., Lucas 1993, 1997, Lucas and Hunt 1993, Lucas and Heckert 1996). This ease of identification, combined with their abundance, broad geographic distribution, and short (typically less than a stage-

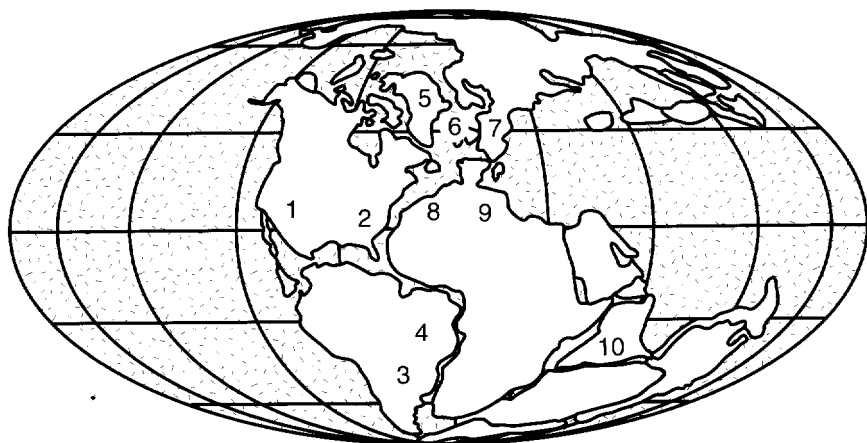


Fig. 1. Distribution of aetosaur fossils across Late Triassic Pangea. 1 = Chinle Group, western United States; 2 = Newark Supergroup, eastern United States; 3 = Ischigualasto and Los Colorados Formations, Argentina; 4 = Santa Maria Formation, Brazil; 5 = Fleming Fjord Formation, Greenland; 6 = Lossiemouth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

age) stratigraphic ranges, make aetosaurs excellent index fossils (Lucas and Heckert 1996).

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

**Institutional Abbreviations**—ANSP, Academy of Natural Sciences, Philadelphia; AUP, Aberdeen University Palaeontological collection, Aberdeen; EM, Elgin Museum, Elgin; MCSNB, Museo di Scienze Naturali Bergamo, Bergamo; MNA, Museum of Northern Arizona, Flagstaff; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; PVL, Miguel Lillo Institute, Tucumán, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart; UCMP, University of California Museum of Paleontology, Berkeley; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

## 2. Phylogeny and systematic paleontology

Parrish (1994:206) recently proposed the first cladistic phylogenetic hypothesis for the aetosaurs, defining the Aetosauria, and thus the Stagonolepididae, by the following synapomorphies: possession of an anteriorly edentulous premaxilla,

reduced, nearly conical teeth, a complete carapace consisting of dorsal and ventral elements, sculptured dorsal paramedian osteoderms that are wider than long (and lacking anteriorly or posteriorly projecting lappets, as seen in the rauisuchians), and "stout" limb bones with hypertrophied trochanters (see also Parrish 1994: tables 1 and 2). Long and Murry (1995) recently published a taxon-by-taxon description of the aetosaurs of western North America, and used 23 characters to define the Aetosauria, but did not examine other taxa and thus provided no phylogeny. Heckert et al. (1996) accepted Parrish's (1994) monophyletic Aetosauria and utilized *Aetosaurus* as an outgroup to all other aetosaur taxa to undertake a phylogenetic analysis. Both here and elsewhere (Heckert and Lucas 1999), we have followed Parrish (1994) in designating the Rauisuchia as an outgroup to the Aetosauria, and rely on the well-known taxa *Postosuchus* (Chatterjee 1985, Long and Murry 1995) and *Saurosuchus* (Reig 1959, 1961, Sill 1974) for comparison.

Parrish (1994) conducted his phylogenetic analysis with 15 characters. Heckert et al. (1996) utilized some of those characters and expanded their matrix to 22 characters. Long and Murry (1995:66) independently listed a total of 23 characters that they considered diagnostic of the Aetosauria, and numerous characters useful for diagnosing each aetosaur from the American Southwest, but expressly avoided phylogenetic analyses. We conducted a similar analysis to this one, using 60 characters, when we described *Coahomasuchus* (Heckert and Lucas 1999). Here, we integrate these analyses and add new characters, resulting in a data matrix of 60 characters (see Appendix 1 for a description of characters and character states, and Appendix 2 for a data matrix). These characters are ordered by position on the body, with skull and mandible characters listed first, followed by characters of the axial skeleton, appendicular skeleton, and the armor. Armor characters are subdivided into those for dorsal paramedian, lateral, ventral, and appendicular scutes. Within each subdivision, we list characters utilized by Parrish (1994) and Long and Murry (1995) first, followed by additional characters we have identified and examined.

Unfortunately, many existing aetosaur genera cannot be evaluated for Long and Murry's (1995) characters, as 13 of these are found on either the skull or mandible, elements that are infrequently preserved relative to the armor, which we rely on for 32 characters. Furthermore, another six of Long and Murry's characters are synonymous with characters identified by Parrish (1994), with character 3 "premaxilla edentulous anteriorly with an anteroventrally inclined mediolaterally expanded 'shovel' at anterior end" (Parrish 1994:table 1) accounting for two of Long and Murry's characters. We also did not consider the last character of Long and Murry (1995:66), "tendency toward spinescence within lateral armor" to be quantifiable in cladistic terms, and instead utilize several characters to evaluate changes in lateral scute morphology. Two of Long and Murry's (1995) characters, "anterior portion of dentary edentulous" and "dentary with reduced dentition," are linked, but were maintained as separate characters. We feel this is justified because all aetosaurs with preserved jaw material have an edentulous anterior dentary, but within the aetosaurs, tooth counts in the dentary range from more than 10 to as few as five, and we consider the latter condition relatively derived.

To conduct this analysis we examined specimens of and/or primary literature on the following aetosaurs (important citations listed with each taxon): *Aetosaururus*, including both *A. ferratus* and *A. crassicauda* (O. Fraas 1877, E. Fraas 1907, Huene 1920b, 1921, Walker 1961, Wild 1989, Small 1998), *Stagonolepis*, including both *S. robertsoni* and *S. wellesi* (Agassiz 1844, Huxley 1859, 1875, 1877, Case 1932, Walker 1961, Long and Ballew 1985, Long and Murry 1995); *Acompsosaurus wingatensis* (Mehl 1915, Mehl et al. 1916); *Desmatosuchus* (Case 1920, 1922, Long and Ballew 1985, Small 1985, 1989, Long and Murry 1995); *Longosuchus* (Sawin 1947, Hunt and Lucas 1990, Parrish 1994, Long and Murry 1995), *Paratypothorax* (Long and Ballew 1985, Hunt and Lucas 1992, Long and Murry 1995); *Typothorax* (Cope 1875, Long and Ballew 1985, Hunt et al. 1993, Long and Murry 1995), *Ebrachosaurus* (Kuhn 1933, 1936); *Aetosauroides* (Casamiquela 1960, 1961, 1967); *Neoetosauroides* (Bonaparte 1967, 1971a, b, 1978); *Redondasuchus* (Hunt and Lucas 1991, Heckert et al. 1996), *Acaenasuchus* (Long and Murry 1995); and *Lucasuchus* (Long and Murry 1995). All named aetosaur genera were considered, subject to the following caveats: *Argentinosuchus* (Casamiquela 1960) is clearly a junior synonym of the Ischigualasto Formation aetosaur, herein referred to *Stagonolepis* (= *Aetosauroides*, see below). The type specimen of *Chilenosuchus* (Casamiquela 1978) is lost, is almost certainly not an aetosaur, and may not even be from Triassic rocks (Breitkreuz et al. 1992). A detailed osteology of *Stegomus* (Marsh 1896, Jepsen 1948, Baird 1986) is not possible from the known specimens, which are indistinguishable from *Aetosaururus* (Lucas et al. 1998). Heckert and Lucas (1999) published the name of a new aetosaur, *Coahomasuchus kahleorum*, from the Colorado City Member of the Dockum Formation in west Texas. This aetosaur was briefly described and illustrated by Lucas et al. (1993), and is herein referred to as *Coahomasuchus*. Murry and Long (1996) reported a new, "carnivorous" aetosaur from the same horizon as *Coahomasuchus*, but this aetosaur, while distinct, has not been described sufficiently for us to include it in our phylogenetic analysis. Herein, we refer to this aetosaur as the "carnivorous aetosaur."

With these considerations in mind we constructed a data matrix of 60 characters for the 12 taxa listed above. Initial runs of PAUP (Swofford 1993) analyses using both the branch-and-bound and exhaustive algorithms and incorporating all the taxa in the data matrix yielded 16 most parsimonious trees. The strict consensus of these trees bore out our initial suspicions that *Stagonolepis robertsoni* and *Aetosauroides scagliai* are congeneric, as are *Desmatosuchus* and *Acaenasuchus*, and *Longosuchus* and *Lucasuchus*. Accordingly, we removed *Aetosauroides*, *Acaenasuchus* and *Lucasuchus* from the matrix and here regard them as junior subjective synonyms of *Stagonolepis*, *Desmatosuchus* and *Longosuchus*, respectively. We also remain skeptical regarding the distinctiveness of the Chinle species *Stagonolepis wellesi* (Long and Ballew 1985) from the European *S. robertsoni*. Although Long and Ballew (1985) and Long and Murry (1995) note the presence of spikes on the cervical lateral scutes as well as wider transverse processes on *S. wellesi*, these features are not convincingly associated with UMMP 13950, the type specimen of *S.* (= *Calyptosuchus*) *wellesi* (Long and Ballew 1985). Indeed, the type

specimen is a mid-dorsal to mid-caudal carapace, associated vertebrae, pelvis, and miscellaneous appendicular scutes, and thus lacks cervical lateral scutes entirely. Otherwise, these taxa score almost identically throughout the matrix. The same is true of the two distinct German species of *Aetosaurus*, *A. ferratus* and *A. crassicauda*, which differ primarily in size (O. Fraas 1877, E. Fraas 1907, Huene 1920, Wild 1989, Small 1998). Although we consider *Redondasuchus* distinct from *Tytophorax* (Heckert et al. 1996; *contra* Long and Murry 1995, Small 1998), we determined that it was too incompletely known (only 29 of 60 characters could be coded) to include in our analyses. Therefore, in our final analysis we chose to include only a single species of *Stagonolepis* (*S. robertsoni*) as well as the taxa *Aetosaurus ferratus*, *Coahomasuchus*, *Desmatosuchus haplocerus*, *Longosuchus meadei*, *Neoaetosauroides engaeus*, *Paratytophorax andressorum*, and *Tytophorax coccinarum*, and utilized the rauisuchians as an outgroup.

The result of this analysis was a single most parsimonious tree (Fig. 2). This tree has a treelength of 76, a consistency index of 0.74, and a retention index of 0.56. This analysis demonstrates that the aetosaurs are a monophyletic group, with *Aetosaurus* a sister taxon to the other aetosaurs, composed of two clades, (*Coahomasuchus* + *Stagonolepis*) and (*Neoaetosauroides* + ((*Tytophorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratytophorax*))). The conclusions of this analysis are broadly similar to those reached by other workers, both using cladistics (Parrish 1994, Heckert et al. 1996) and older, non-cladistic phylogenetic hypotheses (e.g., Walker 1961). The following is our systematic description of the results of this analysis.

### **Systematic Paleontology**

#### **Class Reptilia Laurenti 1768**

#### **Order Crocodylotarsi Benton and Clark 1988**

#### **Suborder Aetosauria Nicholson and Lydekker 1889**

#### **Family Stagonolepididae Lydekker 1887**

We present a new diagnosis of the Aetosauria, and thus the Stagonolepididae, although we hesitate to present a cladistic definition of these taxa. The aetosaurs are clearly a monophyletic assemblage, but interpretations of archosaur relationships are sufficiently uncertain that the identification of sister-groups to the Aetosauria varies widely from worker to worker. We suggest that Aetosauria be diagnosed as a stem-based taxon, consisting of all crurotarsans more closely related to *Desmatosuchus* than the immediate sister group, recognizing that the sister-group may be rauisuchians (Benton and Clark 1988, Parrish 1993, 1994), prestosuchians (Jülich 1994), or another suchian taxon (Sereno 1991). With this admittedly tentative definition, we define the Stagonolepididae as the node-based taxon consisting of the last common ancestor (and all of its descendants) of *Aetosaurus* and *Desmatosuchus*.

We recognize the following 18 synapomorphies as diagnostic of the Stagonolepididae (numbering follows that used in our data matrix – see Appendix): 1, premaxilla edentulous anteriorly, with an anteroventrally inclined, mediolaterally expanded “shovel” at the anterior end (unknown in *Coahomasuchus* and *Paraty-*

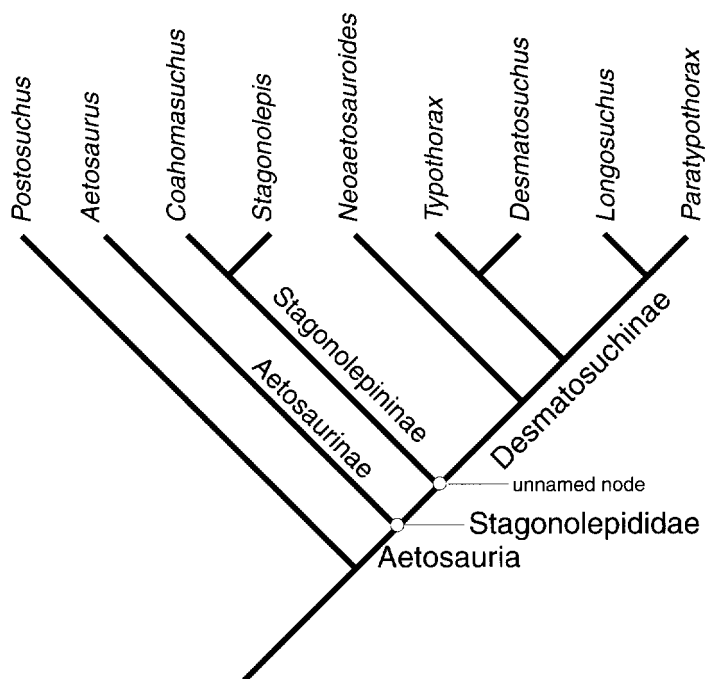


Fig. 2. Single most parsimonious tree of the eight best-known aetosaur genera, with the rauisuchian *Postosuchus* used as an outgroup. As discussed in the text, Aetosauria is a stem-based taxon, as are all sub-families. Stagonolepididae is defined at the node that represents the last common ancestor of *Desmatosuchus* and *Aetosaurus*. Treelength is 76, consistency index is 0.74, retention index is 0.56. See text for details and appendices for character lists and data matrix.

*pothorax*); 2, teeth reduced in size, conical or nearly conical (unknown in *Coahomasuchus* and *Paratypothorax*); 8, external nares longer than antorbital fenestra (unknown in *Coahomasuchus* and *Paratypothorax*); 10, supratemporal fenestra exposed laterally, not dorsally (unknown in *Coahomasuchus* and *Paratypothorax*); 11, parietal short (unknown in *Coahomasuchus* and *Paratypothorax*); 12, posterior margin of parietal modified to receive paramedian scutes (unknown in *Coahomasuchus* and *Paratypothorax*, but very likely present in *Coahomasuchus*); 13, maxilla included in external nares (unknown in *Coahomasuchus*, *Paratypothorax*, and *Neoetosauroides*); 14, jugal downturned (unknown in *Coahomasuchus* and *Paratypothorax*); 15, "slipper-shaped" mandible, consisting of robust posterior bones and processes with dorsally concave, less robust dentary (unknown in *Paratypothorax*); 17, presacral vertebral column massively constructed (unknown in *Paratypothorax*); 22, apex of scapula broadly expanded (unknown in *Coahomasuchus* or *Paratypothorax*); 23, manus short, broad, and small, effectively wider than long (unknown in *Paratypothorax*); 24, well-developed, robust,

short anterior iliac blade (unknown in *Paratypothorax*); 27, pubes broadened transversely and fused, forming a "pubic apron" in anterior view (unknown in *Coahomasuchus*, *Longosuchus*, *Neoaetosauroides* and *Paratypothorax*); 28, dorsal paramedian plates wider than long, sculptured, lacking anteriorly or posteriorly projecting lappets; 57, dermal lateral scutes articulating with larger paramedian plates; 59, dermal ventral scutes articulating with each other to form a ventral carapace (unknown in *Typothorax*, *Desmatosuchus*, and *Paratypothorax*); and 60, dermal scutes covering the appendages, at least in part (unknown in *Desmatosuchus*, *Neoaetosauroides* and *Paratypothorax*).

### Subfamily Aetosaurinae, new taxon

We erect the taxon Aetosaurinae for the most primitive aetosaurs. Currently, the Aetosaurinae is a monogeneric taxon, and includes only *Aetosaurus*. Consequently, the Aetosaurinae are diagnosed by the same features that diagnose *Aetosaurus* (see below). A cladistic definition of the Aetosaurinae would include all taxa more closely related to *Aetosaurus* than the last common ancestor of *Aetosaurus* and *Desmatosuchus*. This may include the carnivorous aetosaur (Murry and Long 1996), but until this taxon is fully described we withhold judgment on its phylogenetic position.

### Genus *Aetosaurus* O. Fraas 1877

(Fig. 3A-D, F)

Revised diagnosis: *Aetosaurus* is distinguished from all other aetosaurs by the presence of conical, recurved teeth and dorsal paramedian scutes that are moderately wide (width/length [W:L] = 2–3.5) that possess a radial pattern of elongate pits and ridges and a low dorsal boss that does not contact the posterior margin of the scute.

*Aetosaurus* was named by O. Fraas (1877) for 22 articulated skeletons collected from the Lower Stubensandstein at Heselach in Germany. This aetosaur is widely considered the most primitive member of the Stagonolepididae, a conclusion borne out by our analysis. Of the three species, *A. ferratus*, *A. crassicauda* (E. Fraas 1907), and *A. arcuatus* (Marsh 1896), *A. ferratus* is the best known. Wild (1989) summarized the evidence demonstrating the validity of the two European species (see below), and Lucas et al. (1999) have demonstrated that *Stegomus arcuatus* from the eastern U.S. A. is a junior subjective synonym of *Aetosaurus*. Recently, Jenkins et al. (1994) reported *Aetosaurus* from the Fleming Fjord Formation in Greenland, and Heckert and Lucas (1998) and Small (1998) have reported *Aetosaurus* from the Chinle Group in the western U.S.A. One isolated scute from the fissure fill in Cromhall, England, reported by Fraser (1988) also pertains to *Aetosaurus*. All occurrences of *Aetosaurus* are from strata of Norian age (Lucas and Heckert 1996, Heckert and Lucas 1998, Lucas et al. 1998).



***Aetosaurus ferratus* O. Fraas 1877**

(Fig. 3A, D)

- 1877 *Aetosaurus ferratus* O. Fraas, p. 1, figs. 2–3 (unnumbered), pl. 1–3.
- 1896 *Aetosaurus ferratus*: E. Fraas, p. 17, tab. 4.
- 1907 *Aetosaurus ferratus*: Huene, p. 392, figs. 345–346, 350.
- 1914 *Aetosaurus ferratus*: Huene, p. 18, figs. 43–44.
- 1915 *Aetosaurus ferratus*: Lull, p. 101, fig. 9.
- 1920a *Aetosaurus ferratus*: Huene, p. 161, fig. 1.
- 1920b *Aetosaurus ferratus*: Huene, p. 465, figs. 1–50.
- 1928 *Aetosaurus ferratus*: Schmidt, p. 419, figs. 1175a–f.
- 1938 *Aetosaurus ferratus*: Berckhemer, p. 191, fig. 48.
- 1955 *Aetosaurus ferratus*: Hoffstetter, p. 672, fig. 5.
- 1956 *Aetosaurus ferratus*: Huene, p. 450, fig. 484a, b.
- 1956 *Aetosaurus ferratus*: Romer, p. 131, fig. 69e.
- 1961 *Aetosaurus ferratus*: Walker, p. 164, figs. 24a, 40–45, tab. 13.
- 1976 *Aetosaurus*: Krebs, p. 78, fig. 26a.
- 1978 *Aetosaurus*: Bonaparte, p. 300, fig. 13a.
- 1988 Possible aetosaur?: Fraser, p. 132, fig. 4.
- 1989 *Aetosaurus ferratus*: Wild, figs. 1–3, 4a.
- 1994 *Aetosaurus* sp.: Jenkins et al. figs. 8–9.
- 1998 *Aetosaurus* sp.: Small, figs. 2–4.

Lectotype: Individual number XVI, a complete skull, skeleton, and articulated carapace from the block of 22 specimens, SMNS 5770 (Walker 1961).

Type locality: Lower Stubensandstein, Heslach, Baden-Württemberg, Germany.

Revised diagnosis: A species of *Aetosaurus* distinguished from *A. crassicauda* by its small (< 1 m long) size and elongate dorsal boss (keel) on dorsal paramedian scutes and from *A. arcuatus* by the presence of an elongate, prominent dorsal boss (keel) and elongate, deeply incised pits and prominent ridges on the paramedian scutes (Fig. 3A,D).

Distribution: The type locality in the Lower Stubensandstein, at Heslach, Baden-Württemberg, Germany, the Calcare di Zorzino Formation at Cene near Bergamo, Italy (Wild 1989), the Ørsted Dal Member of the Fleming Fjord Formation in eastern Greenland (Jenkins et al. 1994), the Chinle Formation in Colorado, U.S.A. (Small 1998), and the fissure fill at Cromhall, Avon, in the United Kingdom (Fraser 1988, see below).

Discussion: Wild (1989) differentiated *A. ferratus* from *A. crassicauda* based on its smaller size (90 cm maximum adult length), elongate keels on the dorsal paramedian scutes, and densely packed, deeply incised radial patterns of pits and grooves on the scutes. The Greenland specimens represent *A. ferratus* (Jenkins et al. 1994), as do at least some of the Chinle specimens (Small 1998).

Fraser (1988:fig. 4) illustrated a small aetosaur scute and an associated possible partial maxilla from the Cromhall Quarry in Avon, a fissure-fill deposit in the

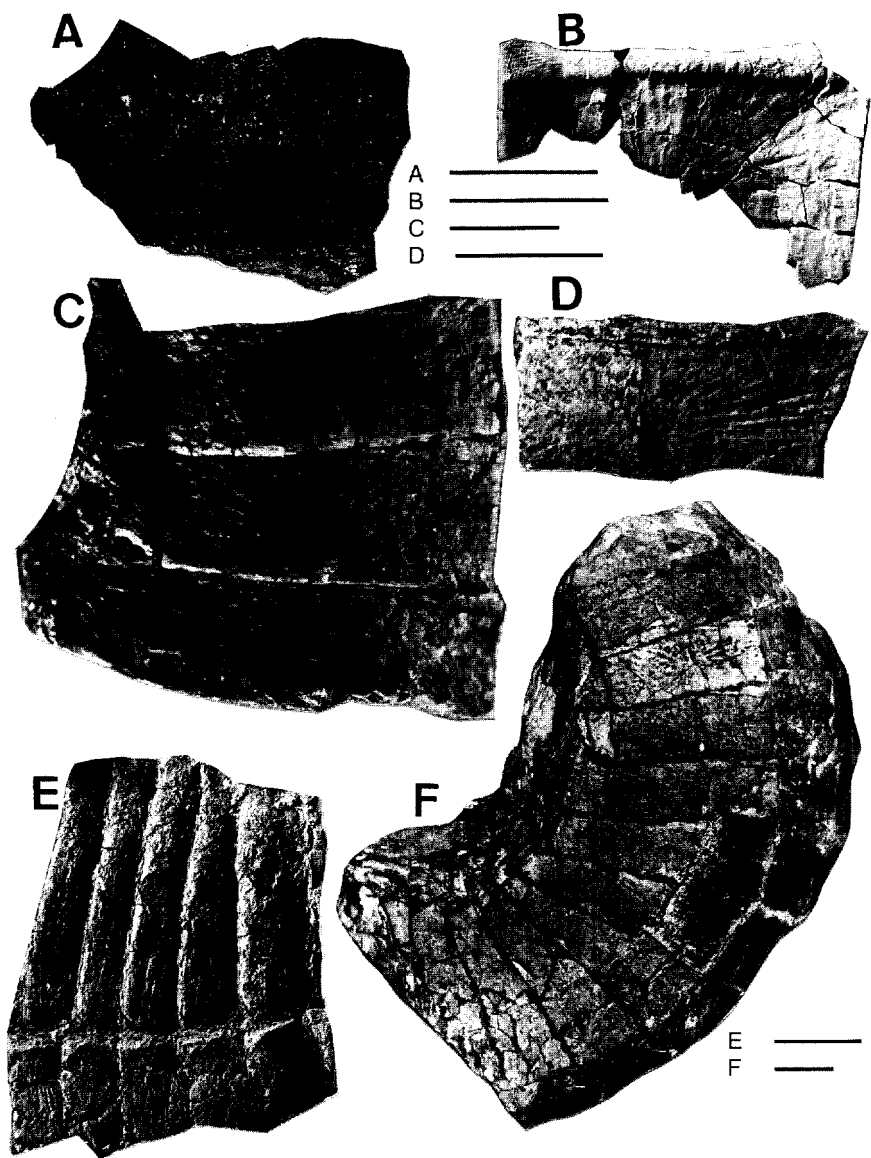


Fig. 3. Selected scutes of *Aetosaurus* (A-D, F) and *Coahomasuchus* (Fig. 3E), all in dorsal view. A, MCSNB 4864, right dorsal paramedian scutes, partial left dorsal paramedian scutes, and partial right lateral scutes of *A. ferratus* from the Calcare di Zorzino Formation, Italy; B, NMMNH P-17212, right dorsal paramedian scute of *A. arcuatus* from the Bull Canyon Formation, New Mexico; C, F, close-up (C) and distant (F) views of the holotype of *A. crassicauda* from the Middle Stubensandstein, Pfaffenhoffen, Germany; D, topotypic right dorsal paramedian scute of *A. ferratus* from SMNS 5770, Lower Stubensandstein, Heselach, Germany; E, NMMNH P-18496 right dorsal paramedian and lateral scutes of the holotype of *Coahomasuchus kahleorum* from the Colorado City Member of the Dockum Formation, Texas. All scale bars are 2 cm.

United Kingdom. The scute strongly resembles the lateral scutes of *A. ferratus* in size, shape, ornamentation, and possession of an anterior bar. The small size of the Cromhall scute, combined with the longitudinal ridge down the middle of the paramedian scute, indicates that it pertains to *A. ferratus*. Further, the associated maxilla is similar to *A. ferratus* and appears to have sockets for at least six teeth, including sockets at the anteriormost point of the jaw. As the most primitive aetosaur, *Aetosaurus* has the least edentulous maxillae of the aetosaurs, and, unlike every aetosaur but *Desmatosuchus*, has teeth anterior to the posterior margin of the external naris. Therefore, we assign specimens AUP 11300, a lateral scute, and AUP 11297, a partial right maxilla, to *Aetosaurus ferratus*.

### ***Aetosaurus crassicauda* E. Fraas 1907**

(Fig. 3C,F)

- 1907 *Aetosaurus crassicauda* E. Fraas, p. 101, pl. 1–2.  
1921 *Aetosaurus crassicauda*: Huene, p. 329, figs. 4, pl. 1 (figs. 3, 7–8).  
1928 *Aetosaurus crassicauda*: Schmidt, p. 420, fig. 1176.  
1938 *Aetosaurus crassicauda*: Berckhemer, p. 192, tab. 52 (figs. 34–35).  
1955 *Aetosaurus crassicauda*: Hoffstetter, p. 677, fig. 5.  
1956 *Aetosaurus crassicauda*: Huene, p. 450, fig. 484b.  
1989 *Aetosaurus crassicauda*: Wild, p. 1, fig. 4c.

Holotype: SMNS 11837, a partial skeleton consisting of an articulated carapace from the mid-dorsal to mid-caudal region, mid-dorsal, sacral, and proximal caudal vertebrae, and part of the pelvis.

Type locality: Middle Stubensandstein, Pfaffenhofen, Baden-Württemberg, Germany.

Revised diagnosis: A species of *Aetosaurus* distinguished from both *A. ferratus* and *A. arcuatus* by development of the dorsal boss into a knob on the paramedian scutes, from *A. ferratus* by its larger size (total body length approximately 1.5 m), the prevalence of pitting at the expense of grooves on the dorsal paramedian scutes, and strong transverse arching of the anterior caudal paramedian scutes, and from *A. arcuatus* by the more developed boss and prominent pitting on the dorsal paramedian and lateral scutes (Fig. 3C, F).

Distribution: Middle Stubensandstein, Pfaffenhofen, Baden-Württemberg, Germany.

Discussion: E. Fraas (1907) described *A. crassicauda* from a partial carapace from the Middle Stubensandstein at Pfaffenhofen, Germany. As Wild (1989) noted, the most obvious differences between *A. ferratus* and *A. crassicauda* are the latter's larger size (up to 1.5 m adult length), shallow and lightly incised pitting, development of the dorsal keel on the paramedian scutes into a knob, and the strong transverse arching of the anterior caudal paramedians (compare Fig. 3C, F). The largest specimens of *A. arcuatus* are approximately as large as specimens of *A. crassicauda*, but have much less well developed sculpturing on the scutes

(Heckert and Lucas 1998, Lucas et al. 1998). Huene (1921) referred additional material to *A. crassicauda*, but we concur with Walker (1961:p. 173–174) that some of those elements were misidentified, and have restricted our assignments accordingly.

### *Aetosaurus arcuatus* (Marsh) 1896

(Fig. 3B)

- 1896 *Stegomus arcuatus* Marsh, p. 60, pl. 1.
- 1914 *Stegomus arcuatus*: Huene, p. 19, fig. 49.
- 1915 *Stegomus arcuatus*: Lull, p. 79, pl. 5.
- 1948 *Stegomus arcuatus jerseyensis*: Jepsen, p. 9, pls. 1–2.
- 1953 *Stegomus arcuatus*: Lull, p. 79, pl. 5.
- 1980 *Stegomus arcuatus*: Olsen, p. 42, fig. 3.4a, tab. 3.1.
- 1986 *Stegomus arcuatus*: Baird, p. 142, figs. 12–13, 14a.
- 1993 *Stegomus* cf. *Stegomus arcuatus*: Huber et al. p. 179, fig. 5.
- 1998 *Aetosaurus arcuatus*: Heckert and Lucas, p. 604 figs. 2–3.
- 1998 *Aetosaurus arcuatus*: Lucas et al., (1998) figs. 2–5.

Holotype: YPM 1647, natural cast of ventral aspect of part of dorsal carapace.

Type locality: New Haven Formation, Fair Haven, Connecticut, U.S.A.

Revised diagnosis: A species of *Aetosaurus* distinguished from *A. ferratus* and *A. crassicauda* by its minimal ornamentation on dorsal paramedian scutes, consisting of a subdued boss with a faint pattern of elongate pits and grooves (Fig. 3B); lateral margin of dorsal paramedian scutes slightly angled, with scute wider anteriorly and narrower posteriorly; and dorsal paramedian scutes that are up to 3.5 times wider than long; and tail that tapers rapidly posteriorly; also distinguished from *A. ferratus* by its larger size (adults up to 1.5 m body length).

Distribution: *A. arcuatus* is known from the type locality in the New Haven Formation, Fair Haven, Connecticut, from the Passaic Formation in Somerset and Huntendon Counties, New Jersey, "Lithofacies Association II" (= Lower Sanford Formation), North Carolina, and the Bull Canyon Formation, New Mexico, all in the U.S.A.

Discussion: *A. arcuatus* was originally named *Stegomus arcuatus* by Marsh (1896). Since then, all relatively small aetosaur specimens found in the Newark Supergroup were referred to *Stegomus*. Jepsen (1948) attempted to distinguish subspecies, his *S. arcuatus jerseyensis* and *S. arcuatus arcuatus*, but these are based on specimens that lack the necessary overlap of homologous parts, and the minor differences he describes fall well within the range of variation of a single aetosaur species (Lucas et al. 1998). No subsequent worker has attempted to follow this scheme. Lucas et al. (1998) recently demonstrated that none of the specimens assigned to *Stegomus*, including the type, are significantly different from the known species of *Aetosaurus*. Accordingly, they reassigned the type species,

*Stegomus arcuatus*, to *Aetosaurus*. The second nominal species of “*Stegomus*,” *S. longipes* Emerson and Loomis (1904), is based on a partial skeleton of a sphenosuchian and was renamed *Stegomosuchus longipes* by Huene (1914).

**Unnamed Clade: (*Coahomasuchus* + *Stagonolepis*) + (*Neoaetosauroides* + (*Desmatosuchus* + *Tytophorax*) + (*Longosuchus* + *Paratytophorax*))**

This taxon is the other stem-based counterpart to the Stagonolepididae, defined as all aetosaurs more closely related to *Desmatosuchus* than the last common ancestor of *Desmatosuchus* and *Aetosaurus*, and consists of all valid, named, aetosaur genera except *Aetosaurus*. These taxa are united by the following three synapomorphies: 3, teeth conical, not recurved (unknown in *Coahomasuchus* and *Paratytophorax*); 4, anterior part of dentary edentulous (unknown in *Coahomasuchus* and *Paratytophorax*); 5, maxillary tooth row does not extend anterior to the posterior end of the external naris (unknown in *Coahomasuchus*, *Neoaetosauroides*, and *Paratytophorax*; reversed in *Desmatosuchus*).

### Subfamily Stagonolepininae

(*Coahomasuchus* + *Stagonolepis*):

Huene (1942) erected the subfamily “Stagonolepininae” for the aetosaur *Stagonolepis*. The proper Linnaean construction for this subfamily name is Stagonolepininae, as we use here. We define the Stagonolepininae as all aetosaurs more closely related to *Stagonolepis* than the last common ancestor of *Stagonolepis* and *Desmatosuchus*. In this paper, the Stagonolepininae consists of the genera *Stagonolepis* and *Coahomasuchus*.

*Coahomasuchus* and *Stagonolepis* are united by the following two synapomorphies: 7. Presence of a deep, hemispherical fontanelle in the bottom of the basisphenoid between the basal tubera and basiptyergoid processes (unknown in *Neoaetosauroides* and *Paratytophorax*; convergent with *Longosuchus* and *Desmatosuchus*). 36. Absence of raised bosses on cervical paramedian scutes (convergent with *Tytophorax*).

### *Coahomasuchus kahleorum* Heckert and Lucas 1999

(Fig. 3E)

1993 New aetosaur genus: Lucas et al., p. 241, fig. 5.

1999 *Coahomasuchus kahleorum* Heckert and Lucas, p. 50, figs. 3–8.

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

Type locality: Colorado City Member, Dockum Formation, Otis Chalk, Texas, U.S.A.

Revised diagnosis: *Coahomasuchus* can be diagnosed from all other aetosaurs by the following characteristics: presacral dorsal paramedian scutes with faint ornamentation consisting of sub-parallel, non-radial grooves and ridges (Fig. 3E); lateral scutes latero-medially flat, lacking keels, spikes, or flanges with a radial pattern of pits emanating from the center of the medial third of the specimen; small, subcircular to ovate, posteriorly tapering cervical ventral scutes; anterior ventral thoracic scutes hexagonal; thoracic scutes articulated in as few as four and as many as ten columns.

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

Distribution: Known only from the type locality.

Discussion: *Coahomasuchus* represents one of the least derived aetosaurs. Although it is still relatively small, it is at least as robust as the largest specimen of *A. crassicauda* and much larger than *A. ferratus*. As the oldest primitive aetosaur, *Coahomasuchus* is important because it documents the presence of a basal aetosaur among the first aetosaur records.

### *Stagonolepis robertsoni* Agassiz 1844

(Fig. 4)

- 1844 *Stagonolepis robertsoni* Agassiz, p. 139, pl. XXXI, figs. xiii, xiv.
- 1859 *Stagonolepis robertsoni*: Huxley, p. 440, pl. XIV figs. 1–3.
- 1877 *Stagonolepis robertsoni*: Huxley, p. 1, pl. I–X.
- 1907 *Stagonolepis robertsoni*: Huene, p. 392, figs. 347–348.
- 1915 *Acompsosaurus wingatensis* Mehl et al., p. 29, figs. 12–14, pl. 3.
- 1922 Phytosaur, Case, p. 70, fig. 27, pl. 13a.
- 1932 Phytosaur, Case, p. 57, figs. 1–6, pl. 1–3, pl. 4 (fig. 1).
- 1936 *Ebrachosaurus singularis* Kuhn, p. 85, fig. 6–8, pl. XI (fig. 1,3), pl. XII (fig. 2), pl. XIII (fig. 4).
- 1936 *Stagonolepis robertsoni*: Huene, p. 207, fig. 3.
- 1942 *Stagonolepis robertsoni*: Huene, p. 223, figs. 45–49.
- 1960 *Aetosauroides scagliai* Casamiquela, p. 2, figs. 1–2.
- 1960 *Argentinosaurs bonapartei* Casamiquela, p. 2, figs. 3–5.
- 1961 *Aetosauroides scagliai*: Casamiquela, p. 4, figs. 1–26, pl. 1.
- 1961 *Argentinosaurs bonapartei*: Casamiquela, p. 4, figs. 27–32.

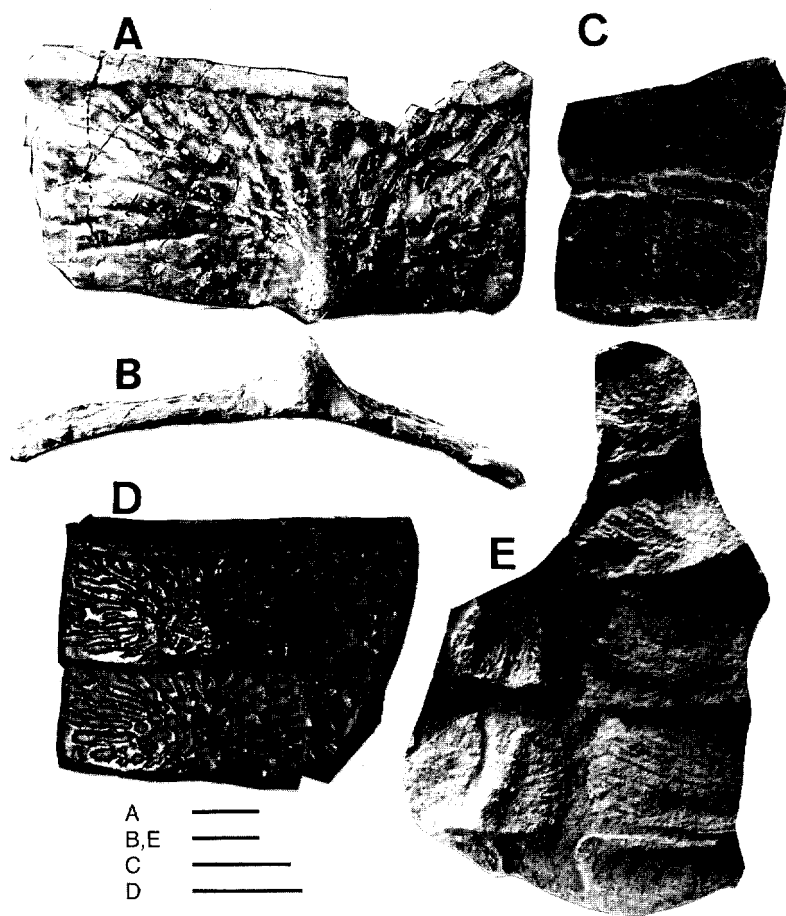


Fig. 4. Selected scutes of *Stagonolepis robertsoni*; all in dorsal view. A-B, MNA V-2930, left dorsal paramedian scute of *Stagonolepis* from the Placerias quarry, Bluewater Creek Formation, Arizona; C, E, dorsal paramedian scute (C) and left lateral and dorsal (E) paramedian scutes of the type of *Ebrachosaurus singularis* Kuhn, 1936, from the Blasensandstein, Ebrach, Germany (reproduced from Kuhn, 1936:pl. XI, figs. 1,3); D, PVL 2073, two dorsal paramedian scutes from the carapace of *Aetosauroides scagliai* (= *Stagonolepis robertsoni*), Ischigualasto Formation, Argentina.

- 1961 *Stagonolepis robertsoni*: Walker, p. 103, figs. 2–23, 24b, 25b, pl. 9–12.  
 1967 *Aetosauroides scagliai*: Casamiquela, p. 173, figs 1–3, pl. I–XV.  
 1971b *Aetosauroides scagliai*: Bonaparte, p. 671, fig. 15.

- 1971b *Argentinosuchus bonapartei*: Bonaparte, p. 671, fig. 16.
- 1976 *Stagonolepis*: Krebs, p. 77, fig. 26b.
- 1976 *Stagonolepis robertsoni*: Krebs, p. 78, fig. 3, 4, 9, 10d, 12, 15, 16, 17c-e, 19d-e, 20d-e, 27.
- 1978 *Aetosauroides scagliai*: Bonaparte, p. 300, figs. 137b, 138.
- 1978 *Stagonolepis* [sic]: Bonaparte, p. 300, fig. 136b.
- 1982 *Aetosauroides*: Bonaparte, p. 108, fig. 4d.
- 1985 *Calypotosuchus wellesi* Long and Ballew, p. 45, figs. 13-16, pl. 4-5.
- 1986 *Stagonolepis robertsoni*: Baird, p. 125, figs. 14b-c, 15.
- 1986 *Stagonolepis*: Parrish, p. 8, fig. 6, 14c3.
- 1986 *Calypotosuchus*: Parrish, p. 15, fig. 17h.
- 1988 *Stagonolepis*: Carroll, p. 273, figs. 13-15, 13-16.
- 1988 *Stagonolepis*: Fraser, p. 132, fig. 5b.
- 1989 *Calypotosuchus* sp.: Hunt et al., p. 8, fig. 1-34.7f,g,h.
- 1991 *Stagonolepis*: Sereno, p. 11, fig. 10, 27f.
- 1995 *Stagonolepis wellesi*: Long and Murry, p. 1, figs. 68-70, 71a, b, c, d, 72-84.
- 1996 *Stagonolepis*: Lucas and Heckert, p. 57, fig 4 (*Stagonolepis*).

Holotype: EM 27R, a segment of the ventral carapace.

Type locality: Lossiemouth Sandstone Formation, Lossiemouth, Scotland

Revised diagnosis: *Stagonolepis* is readily diagnosed from other aetosaurs by its relatively narrow (W:L = 2.5:1) dorsal paramedian scutes with a radial pattern of pits and grooves radiating from a prominent keel or knob that contacts the posterior margin of the scutes (Fig. 4); transverse processes on vertebrae exceed twice centrum length; neural spines on posterior dorsal, sacral, and anterior caudal centra tall (see Walker 1961, for a detailed osteology of *Stagonolepis*).

Distribution: *Stagonolepis* is the most widely distributed aetosaur. When all of the junior subjective synonyms are accounted for (see below), *Stagonolepis* is known from Elgin, Scotland, the Chinle Group in the U.S.A., the Ischigualasto Formation in Argentina, the Santa Maria Formation in Brazil, and the Blasensandstein in Germany.

Discussion: *Stagonolepis* was the first aetosaur to be described, albeit as a fish (Agassiz 1844). Huxley (1859, 1875, 1877) was the first to recognize its reptilian affinities. This relatively primitive aetosaur is slightly more derived than *Aetosaurus*, based on the synapomorphies listed for the clade (*Coahomasuchus* + *Stagonolepis*), as well as numerous other skeletal features (see Walker 1961). Three species of aetosaurs, *Argentinosuchus bonapartei* Casamiquela 1960, *Aetosauroides scagliai* (Fig. 4D), Casamiquela 1960, and *Calypotosuchus wellesi* Long and Ballew 1985, are definitely junior subjective synonyms of *Stagonolepis robertsoni*. Furthermore, although the type material of *Ebrachosaurus singularis* is lost, Kuhn's published illustrations (Kuhn 1936: textfig. 6-8, pl. XI figs. 1,3) (Fig. 4C, E) indicate an aetosaur nearly identical to *Stagonolepis*, so we also consider *Ebrachosaurus* a junior subjective synonym of *Stagonolepis*. The holotype of *Acompso-saurus wingatensis* Mehl, which consists of a nearly complete pelvis collected



from the Bluewater Creek Formation in western New Mexico, U.S.A., is lost, but generally resembles *Stagonolepis* (Hunt and Lucas 1989, Long and Murry 1995, Heckert 1997).

At this time, we only recognize one species of *Stagonolepis*, *S. robertsoni*. Long and Murry (1995) argued that *Calyptosuchus wellsi* from the Chinle Group is congeneric with *Stagonolepis*, but reiterated the position of Murry and Long (1989) that the Chinle form is a different species, *S. wellsi*. We have maintained the distinction in the appendices based on their descriptions, but note here that we are not convinced that these characteristics are demonstrably associated with their holotype of *S. wellsi*. Including *S. wellsi* in the analysis results in no change in tree topology (it is a sister taxon to *S. robertsoni*), but lowers the consistency and retention indices due to the reported presence of lateral spikes, indicating convergence with the derived clade of ((*Typhothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratyphothorax*)). All reported specimens of *Stagonolepis* occur in strata of Adamanian (latest Carnian) age (Lucas and Heckert 1996).

### Subfamily Desmatosuchinae Huene 1942

*Neoetosaurioides* + ((*Typhothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratyphothorax*))

Huene (1942) erected the subfamily Desmatosuchinae for the aetosaurs *Desmatosuchus*, *Acompsosaurus* (= *Stagonolepis*) and ?*Hoplitosuchus*. We define the Desmatosuchinae as all aetosaurs more closely related to *Desmatosuchus* than the last common ancestor of *Stagonolepis* and *Desmatosuchus*. In this paper, the Desmatosuchinae consist of *Neoetosaurioides* + ((*Typhothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratyphothorax*)).

Various characters loosely tie *Neoetosaurioides* to the more derived aetosaurs by the overlap of some derived character states. Additionally, these aetosaurs typically have slightly more robust limb bones (lower length:width ratios) than the other aetosaurs. This clade is weakly supported by the following synapomorphy: 9, infratemporal fenestra equant to square (unknown in *Typhothorax*, *Coahomasuchus*, and *Paratyphothorax*).

### *Neoetosaurioides engaeus* Bonaparte 1967

- 1967 *Neoetosaurioides engaeus* Bonaparte, p. 283, figs. 7–8.
- 1971a *Neoetosaurioides engaeus*: Bonaparte, p. 87, figs. 34–42.
- 1971b *Neoetosaurioides engaeus*: Bonaparte, p. 171, fig. 17.
- 1978 *Neoetosaurioides engaeus*: Bonaparte, p. 300, fig. 139.
- 1982 *Neoetosaurioides*: Bonaparte, p. 108, fig. 4e.
- 1985 *Neoetosaurioides*: Cruickshank and Benton, p. 716, fig. 2a.

Holotype: PVL 3525, a partial skeleton including partial jaws, a nearly complete, poorly preserved carapace, most of the axial skeleton, and nearly complete limbs.

Type locality: Los Colorados Formation, Argentina.

Revised diagnosis: *Neoaetosauroides* is diagnosed from all aetosaurs by its greatly reduced dentition, consisting of as few as six dentary teeth, the presence of a postglenoid process on the coracoid, and reduction of the fifth metatarsal, and from all aetosaurs but *Aetosaurus* by its narrow, unornamented dorsal paramedian scutes.

Distribution: *Neoaetosauroides* is known from three specimens collected from the Los Colorados Formation in Argentina (Bonaparte 1967, 1971a, b, 1978).

Discussion: *Neoaetosauroides* is notable for its postglenoid process on the coracoid and reduction of the fifth metatarsal (Parrish 1994) as well as its greatly reduced dentary tooth count. A character we have observed but which was not included in the phylogenetic analysis that may support inclusion of *Neoaetosauroides* with the more derived aetosaurs listed below is its relatively stout limb proportions. Recently one of us (ABH) restudied the type specimen and currently we are preparing a manuscript redescribing the taxon. *Neoaetosauroides* is of Coloradan age = Apachean (late Norian-Rhaetian) (Lucas and Heckert 1996).

**Unnamed Clade: (*Typothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paraty-pothorax*)**

These aetosaurs share the following seven synapomorphies: 39, dorsal bosses form a distinct knob, especially over the posterior paramedian scutes (convergent with *Stagonolepis*); 41, dorsal paramedian caudal scutes not transversely arched; 48, posterior emargination of lateral scute, revealing hollow on the posterior side of the lateral spike (reversed in *Typothorax*); 49, lateral spikes on cervical lateral scutes; 50, lateral spikes on dorsal ("trunk") lateral scutes; 52, lateral scutes sharply angulated with two distinct flanges that meet at an angle of approximately 90° or more; and 54, dorsal paramedian scutes not constricted anterior to sacrum.

The following synapomorphy may also unite these taxa, except that it is unknown in *Longosuchus* and *Paraty-pothorax*: 6, posterior premaxillary teeth absent (1).

**Unnamed Clade: *Typothorax* + *Desmatosuchus***

*Typothorax* and *Desmatosuchus* are united by the following four synapomorphies: 6, posterior premaxillary teeth absent (unknown in *Longosuchus* and *Paraty-pothorax*); 32, random pitting on cervical paramedian scutes, no elongate radial grooves and ridges; 33, random pitting on dorsal paramedian scutes, no elongate radial grooves and ridges; 47, random pitting on lateral scutes, no elongate radial grooves and ridges.

***Typothorax coccinarum* Cope 1875**

(Fig. 5A-C)

- 1877 *Typothorax coccinarum* Cope, p. 265, pl. 22, figs. 1–9.
- 1887 *Typothorax coccinarum*: Cope, p. 210, pl. 1.
- 1915 *Typothorax coccinarum*: Huene, p. 485, figs. 1–10, 12–15, 18–19, 22–27.
- 1953b “Type material of *Episcoposaurus horridus*.” Gregory, p. 1, fig. 17.
- 1985 *Typothorax coccinarum*: Long and Ballew, p. 45, figs. 8–12, pl. 2–3.
- 1985 Phytosaur: Lucas et al., p. 199, fig. 3a-b.
- 1985 *Typothorax* sp.: Lucas et al., p. 199, fig. 3c-Ee.
- 1986 *Typothorax*: Parrish, p. 7, figs. 17F, 20G, 28.
- 1989 *Typothorax coccinarum*: Long et al., p. 65, fig. 3a.
- 1989 *Typothorax coccinarum*: Small, p. 301, pl. 4j,l, 5j.
- 1992 *Typothorax coccinarum*: Lucas and Hunt, p. 151, figs. 13f, 14f-q.
- 1993 *Typothorax coccinarum*: Hunt et al., p. 209, figs. 1–2.
- 1995 *Typothorax coccinarum*: Long and Murry, p. 1, figs. 99–112.
- 1995 *Typothorax coccinarum*: Spamer and Daeschler, p. 430, fig. 15.
- 1996 *Typothorax*: Lucas and Heckert, p. 58, fig. 4 (*Typothorax*).

Lectotype: USNM 2586, a fragment of a dorsal paramedian scute (Lucas and Hunt 1992:fig. 13F), designated by Hunt and Lucas, 1993.

Type locality: Petrified Forest Formation, Chinle Group, Rio Arriba County, New Mexico.

Revised diagnosis: This genus is distinguished from other aetosaurs by its very broad dorsal paramedian scutes (width:length > 4:1) with ornamentation consisting of a random pattern of pits and prominent ventral keels that extend across the entire width of the scute (Fig. 4A, C), and its dorso-ventrally tall ilium with its highly unusual constriction above the acetabulum (e.g., Long and Murry 1995: fig. 106).

Distribution: *Typothorax* is restricted to the Chinle Group of the western U.S.A., where it is one of the most abundant vertebrate fossils in strata of early-mid Norian age (Lucas and Heckert 1996). As Gregory (1953b) noted, the unillustrated type material of *Episcoposaurus horridus* Cope (1887) pertains to *Typothorax*, thus rendering *Episcoposaurus* a junior subjective synonym of *Typothorax*.

Discussion: *Typothorax*, known from numerous localities in the Chinle Group, was the first aetosaur described from the U.S.A. (Cope 1875). Hunt et al. (1993) published a preliminary description of a nearly complete, articulated skeleton currently being prepared at the NMMNH (Fig. 5A-C), and Long and Murry (1995) presented a discussion and photographs of numerous specimens of *Typothorax* postcrania. To date, *Typothorax* occurrences are restricted to the Chinle Group, where it occurs at a large number of localities of Revueltian (early-mid Norian) age.

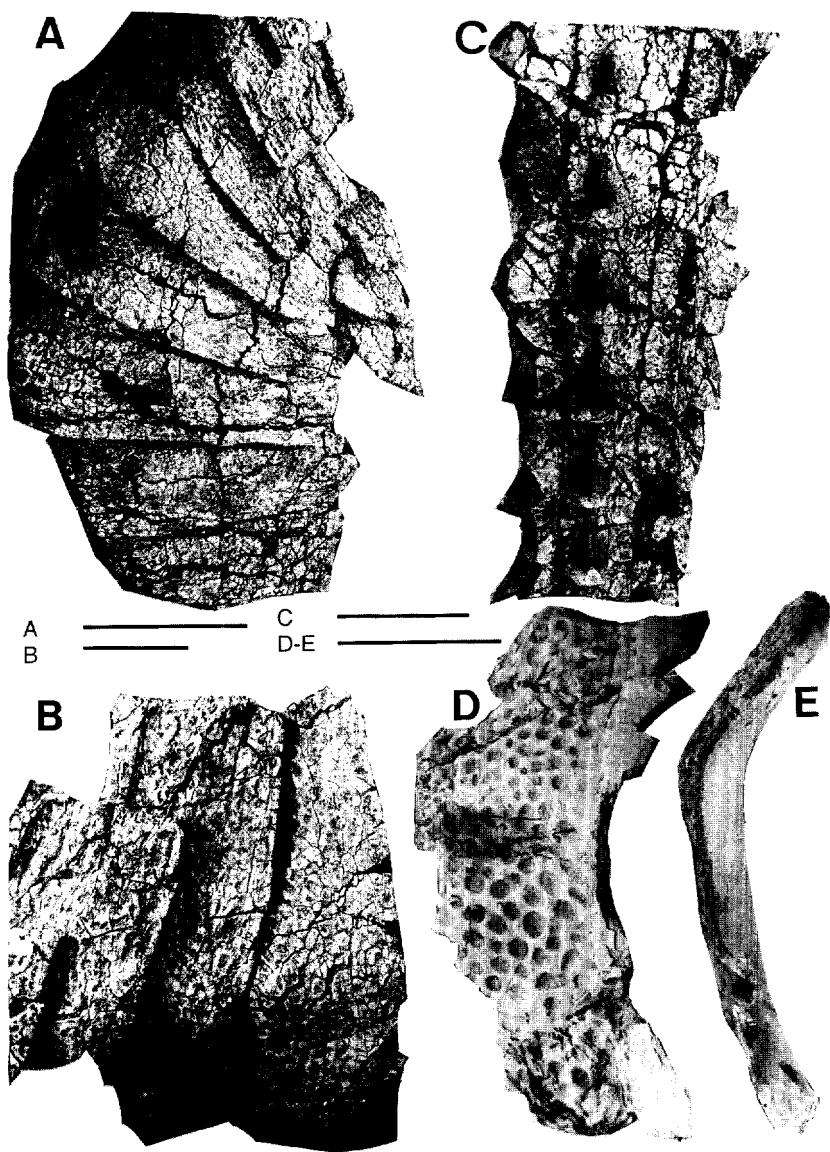


Fig. 5. Selected scutes of *Typothorax* (A-C) and *Redondasuchus* (D-E). A-C: NMMNH P-12964, nearly complete, articulated skeleton of *Typothorax coccinarum* from the Bull Canyon Formation, New Mexico, including distant (A) and close-up (B) dorsal views of dorsal paramedian scutes and (C) lateral view of lateral spikes developed on caudal paramedian scutes; D-E, UCMP 65415, holotype left dorsal paramedian scute of *Redondasuchus reseri* from the Redonda Formation, New Mexico, in dorsal (D) and anterior (E) views.

***Desmatosuchus haplocerus* (Cope 1892)**

(Fig. 6A-C)

- 1892 *Episcoposaurus haplocerus* Cope, p. 129.
- 1920 *Desmatosuchus spurensis* Case, p. 524, figs. 1–4.
- 1921 *Desmatosuchus spurensis*: Case, p. 133, pl. 3.
- 1922 *Desmatosuchus spurensis*: Case, p. 26, figs. 7–20, pl. 5–10.
- 1922 *Phytosaur*: Case, p. 70, fig. 27B, pl. 13a.
- 1929 *Desmatosuchus spurensis*: Case, p. 50, fig. 21.
- 1932 *Phytosaurus*: Case, p. 72, pl. 4 (figs. 2–3).
- 1942 *Desmatosuchus spurensis*: Huene, p. 233, fig. 50.
- 1953b *Desmatosuchus haplocerus*: Gregory, p. 1, figs. 1–14.
- 1954 *Desmatosuchus spurensis*: Brady, p. 19, figs. 1–2.
- 1958 *Desmatosuchus*: Brady, p. 61, figs. 1–4.
- 1961 *Desmatosuchus*: Walker, p. 179, fig. 24d.
- 1976 *Desmatosuchus*: Krebs, p. 78, fig. 26a.
- 1978 *Desmatosuchus*: Bonaparte, p. 300, fig. 136d.
- 1985 *Desmatosuchus haplocerus*: Long and Ballew, p. 45, figs 1–7, pl. 1.
- 1986 *Desmatosuchus haplocerus*: Murry, p. 122, fig. 9.12a.
- 1986 *Desmatosuchus*: Parrish, p. 7, figs. 12f, 16h, 17g, 19f, 20f, 21c, 22b
- 1986 *Desmatosuchus*: Parrish and Carpenter, p. 152, fig. 11.3.
- 1989 *Desmatosuchus haplocerus*: Long et al. fig., p. 69, 2b-c.
- 1989 *Desmatosuchus haplocerus*: Small, p. 301, fig. 1B, pl. 5a-f, i.
- 1993 *Desmatosuchus haploceros*[sic]: Parrish, p. 298, fig. 6b.
- 1994 *Desmatosuchus* sp.: Lucas and Heckert, p. 249, fig. 9.
- 1994 *Desmatosuchus*: Lucas, p. 107, fig. 5d-e.
- 1995 *Desmatosuchus haplocerus*: Long and Murry, p. 1, figs. 85–98.
- 1995 *Acaenasuchus geoffreyi* Long and Murry, p. 1, figs. 112–113.
- 1995 *Episcoposaurus haplocerus*: Spamer and Daeschler, p. 430, fig. 21.
- 1996 *Desmatosuchus*: Lucas and Heckert, p. 57, figs. 2, 4 (*Desmatosuchus*).
- 1997 *Desmatosuchus* sp.: Lucas et al., p. 23, fig. 6f-h.
- 1997 *Desmatosuchus* sp.: Heckert, p. 29, fig. 3c-e.

Holotype: ANSP 14688, “A dorsal and probably two caudal vertebrae; a scapula of the right side, a few fragments of ribs, and about thirty dermal bones” (Cope 1892:129).

Type locality: Tecovas Member, Dockum Formation, Chinle Group, Dickens County, Texas.

Diagnosis: Aetosaur genus readily diagnosed from all other aetosaurs by the presence of anterior laminae on the paramedian and lateral scutes (Fig. 6B-C), and dorso-ventrally thickened cervical paramedian scutes that are longer than wide, cervical lateral scutes that bear large, posteriorly recurved spikes (Fig. 6A); diagnosed from all aetosaurs but *Tyothorax* and *Redondasuchus* by the absence of elongate grooves and ridges on paramedian and lateral scutes.

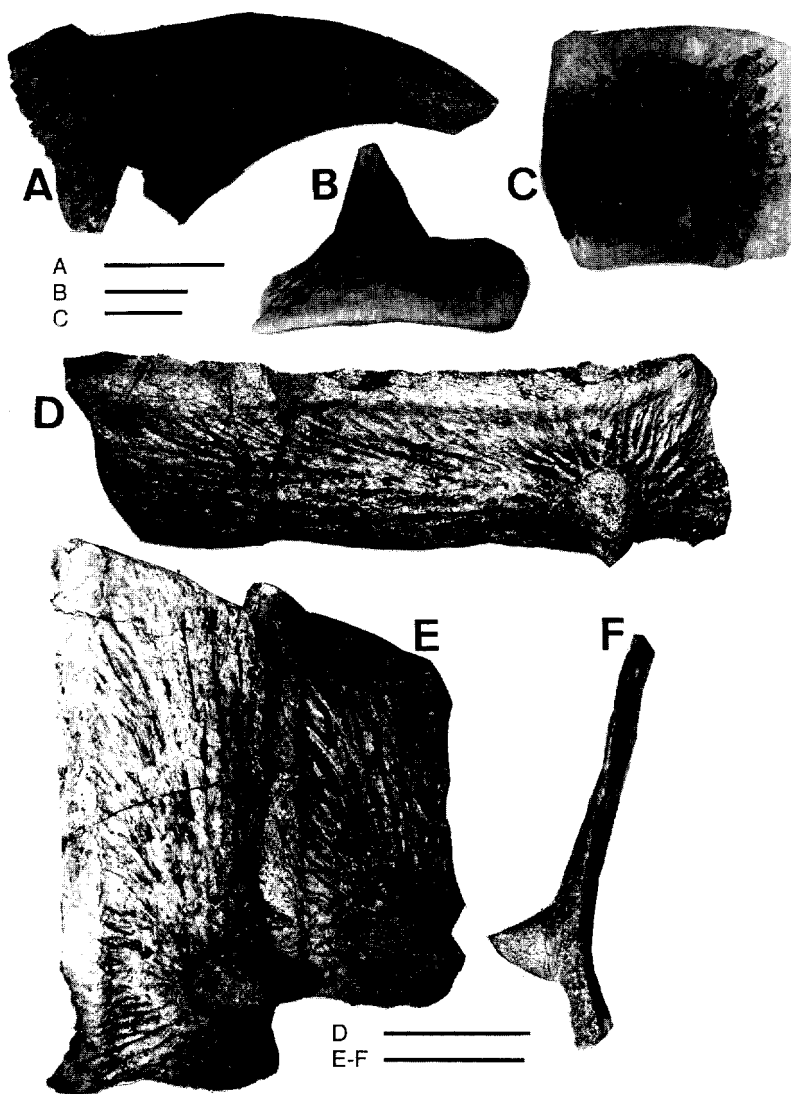


Fig. 6. Selected scutes of *Desmatosuchus haplocerus* (A-C) and *Paratypothorax andressorum* (D-F). A, UCMP 33208, right lateral cervical spike from the Bluewater Creek Formation, Arizona, in dorsal view; B-C, anterior (B) and dorsal (C) views. D-F, dorsal paramedian scutes of unnumbered SMNS syntype specimens of *Paratypothorax andressorum* from the Middle Stubensandstein, Pfaffenhoffen, Germany in dorsal (D-E) and posterior (F) views.

Discussion: Gregory (1953b) demonstrated that the holotype of *D. spurensis* Case (1920) is congeneric with the unillustrated type material of *Episcoposaurus haplocerus* Cope 1892 and that the type species of *Episcoposaurus*, *E. horridus* Cope 1875, is almost certainly a synonym of *Typothorax coccinarum* Cope 1875, as noted previously. Thus, the type and only species of *Desmatosuchus* is *D. haplocerus*. *Desmatosuchus* is one of the best known Chinle aetosaurs, and is easily recognized by the giant recurved lateral spikes developed on anterior lateral scutes and the lack of anterior bars on the paramedian and lateral scutes. This latter feature, as well as the random pitting on dorsal paramedian scutes, also occurs in the small aetosaur *Acaenasuchus*, which is one of the reasons we consider *Acaenasuchus* to represent juveniles of *Desmatosuchus* as Long and Ballew (1985) and Murry and Long (1989) originally suggested and has been argued elsewhere (Estep et al. 1998). Recent descriptions of *Desmatosuchus* include Small (1985, 1989), and Long and Murry (1995). *Desmatosuchus* occurs in strata of late Carnian to early-mid Norian age (Lucas and Heckert 1996), including a possible record in the Zarzaitine Series in Algeria (Jalil et al. 1995, fig. 1e-f).

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

*Longosuchus* and *Paratypothorax* are united by the following synapomorphy: 35, Bosses on dorsal paramedian scutes touching to overlapping posterior margin of scute (shared with *Stagonolepis*).

#### *Longosuchus meadei* (Sawin 1947)

- 1947 *Typothorax meadei* Sawin, p. 201, figs. 1–13, pl. 34.
- 1961 *Typothorax*: Walker, p. 177, fig. 24c.
- 1976 *Typothorax meadei*: Krebs, p. 78, fig. 20.
- 1976 *Typothorax*: Krebs, p. 78, fig. 26c.
- 1978 *Typothorax*: Bonaparte, p. 300, fig. 136d.
- 1986 *Typothorax meadei*: Murry, p. 123, fig. 9.12b.
- 1986 *Typothorax meadei*: Parrish, p. 11, fig. 12G, 13D, 33h.
- 1989 *Typothorax meadei*: Small, p. 301, fig. 1a.
- 1990 *Longosuchus meadei* Hunt and Lucas, p. 317, figs. 2–3.
- 1992 *Longosuchus*: Lucas and Hunt, p. 151, fig. 13c.
- 1994 *Longosuchus meadei*: Parrish, p. 196, figs. 1–6.
- 1995 *Longosuchus meadei*: Long and Murry, p. 1, fig. 58–63.
- 1995 *Lucasuchus hunti*: Long and Murry, p. 1, figs. 64–65.
- 1995 *?Lucasuchus hunti*: Long and Murry, p. 1, figs. 66–67.
- 1998a *Longosuchus meadei*: Lucas, p. 589, fig. 2.

Lectotype: TMM 31185-84a, "skull with lower jaws, cervical and dorsal scutes, partial vertebral column, limbs and fragmentary girdles" (Hunt and Lucas 1990:320).

Type locality: Colorado City Member, Dockum Formation, Chinle Group, TMM quarry 3a near Otis Chalk, Texas.

Revised diagnosis: *Longosuchus* is distinguished from all other aetosaurs by the presence of faceted spikes on the lateral scutes and prominent dorsal bosses projecting vertically from the paramedian scutes.

Distribution: *Longosuchus* is known from the Colorado City Member of the Dockum Formation, Texas, the Salitral Formation in north-central New Mexico, the Pekin Formation in North Carolina, all in the U.S.A., and the Timesgadiouine Formation, Argana Group, in Morocco (Lucas 1998a). All occurrences of *Longosuchus* (= *Lucasuchus*) are from strata of early late Carnian age (Lucas and Heckert 1996).

Discussion: Hunt and Lucas (1990) separated the holotype of *Typosuchus meadei* from *Typosuchus* as a new genus, *Longosuchus*, based on numerous characteristics, including the extremely distinctive armor. Parrish (1994) recently re-described the skull of *Longosuchus*. Long and Murry (1995) split *Longosuchus* into two genera: *Longosuchus* from Texas and their new genus *Lucasuchus*. Their diagnosis of *Lucasuchus* is based on minor differences in scute morphology, some so subjective that they cannot be replicated. Although some of the material they subsequently referred to *Lucasuchus* probably represents a different species, little if any of this material is associated with the holotype of *Lucasuchus*. Therefore, we regard *Lucasuchus* (type species *Lucasuchus hunti*) as a junior subjective synonym of *Longosuchus meadei*.

### ***Paratyposuchus andressorum* Long and Ballew 1985**

(Fig. 6D-F)

- 1861 *Belodon*: Meyer, p. 337, pl. 43 (figs 1,2,4,5).
- 1865 *Belodon*: Meyer, p. 118, pl. 28 (figs 1-9).
- 1911 *Phytosaurus kapffii*: Huene, p. 103, fig. 25.
- 1913 *Phytosaurus kapffii*: Huene, p. 282, fig. 13.
- 1932 *Phytosaurus?*: Case, p. 72, pl. 4 (figs. 4-6).
- 1953a Pseudosuchian allied to *Typosuchus*: Gregory, p. 1, fig. 1.
- 1953b cf. *Typosuchus* sp.: Gregory, p. 1, fig. 16.
- 1974 *Nicrosaurus*: Wild, p. 22, fig. 9.
- 1985 *Paratyposuchus andressi* Long and Ballew, p. 45, fig. 17, pl. 6-7.
- 1989 *Paratyposuchus*: Small, p. 301, pl. 5g-h.
- 1992 *Paratyposuchus andressi*: Hunt and Lucas, p. 147, figs. 2-4.
- 1992 *Paratyposuchus*: Lucas and Hunt, p. 164, fig. 13b.
- 1994 "large paramedian scute...of *P. andressi*": Jenkins et al, p. 13, fig. 10.
- 1995 *Paratyposuchus andressi*: Long and Murry, p. 1, figs. 113-115.
- 1995 *Paratyposuchus* sp.: Jalil et al., p. 173, fig. 1a,c.
- 1995 *Paratyposuchus andressi*: Jalil et al., p. 173, fig. 1b,d.
- 1997 *Paratyposuchus* sp.: Heckert, p. 29, fig. 3f.

Holotype: SMNS unnumbered left anterior caudal paramedian scute.



Type locality: Lower Stubensandstein of Stuttgart-Heslach, Baden-Württemberg, Germany.

Revised diagnosis: *Paratypothorax* is diagnosed from all aetosaurs but *Tytophorax* by its wide (W:L > 4:1), strap-like paramedian scutes, and from *Tytophorax* by the presence of a deeply incised pattern of radial pits and grooves and a prominent dorsal boss that contacts, and may overlap, the posterior margin of the paramedian scute (Fig. 6D-F).

Distribution: *Paratypothorax*, while not common in any one fauna, was widespread, and is known from several localities in the Chinle Group in the southwestern U.S.A., the Ørsted Dal Member of the Fleming Fjord Formation in Greenland, the type locality at Stuttgart-Heslach, and the in the Middle Stubensandstein of Baden-Württemberg, Germany.

Discussion: Long and Ballew (1985) named this aetosaur for very distinctive specimens collected from the Lower Stubensandstein in Germany and noted its presence in the Chinle Group in the southwestern U.S.A. Unfortunately, little of the skeleton is known other than the armor, although Long and Murry (1995) illustrate much associated material that may pertain to *Paratypothorax*. Jenkins et al. (1994) reported *Paratypothorax* from the Fleming Fjord Formation in Greenland. An aetosaur scute of unknown provenance in Germany was described by Gregory (1953a), and other material illustrated by him (Gregory 1953a: fig. 1; 1953b: fig. 16.) also pertains to *Paratypothorax*, not *Tytophorax*. Because the specific epithet was designated to honor the Andress family, the proper Linnaean form of the name is *Paratypothorax andressorum*.

### **Stagonolepididae incertae sedis**

#### ***Redondasuchus reseri* Hunt and Lucas 1991**

(Fig. 5D-E)

1985 *Tytophorax* sp.: Lucas et al., p. 199, figs. 3f-g.

1991 *Redondasuchus reseri* Hunt and Lucas, p. 728, figs. 2-3.

1996 *Redondasuchus reseri*: Heckert et al., p. 619, figs. 3-6.

Holotype: UCMP 65415, a nearly complete left dorsal paramedian scute.

Type locality: Redonda Formation, Chinle Group, Apache Canyon, Quay County, New Mexico, U.S.A.

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 (Fig. 5D-E), possess a discontinuous ventral keel, lack raised bosses on the dorsal surface, and ornamentation consisting solely of densely packed pits that lack a radial pattern.

Distribution: Currently, *Redondasuchus* is known only from several isolated scutes and an associated rib from two localities in the Redonda Formation of eastern New Mexico.

**Discussion:** Although Long and Murry (1995) and Small (1998) consider *Redondasuchus* a junior subjective synonym of *Typothorax*, comparison of the isolated material of *Redondasuchus* with a complete skeleton of *Typothorax* at NMMNH (see Hunt et al. 1993) indicates that the scutes associated with *Redondasuchus* fall outside the range of variation seen in *Typothorax* (Heckert et al. 1996). Although *Redondasuchus* is too incomplete to consider in this phylogenetic analysis, Heckert et al. (1996) demonstrated that it is a sister taxon to *Typothorax*, and analyses run with the data matrix presented here consistently support that hypothesis. Therefore, we consider *Redondasuchus* to represent a highly derived sister taxon of *Typothorax* and thus a probable Desmatosuchine.

### Other records

Chatterjee and Roy-Chowdhury (1974) mentioned an aetosaur from the Maleri Formation in India and indicated that it had affinities to *Typothorax*. At that time, the only well-known aetosaur referred to *Typothorax* was "*Typothorax*" *meadei* Sawin 1947. Although various authors suggested that "*Typothorax*" *meadei* was distinct from the type species *Typothorax coccinarum* Cope (1875), it was not until 1990 that Hunt and Lucas renamed the holotype *Longosuchus*. This, and the description given by Chatterjee and Roy-Chowdhury (1974:107), strongly suggests that these scutes pertain to *Longosuchus*, although Small (1998, pers. comm.) has seen the scutes and maintains that they are distinct from *Longosuchus*.

A wide (W:L = 3.4:1), strap-like paramedian scute and associated horn-like lateral scute reported by Lucas et al. (1995: figs. 2–3) probably belong to a species of *Paratypothorax*. They may even represent cervical scutes of *P. andressorum*, which normally exhibits a relatively strong dorsal boss. Most aetosaurs with known articulated carapaces exhibit an increase in dorsal boss size posteriorly (e.g., Case 1922:pl. 9B; 1932:pl. I). Therefore, the absence of a dorsal boss on this otherwise *Paratypothorax*-like scute may reflect its position in the carapace, not a taxonomic difference.

Murry and Long (1996) published a very preliminary description of a new, carnivorous aetosaur from the Colorado City Member of the Dockum Formation in Texas. This aetosaur can be diagnosed from all previously described taxa by the presence of flat, triangular lateral scutes, among other features (Murry and Long, 1996), so it does not represent a more complete specimen of the less well-known taxa. The presence of recurved teeth suggests affinities with *Aetosaurus*, as we mentioned in the diagnosis of the Aetosaurinae previously, but until this taxon is fully described we withhold judgment on its phylogenetic position.

### 3. Biostratigraphy

Tetrapod fossils provide one of the principal bases for the correlation of non-marine Triassic strata across Pangea (Ochev and Shishkin 1989, Lucas 1990, 1997, 1998b). During the Late Triassic, two archosauromorph groups – phytosaurs (Par-

asuchidae) and aetosaurs – were broadly distributed across Pangea and are abundant in Upper Triassic nonmarine strata.

Phytosaurs have long been used for correlation of these strata (Camp 1930, Gregory 1957, Westphal 1976, Ballew 1989), but are not ideal index fossils because: (1) nearly an entire phytosaur skull is needed to make a genus – or species – level identification, whereas the vast majority of phytosaur fossils are isolated bones and skull fragments; and (2) phytosaur taxonomy is not well agreed on and generally oversplit, with as many as four different taxonomic schemes (Westphal 1976, Ballew 1989, Long and Murry 1995, Hunt 1994a, b) in use.

In contrast, aetosaurs make ideal index fossils for the correlation of nonmarine Upper Triassic strata. An ideal index fossil should be widely distributed geographically, abundant, have a short temporal range, and easily identifiable. Aetosaurs meet all four criteria:

(1) Aetosaur fossils are found throughout most of Late Triassic Pangea (Fig. 1). Indeed, they have a broader distribution than phytosaurs, most notably being known from Argentina, Brazil, and Greenland, where phytosaurs do not occur.

(2) Aetosaurs are the most abundant tetrapod fossils in the Chinle Group (western U.S.A.) (Long and Ballew 1985, Lucas 1993, 1997) and are also relatively abundant in the Ischigualasto Formation of Argentina (Rogers et al. 1993). They are common in many other Upper Triassic deposits.

(3) Stratigraphically, most aetosaurs have relatively limited ranges. Temporal ranges of aetosaur genera are also usually short – much less than a stage/age (see below). Of the 10 genera recognized here, only *Paratypothorax* and *Desmatosuchus* have ranges that cross the Carnian-Norian boundary. All other aetosaur genera are known from stratigraphic intervals shorter than any given stage-age.

(4) Aetosaurs are easy to identify because their body armor is highly distinctive at the genus level, as we have demonstrated throughout this paper (see Figs. 3–6). A single piece or fragment of aetosaur armor, sometimes even as small as a postage stamp, can be very precisely identified.

As a consequence of these features, we are able to present a correlation of numerous Upper Triassic depositional units based on the occurrence of various aetosaur taxa (Fig. 7). These correlations are particularly powerful when integrated with the extensive biochronology based on aetosaurs and other taxa we present in the following section.

#### 4. Biochronology

We exploit the excellent record of aetosaurs to propose a Late Triassic aetosaur biochronology (Fig. 8). Based primarily on the stratigraphic succession of aetosaurs in the upper Carnian-Rhaetian Chinle Group of the western USA, we can recognize seven aetosaur biochrons. Although this biochronology can be tied to the global chronostratigraphic time scale, we instead use the nonmarine Triassic time scale based on land-vertebrate faunachrons (LVF) erected by Lucas (1998b). The advantage of this scheme is that, while it can be tied to the marine time scale,



Stage	Land-vertebrate faunachron (LVF) of Lucas (1998b)	Genus	Location(s) and lithostratigraphic unit(s)							
			Chinle Group (USA)	Newark Supergroup (USA)	South America	Greenland	Europe	Africa	India	
202 Ma Rhaetian 208 Ma	Apachean									
Norian	Revuelitian	<div>Paratypothorax</div> <div>Desmatosuchus</div>	Both taxa present in numerous formations			Fleming Fjord Formation (Paratypo- thorax)	Lower Stubensand- stein, German Keuper (Paratypo- thorax)			
218 Ma	Adamanian		Both taxa present in numerous formations						Zarzaitine Series, Morocco (Paratypo- thorax and aff. Desmato- suchus)	
228 Ma			Numerous Formations (Desmato- suchus)	Pekin Fm., North Carolina (Desmato- suchus)						
Carnian	Otischalkian									

Fig. 7. Correlation chart of Upper Triassic strata based on aetosaurs. Upper chart shows correlations based on the aetosaurs *Longosuchus*, *Stagonolepis*, *Typothorax*, and *Aetosaurus*, and indicates the age of *Redondasuchus* and *Neoaetosaurioides*. Lower chart shows correlations based on the aetosaurs *Desmatosuchus* and *Aetosaurus*. Faunachrons follow Lucas and Hunt (1993) and Lucas (1998b).

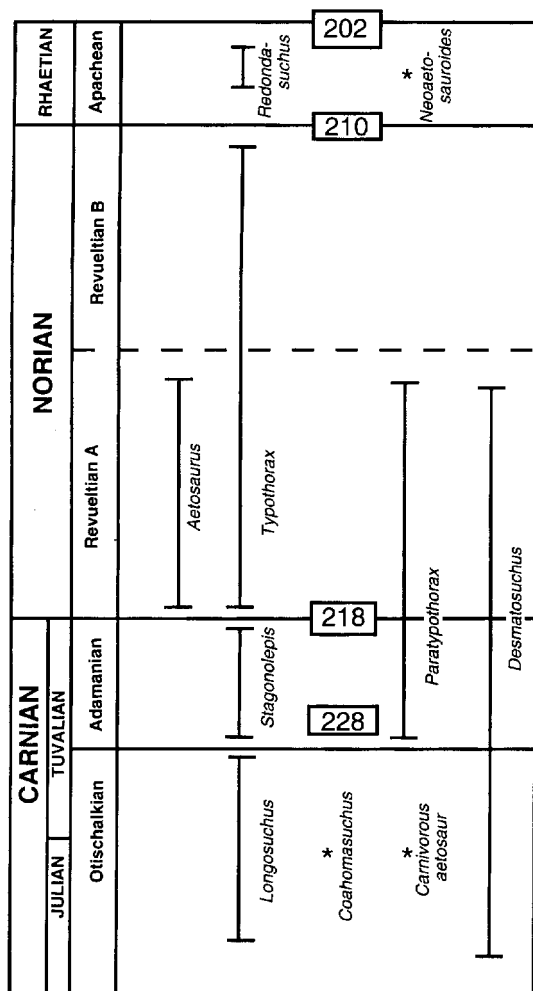


Fig. 8. Biochronology of the aetosaur genera discussed here. Faunachrons follow Lucas and Hunt (1993) and Lucas (1998b). Singleton occurrences marked by asterisks (\*).

it also stands alone, and is particularly useful when attempting to correlate to inland basins such as the Ischigualasto and Santa Maria Formations. The four land-vertebrate faunachrons of Lucas (1998b) that are pertinent to this discussion, and their correlation to the global chronostratigraphic time scale are: Otischalkian (early and late Carnian: Julian-Tuvalian), Adamanian (latest Carnian: late Tuvalian), Revueltian (early-mid Norian: Lacin-Alaunian); and Apachean (latest Norian-Rhaetian).

The seven aetosaur biochrons we recognize are: (1) *Longosuchus* biochron of Otischalkian age; (2) *Desmatosuchus* biochron of Otischalkian-Revueltian age; (3) *Stagonolepis* biochron of Adamanian age; (4) *Paratypothorax* biochron of Adamanian-Revueltian age; (5) *Typothorax* biochron of Revueltian age; (6) *Aeto-*

*saurus* biochron of Revueltian age; and (7) *Redondasuchus* biochron of Apachean age. Many of these biochrons correlate strata across much of Pangea. Additionally, a marine occurrence of *Aetosaurus* from the Calcare di Zorzino in Italy (middle-late Norian = younger portion of the *Himavatites columbianus* Ammonite Zone) directly correlates the *Aetosaurus* biochron, including strata in the U.S.A., Greenland, and Germany, to the global marine timescale. An eighth biochron, the *Neoaetosauroides* biochron of late Norian-Rhaetian age, is based on specimens restricted to the Los Colorados Formation in Argentina.

The Chinle Group in the western United States is critical to establishing an aetosaur biochronology of the Late Triassic. This is because the Chinle has a prolific aetosaur record that includes all of the known aetosaur genera except *Neoaetosauroides*, and the fossils can be arranged in an unambiguous stratigraphic succession that spans the late Carnian, Norian, and Rhaetian. Eight named aetosaur genera are found in the Chinle, and six of these establish biochrons that can be used to correlate Upper Triassic strata between multiple Pangean basins.

#### 4.1 *Longosuchus* biochron

*Longosuchus meadei* (Sawin) is one of the oldest Chinle aetosaurs, found in strata of Otischalkian age (Hunt and Lucas 1990, Lucas and Hunt 1993, Lucas and Heckert 1996). Its occurrence in the Pekin Formation of the Newark Supergroup in North Carolina provides a direct Chinle-Newark aetosaur-based correlation (Huber et al. 1993b).

Long and Murry (1995, p. 203) claimed that their taxonomy, which restricted *Longosuchus* to West Texas and identified *Lucasuchus* from West Texas, New Mexico and North Carolina, "negates the utility of *L[ongosuchus] meadei* as a biochron fossil." Ironically, all Long and Murry (1995) did was redefine the *Longosuchus* biochron of Hunt and Lucas (1990) as a *Lucasuchus* biochron. *Longosuchus* (= *Lucasuchus*) thus remains a robust biochronologic indicator of the early late Carnian.

If the record of "*Typothorax*" *meadei* from the Maleri Formation reported by Chatterjee and Roy-Chowdhury (1974) is of *Longosuchus*, then the *Longosuchus* biochron can be extended to India. The Maleri fauna also includes phytosaurs, metoposaurs, and rhynchosaurs of late Carnian age, including *Paleorhinus* (= *Parasuchus*) (Long and Murry 1995) and *Metoposaurus* (Hunt 1993). Thus, we suggest that the *Longosuchus* biochron can be tentatively extended to India, pending description of the Maleri aetosaurs.

#### 4.2 *Desmatosuchus* biochron

*Desmatosuchus* co-occurs with *Longosuchus* in the early late Carnian (Otischalkian) (Case 1922, Hunt and Lucas 1990, Lucas and Hunt 1993, Lucas and Heckert 1996) and has a temporal range extending through the Adamanian into

the early Revueltian, but not through the end of Revueltian time (Fig. 8). *Desmatosuchus* is abundant in the Adamanian of the Chinle Group, so this can be termed its abundance biochron ("acme zone"). *Desmatosuchus* is also known from the Pekin Formation of the Newark Supergroup, providing another Chinle-Newark, aetosaur-based correlation. A *Desmatosuchus*-like scute from the Zarzaitine Series of Algeria is the only other possible record (Jalil et al. 1995).

### 4.3 *Stagonolepis* biochron

*Stagonolepis* occurrences in North America are restricted to Adamanian strata of the Chinle Group (Figs. 7, 8), where it has been referred to as both *S. robertsoni* and *S. wellesi* (Long and Murry 1995). *Stagonolepis robertsoni* is well known from its type locality, the Lossiemouth Sandstone near Elgin, Scotland (Walker 1961), which supports an Adamanian age for the Elgin tetrapod fauna.

The synonymy of *Ebrachosaurus singularis* and *Stagonolepis robertsoni* indicates that the Blasensandstein at Ebrach is of earliest Adamanian age. Notably, the phytosaur *Paleorhinus* is also known from Ebrach. Although *Paleorhinus* is usually taken to indicate an Otischalkian age (Lucas and Hunt 1993, Lucas 1997, 1998), it co-occurs with *Stagonolepis* low in the Chinle Group at the onset of Adamanian time (Lucas et al. 1997). Therefore, it is possible that the Ebrach fauna is the youngest Carnian fauna from Germany, and marks the only Adamanian fauna from Germany (also see Lucas, this volume).

Further, *Aetosauroides* and *Argentinosuchus* from the Ischigualasto Formation of Argentina are junior subjective synonyms of *Stagonolepis*, indicating that *Stagonolepis* (= *Aetosauroides*) is also known from the Santa Maria Formation in Brazil (Zacarias 1982). Thus, correlation of the *Stagonolepis* biochron indicates a latest Carnian age of the Ischigualasto and Santa Maria faunas, an age assignment supported by other evidence presented by Hunt and Lucas (1991a, b), Lucas et al. (1992), Lucas and Hunt (1993), Heckert and Lucas (1996), and Lucas and Heckert (1996), not the older "middle Carnian" or Ladinian age advocated by some other workers (e.g., Cox 1991, Rogers et al. 1993, Battail 1993).

Perhaps the most important consequence of recognizing the *Stagonolepis* biochron is the fact that this constrains the first appearance of identifiable dinosaur fossils to the latest Carnian across Pangea (Heckert and Lucas 1996). Dinosaurs and probable dinosaurs that co-occur with *Stagonolepis* include *Staurikosaurus* from the Santa Maria Formation in Brazil, *Eoraptor*, *Herrerasaurus*, and *Pisanosaurus* from the Ischigualasto Formation in Argentina, numerous dinosaurs from the Chinle Group (Hunt et al. 1998), and *Saltopus* from the Lossiemouth Sandstone in Elgin, Scotland.



#### 4.4 *Paratypothorax* biochron

Recent collecting by Heckert (1997) has extended the stratigraphic range of *Paratypothorax* in the Chinle Group to the early Adamanian (Bluewater Creek Formation in west-central New Mexico). Small and Sedlmayr (1995) reported scutes we assign to *Paratypothorax* from the Chinle Group of northwestern Colorado. The co-occurrence of *Aetosaurus* at this locality (Small 1998) suggests a Revueltian age (see below). Thus, we now report an Adamanian-Revueltian age range for the *Paratypothorax* biochron (Fig. 8).

In the German Keuper, *Paratypothorax* has a temporal range of early-mid Norian (Hunt and Lucas 1992, Lucas and Heckert 1996). The genus has also been reported from the early-mid Norian Fleming Fjord Formation of Greenland (Jenkins et al. 1994) and is also present in the Zarzaitine Series of Algeria (Jalil et al. 1995). Unfortunately, the long temporal range of this relatively rare, and still poorly known, aetosaur precludes precise correlation using the *Paratypothorax* biochron.

#### 4.5 *Aetosaurus* biochron

Although *Aetosaurus* is now known from the Chinle Group (Heckert and Lucas 1998, Small 1998), it is important to understand the biochronological significance of the European records of *Aetosaurus*. *Aetosaurus* was first reported from the type species, *A. ferratus*, from the Lower Stubensandstein in Germany (O. Fraas 1877), with subsequent discovery of the larger species *A. crassicauda*, from the Middle Stubensandstein (E. Fraas 1907). Numerous workers have studied the biostratigraphy and biochronology of the Stubensandstein, and most recent workers consider the Lower Stubensandstein to be early Norian and the Middle Stubensandstein to be middle Norian (Aigner and Bachmann 1992, Benton 1993, Lucas and Huber 1998).

Wild (1989) reported the most biochronologically important specimen of *A. ferratus* from the marine Calcare di Zorzino Formation (Zorzino Limestone) of the Lombardian Alps in Italy. The fossiliferous level overlies and is in part laterally equivalent to the Dolomia Principale. Palynostratigraphy and conodont biostratigraphy both indicate that the *Aetosaurus*-bearing strata are very close to the Alaunian (middle Norian)-Sevatian (late Norian) boundary (Jadoul et al. 1994, Roghi et al. 1995, Tintori and Lombardo 1996), and thus correlative to the younger portion of the *Himavatites columbianus* zone of the global Triassic ammonite biochronology (Tozer 1994). This occurrence thus provides a direct link between *Aetosaurus* records and the global marine timescale.

More recently, Jenkins et al. (1994) reported *A. ferratus* from the Ørsted Dal Member of the Fleming Fjord Formation in eastern Greenland. As reported by Jenkins et al. (1994) and Lucas et al. (1999), the *Aetosaurus*-bearing fauna most closely resembles the fauna of the Lower Stubensandstein and thus is of early-mid Norian age. With the recognition that *Stegomus* is a junior subjective synonym of *Aetosaurus*, Lucas et al. (1999) demonstrated that correlations based on *Aetosau-*

*rus* can be extended into the Newark Supergroup, where *Stegomus* is known from several localities that span the lower to middle Norian.

Recent collecting efforts have greatly expanded the distribution of *Aetosaurus*. Both Heckert and Lucas (1998) and Small (1998) have reported *Aetosaurus* from the Chinle Group. These records are important for several reasons. The discovery of *Aetosaurus* in the Chinle Group is important because Lucas and Hunt (1993) named the Revueltian LVF for the time equivalent to the assemblage of tetrapods found in the Bull Canyon Formation near Revuelto Creek, 10 km from and stratigraphically equivalent to the *Aetosaurus* locality. The Revueltian LVF has been considered early-mid Norian in age based on cross-correlation with palynostratigraphy, megafossil plant biochronology, and magnetostratigraphy (Lucas 1997). However, the presence of *Aetosaurus* in the Bull Canyon Formation provides a more direct correlation to the marine timescale, where *Aetosaurus* is known from strata of middle Norian age (Figs. 7, 8). Thus, the Chinle record of *Aetosaurus* confirms earlier correlations that indicate that the Bull Canyon Formation and its lateral equivalents, which include the Painted Desert Member of the Petrified Forest Member, are of Norian age. This provides a reliable correlation for many of the most fossiliferous units in the upper Chinle Group.

#### 4.6 *Typothorax* biochron

*Typothorax* is known only from the Chinle Group and is one of the most common tetrapod fossils in strata of Revueltian age (Hunt et al. 1993, Hunt 1994, Long and Murry 1995). It thus provides a robust basis for correlating Chinle Group strata with each other, but thus far cannot be used to correlate to other basins. *Typothorax* occurs throughout the Revueltian, and its stratigraphic range appears to extend into younger strata than either *Desmatosuchus* or *Paratypothorax* (Figs. 7, 8), so there is some utility in recognizing two biochrons associated with *Typothorax*—one in which *Typothorax* co-occurs with *Desmatosuchus* and/or *Paratypothorax* and a mid-late Norian biochron in which *Typothorax* is the only large-bodied aetosaur.

#### 4.7 *Redondasuchus* biochron

*Redondasuchus* Hunt and Lucas 1991c, is known only from Apachean strata of the Chinle Group (Figs. 7, 8). Its restriction to the Redonda Formation of eastern New Mexico limits its biochronologic utility.

#### 4.8 Other aetosaur records

*Coahomasuchus* is known only from the type locality and specimen, and thus has no biochronological significance at this time. Similarly, the carnivorous aetosaur is known from a single specimen from the same horizon as *Coahomasu-*

*chus*. Both of these taxa co-occur with *Desmosuchus* and *Longosuchus*, and thus are of Otischalkian age (Fig. 8). *Neoaetosaurioides* is known from the holotype and two associated specimens collected in the upper part of the Los Colorados Formation in La Rioja Province, Argentina (Bonaparte 1967, 1971a, b). Therefore, it is of limited biochronological utility (Figs 7, 8). Likewise, isolated aetosaur scutes of as-yet undescribed taxa (e.g., Lucas et al. 1995) are not known well enough to incorporate into the biochronological framework described here. However, given the taxonomic utility of isolated aetosaur scutes, we urge other workers to collect and describe them whenever possible as a means of testing the biochronologic hypotheses advanced here.

## 5. Paleobiogeography

The extensive biostratigraphy and biochronology of the Aetosauria we present here indicates increasing provincialization of aetosaurs during the Late Triassic. The most cosmopolitan genera are primarily late Carnian (*Stagonolepis*, *Longosuchus*, *Desmosuchus*) or make a first appearance in the late Carnian (*Paratypothorax*), whereas characteristically Norian genera are more provincial (*Typothorax*) or have evolved into several species (*Aetosaurus*), which may have their own paleobiogeographic significance. Highly provincial are the Rhaetian genera (*Redondasuchus*, *Neoaetosaurioides*). Increasing provincialization of the aetosaurs during the Late Triassic parallels the initial breakup of Pangea.

During the Otischalkian, *Longosuchus* and *Desmosuchus* both make a simultaneous first appearance in the Chinle Group and in the Pekin Formation of North Carolina. Additionally, *Longosuchus* is known from Morocco, and *Desmosuchus* may occur in Algeria. The smaller taxon *Coahomasuchus* and the carnivorous aetosaur, which is of similar size, are known only from the Chinle, but this may in part be a result of a collecting bias toward larger animals.

By the onset of the Adamanian, *Longosuchus* had become extinct but *Stagonolepis* makes a near-simultaneous appearance in Scotland, Germany (= *Ebrachosaurus*), the U.S.A., and South America, where it is known from both the Ischigualasto Formation in Argentina (= *Aetosaurioides*; = *Argentinosuchus*) and the Santa Maria Formation in Brazil (= *Aetosaurioides*). *Paratypothorax* makes its first appearance in the western U.S.A. and in Algeria at this time. Thus, by the end of the Carnian, all of the geographically widespread aetosaurs have made a first appearance, with the exception of *Aetosaurus*.

During the Revueltian *Paratypothorax* is more widespread, and is known from the western U.S.A., Greenland, and Germany. The various species of *Aetosaurus* are known from Germany (*A. ferratus* and *A. crassicauda*), Italy (*A. ferratus*), Greenland (*A. ferratus*), the Newark Supergroup (*A. arcuatus*), and the Chinle Group (*A. arcuatus* and *A. ferratus*). The fissure-fill record of *A. ferratus* is of probable late Revueltian (late Norian) age (Fraser 1988). *Typothorax* makes its first appearance early in the Revueltian and appears to remain restricted to the Chinle Group.

The only Apachean aetosaurs are *Redondasuchus* and *Neoaetosauroides*. Both are endemic. *Redondasuchus* is known from two closely spaced localities in the Chinle, and all specimens of *Neoaetosauroides* are from a single locality in the Los Colorados Formation in Argentina.

Thus, the overall trend of aetosaur paleobiogeography is well-established. With the exception of *Aetosaurus*, all genera which are geographically widespread make their first appearance in the Carnian. Notably, *Aetosaurus* comprises three species, so it appears likely that its original diversification also occurred during the Carnian. Later aetosaurs were more restricted in their distribution, perhaps reflecting vicariance events associated with the breakup of Pangea.

## 6. Evolution of the Aetosaurs

We note here that this analysis produces results broadly similar to those of studies by Walker (1961), Parrish (1994) and Heckert et al. (1996). The phylogenetic analysis described here supports the hypotheses that (1) the aetosaurs are monophyletic, and (2) *Aetosaurus* is the most primitive aetosaur. It is evident from this analysis that aetosaurs diversified rapidly before the late Carnian, splitting into at least three distinct lineages: (1) a primitive lineage that gave rise to *Aetosaurus* in the Norian; (2) a more derived lineage that includes the late Carnian *Coahomasuchus* and the latest Carnian *Stagonolepis*; and (3) a derived lineage that quickly diversified to give rise to *Longosuchus*, *Desmatosuchus*, and *Paratypothorax*, all of which make their first appearance in the late Carnian. These lineages correspond with the subfamily names Aetosaurinae, Stagonolepininae, and Desmatosuchinae used here.

When these phylogenetic hypotheses are integrated into the biostratigraphy and biochronology detailed previously, three phases of aetosaur evolution are evident (Fig. 9). First, prior to Otischalkian time, aetosaurs diverged from the other pseudosuchians. In the ensuing interval they underwent considerable diversification, as our analysis shows that even the most primitive aetosaurs share 18 synapomorphies relative to rauisuchians. By Otischalkian time all three aetosaur lineages must have been present. Body sizes of Otischalkian genera range from 1 m (*Coahomasuchus*) to 5–6 m (*Desmatosuchus*). *Longosuchus* appears to have had a Pangean distribution, and *Desmatosuchus* may be known from the Zarzaitine Series of Algeria (Jalil et al. 1995), but *Coahomasuchus* is restricted to the Chinle. *Coahomasuchus* and *Longosuchus* apparently become extinct at the end of Otischalkian time.

During Adamanian time, wide-bodied aetosaurs made their first appearance in the form of *Paratypothorax*, and the relatively primitive *Stagonolepis* reaches the largest size (3–4 m) of any non-spiked aetosaur. No small-bodied aetosaurs are known from this time, as *Acaenasuchus* is clearly a juvenile of *Desmatosuchus*. *Stagonolepis* and *Desmatosuchus* were both particularly successful during this time – the Adamanian is the abundance biochron of *Desmatosuchus*, and *Stago-*

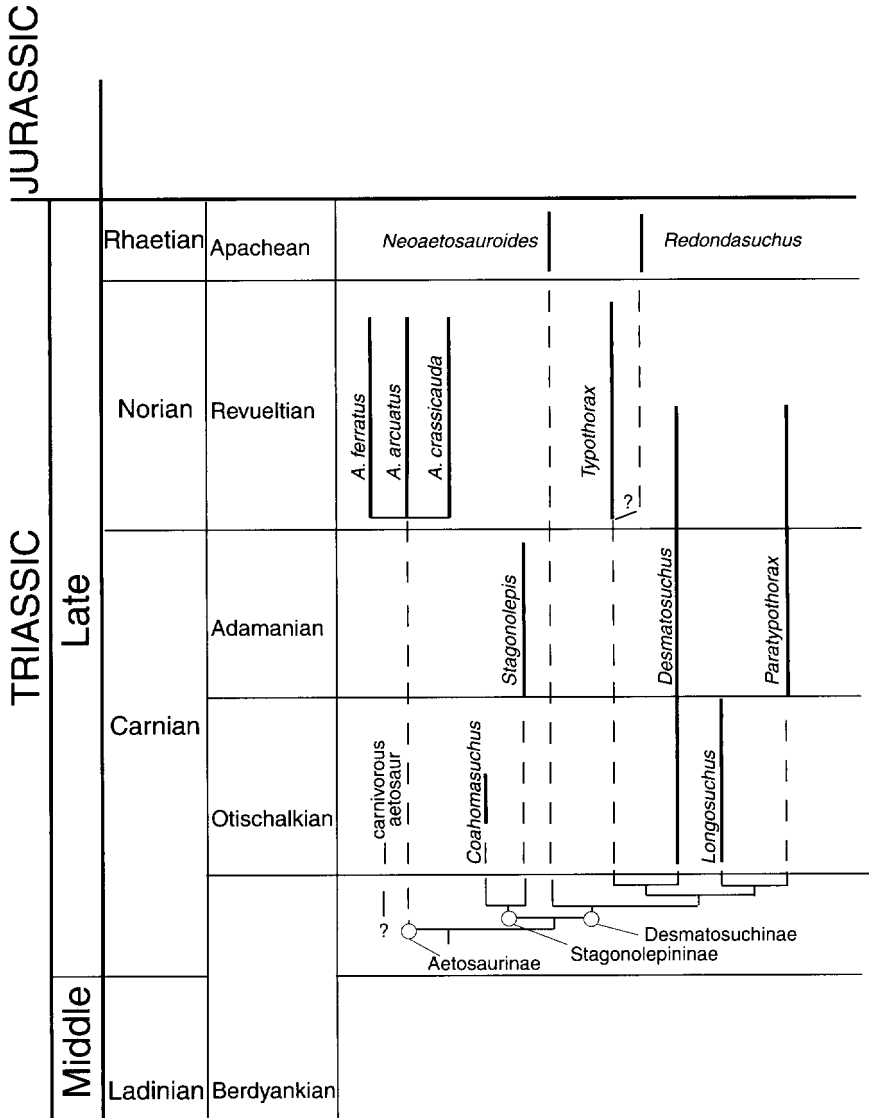


Fig. 9. Evolutionary history of the Stagonolepididae. Solid lines indicate known ranges from Figure 8, dashed lines indicate inferred ranges based on the cladogram in Figure 2.

*nolepis* extended its range across much of Pangea before becoming extinct shortly before the Carnian-Norian boundary.

During the early Revuelitian, wide-bodied aetosaurs become more common as *Paratypothorax* appears in the Lower Stubensandstein in Germany and *Typot-*

*horax* makes its first appearance and rapidly becomes the dominant herbivore and one of the most common Revueltian fossils in the Chinle. The Norian also marks the first appearance of *Aetosaurus*, which is both diverse (3 species) and widespread, with a Laurasian distribution. It is not until the mid-late Norian that *Desmatosuchus* and *Paratypothorax* apparently become extinct. *Typothorax* and *Aetosaurus* appear to have become extinct by the end of the Norian, but this is less well constrained.

By the late Norian-Rhaetian aetosaur diversity and distribution are greatly limited. The only genera are *Redondasaurus*, which is endemic to the Redonda Formation of the Chinle Group, and *Neoaetosauroides*, endemic to the Los Colados Formation in Argentina. There are no Jurassic records of aetosaurs.

From this record several facts are clear. First, the record of aetosaur divergence must be sought in pre-Carnian rocks, as is the case with many other groups that also originate in the Carnian. Second, a Carnian-Norian extinction "event" is not supported by the fossil record of the aetosaurs. Third, after a relatively high period of diversity in the Norian, aetosaurs decline in the latest Norian-Rhaetian and become extinct at or near the Triassic-Jurassic boundary. Fourth, the desmatosuchine aetosaurs appear to have been the most successful aetosaurian subfamily, with a large number of taxa known from every stratigraphic level.

Representatives of the Desmatosuchinae and Stagonolepinae and, by inference, the Aetosaurinae, are present by Otischalkian time. More aetosaur taxa go extinct at the end of Otischalkian time (*Longosuchus*, *Coahomasuchus*, and the carnivorous aetosaur) or persist from the Adamanian into the Revueltian (*Desmatosuchus*, *Paratypothorax*), than go extinct at the end of Adamanian time (*Stagonolepis*). Although *Stagonolepis* is the last stagonolepine, the aetosaurines, represented by *Aetosaurus*, radiate extensively in the Norian. It seems quite likely that the three species of *Aetosaurus* also diverged from each other some time in the latest Carnian. Therefore, the record of aetosaur evolution shows an increase in species and generic diversity across the Carnian-Norian boundary.

## 7. Conclusions

Using characters defined and utilized by both ourselves and previous authors, we have developed a new phylogenetic hypothesis for the relationships of the Aetosauria, indicating that three clades (which we recognize as subfamilies using Linnaean nomenclature) of aetosaurs exist. One of these, the Aetosaurinae consists of the three species of *Aetosaurus*, about which we make no attempt to determine relationships. The second subfamily, the Stagonolepinae, consists of the sister taxa *Stagonolepis* and *Coahomasuchus*. The third subfamily, the Desmatosuchinae, consists of the clade of (*Neoaetosauroides* + ((*Typothorax* + *Desmatosuchus*) + (*Longosuchus* + *Paratypothorax*))).

Recent hypotheses of aetosaur phylogeny (Parrish 1994, Heckert et al. 1996) have shown that certain early-appearing forms, such as *Longosuchus* and *Desmatosuchus*, are among the most derived aetosaurs, whereas more primitive aeto-

saur, particularly *Aetosaurus*, have their first appearance much later. This study indicates that *Coahomasuchus* fills a gap in the aetosaurian record by demonstrating the presence of primitive aetosaurs in the early late Carnian, synchronous with the first appearance of aetosaurs in the fossil record.

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# APPENDIX I: Description of characters used for phylogenetic analysis of the aetosaurs.

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

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

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

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

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

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

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

22. Apex of scapula: un- or modestly expanded (0) or broadly expanded (1).
23. Manus gracile and elongate (longer than wide) (0) or short, broad, and small (wider than long) (1).

- 24. Well-developed, robust, short anterior iliac blade: absent (0) or present (1).
- 25. Openings in pubis: none or one (0) or two (1).
- 26. Coracoid: shallow (0) or robust (1).
- 27. Pubes broadened transversely and fused, forming a "pubic apron" in anterior view: absent (0) or present (1).

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

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

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

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

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

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

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

- 49. Lateral spikes on cervical lateral scutes: absent (0) or present (1).
- 50. Lateral spikes on dorsal ("trunk") lateral scutes: absent (0) or present (1).
- 51. Lateral spikes on caudal lateral scutes: absent (0) or present (1).



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