CHAPTER 8

TAXONOMY OF THE STAGONOLEPIDIDAE

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869

PSEUDOSUCHIA Zittel 1887-1890 *sensu* Gauthier, 1986

SUCHIA Krebs, 1974

STAGONOLEPIDIDAE Lydekker, 1887

Revised diagnosis -- Pseudosuchians that possess the following synapomorphies: premaxilla that is edentulous anteriorly and upturned into a mediolaterally expanded “shovel” at its terminus; external nares much longer than antorbital fenestra; supratemporal fenestra laterally exposed; small peg-like teeth possessing bulbous crowns that are waisted; posterior ramus of jugal downturned; mandible is “slipper-shaped” with an acute anterior terminus; dentary is edentulous anteriorly; posterior margin of parietal modified to receive paramedian scutes; proximal humerus greatly expanded with hypertrophied deltopectoral crest; femur, straight, not twisted, with a hypertrophied, knob-like fourth trochanter; laterally expanded transverse processes in the dorsal series that contain both rib facets; well-developed accessory (hyposphene-hypantrum) articulations on the dorsal vertebrae; iliac blade high, thickened dorsally; anterior iliac blade, short, robust, and slightly recurved ventrally; an extensive carapace of rectangular (wider than long) osteoderms occurring in four distinct rows; and extensive ventral and appendicular armor (Parrish, 1994; Long and Murry, 1995; Heckert and Lucas, 2000; Small, 2002).

The synonymy lists in this chapter are modified from Heckert and Lucas (2000).

STAGONOLEPININAE Heckert and Lucas, 2000

Huene (1942) originally used the name “Stagonolepinae” as a subfamily for *Stagonolepis*. Heckert and Lucas (2000) modified this to Stagonolepininae and defined it cladistically.

Stagonolepininae is defined as a stem-based taxon by Heckert and Lucas (2000:1551) consisting of all stagonolepididids “more closely related to *Stagonolepis* than the last common ancestor of *Stagonolepis* and *Desmatosuchus*.” Stagonolepininae consists of *Coahomasuchus* + *Aetosaurus* + *Stagonolepis* + Typothoraxinae. According to the taxonomy presented herein, Stagonolepininae Heckert and Lucas (2000) is a senior synonym of Aetosaurinae Heckert and Lucas (2000).

Coahomasuchus **Heckert and Lucas 1999**

1993 New aetosaur genus: Lucas et al., p. 241, fig. 5.
1999 *Coahomasuchus kahleorum*: Heckert and Lucas, p. 50, figs. 3-8.
2000 *Coahomasuchus kahleorum*: Heckert and Lucas, p. 1551, fig. 3e.

Type species -- *Coahomasuchus kahleorum* Heckert and Lucas 1999 (by monotypy)

Distribution -- Colorado City Member, Dockum Formation, west Texas. Early late Carnian (Heckert and Lucas, 2000).

Lehman (1994) and Chatterjee (1997) do not accept the validity of the Colorado City Member of the Dockum Formation (Lucas and Anderson, 1993) or the “pre-Tecovas Horizon” of Long and Murry (1995) and instead assign this strata to the Cooper Canyon Formation of the Dockum Group. This has serious implications for biostratigraphy since the Colorado City Member is believed to be Late Carnian in age (Lucas, 1993) while the Cooper Canyon Formation is early Norian (Small, 1989).

Type Locality -- Colorado City Member, Dockum Formation; north of Otis Chalk, Howard County, Texas (Heckert and Lucas, 1999).

Holotype -- NMMNH P-18496, nearly complete, articulated skeleton, including portions of the skull, lower jaws, limbs, girdles, and an almost complete carapace. Completeness of the vertebral column cannot be determined due to dorso-ventral crushing of the carapace.

Diagnosis -- Small aetosaur (1 m. body length) possessing pre-sacral dorsal paramedian plates with a faint ornamentation of sub-parallel, non-radial grooves and ridges. Lateral scutes are flattened, lack spikes, flanges or knobs and have a radial pattern of pits centered in the medial third of the specimen. Cervical ventral scutes are small, sub-circular to oval and taper posteriorly. Anterior ventral thoracic scutes are hexagonal and articulated in columns of four to ten (Heckert and Lucas, 1999).

Discussion -- *Coahomasuchus* is similar to *Aetosaurus* not only in its small body size but also in the possession of flat lateral plates without spikes or keels, faint sub-parallel ridges and anterior bars on the dorsal armor, and gracile post-cranial elements. In their phylogeny, Heckert and Lucas (1999) differentiate these two taxa with only two characters: the presence of a deep, hemispherical fontanelle in the bottom of the basisphenoid, and the lack of raised bosses on the dermal armor in *Coahomasuchus*. A partial braincase is preserved with the holotype of *Coahomasuchus* and Heckert and Lucas (1999:55) state that the basisphenoid is “very deeply excavated” and that “this *may* correspond to the deep hemispherical fontanelle” found in *Desmatosuchus* and

Longosuchus (my emphasis). This character seems ambiguous and its presence in *Coahomasuchus* and its phylogenetic usefulness should be questioned (also see Small, 2002). Therefore, according to Heckert and Lucas (1999) only one character currently separates the two, the lack of pronounced bosses in the dorsal armor of *Coahomasuchus*. However, *Coahomasuchus* also lacks the flexure of the paramedian plates described by Walker (1961) for *Aetosaurus* and *Stagonolepis*, a difference that can be noted in Heckert and Lucas (2000: fig 3).

Also of concern regarding *Coahomasuchus* is its status as an adult animal. Heckert and Lucas (1999) argue that although preservational processes have obscured all cranial sutures, the fact that the bones show no visible gaps suggests that the sutures are fully fused and the specimen is an adult. While this argument does bear merit, additional proof of the maturity of the *Coahomasuchus* type specimen seems necessary, since this is the only indication of such given by the authors. Studies by Brochu (1993) on the postcrania of archosaurs suggest that neurocentral sutures of the vertebrae fuse posteriorly to anteriorly during ontogeny. Indeed, unfused neural arches in archosaurs are considered an indicator of immaturity among many workers. Unfortunately the vertebrae of *Coahomasuchus* are encased within the crushed carapace of the unique specimen (Heckert and Lucas, 1999). However, modern CT-scan technology might be able to elucidate vertebral characters for this taxon and give more support to its status as an adult.

Elder (1978) and Murry and Long (1996) mention the occurrence of another small aetosaur from Howard County. This specimen is of note due to a “varanoid-like” dentition suggestive of a carnivorous diet (Murry and Long, 1996). Unfortunately despite these brief notes this specimen has never been described, although it is very possible that it represents *Coahomasuchus* due to some apparent resemblances including size, armor characteristics, and the fact that they are from the same horizon. If these specimens do both represent *Coahomasuchus* than this taxon would probably be removed from the Stagonolepininae to a more basal position within the Stagonolepididae based on the primitive characteristics of its armor and dentition.

Despite much of the ambiguity surrounding *Coahomasuchus*, it is most likely that Heckert and Lucas (1999) are correct in their assessment of it as a diminutive, primitive aetosaur.

Unnamed Clade: (*Aetosaurus* + *Stagonolepis* + Typothoraxinae)

These taxa are united by the following synapomorphy: moderate to strong ventral flexure of the dorsal paramedian plates along the center of ossification (reversed in the Paratypothoraxini).

Aetosaurus O. Fraas 1877

Type species -- *Aetosaurus ferratus* O. Fraas 1877

Distribution -- Lower Stubensandstein, Germany; Middle Stubensandstein, Germany; Calcare di Zorzino Formation, Italy; Ørsted Dal Member, Fleming Fjord Formation, eastern Greenland; Chinle Formation, Colorado, U. S. A.; New Haven Formation, Connecticut, U. S. A.; fissure fillings, Bristol, U. K. Early-Middle Norian.

Revised diagnosis -- Aetosaur of small adult size (less than 1.5m overall length), the temporal fenestra is large and the orbit small resulting in a longer contact surface between the postorbital and squamosal; the tip of the premaxilla is not laterally expanded; teeth are waisted, slightly pointed and recurved at the tips; dentary tooth count not reduced; dermal armor ornamentation consists of a radial pattern of elongate pits and ridges emanating from a central knob or keel, each row of plates corresponds to an underlying vertebra; cervical paramedian plates are wider than long and not thickened dorsoventrally; paramedian plates are moderately angulated along the center of ossification; lateral plates are quadrangular in shape, show little or no angulation and do not possess spikes or horns; the small longitudinal keel is closer to the medial edge on the lateral armor; plates possess a distinct raised anterior bar; ventral armor possesses a maximum of twelve scutes in each transverse row (Walker, 1961; Wild, 1989).

Discussion -- Heckert and Lucas (2000) place *Aetosaurus* in a separate subfamily, the Aetosaurinae, based on three synapomorphies: 1) conical teeth, not recurved; 2) anterior part of dentary edentulous; and 3) maxillary tooth row does not extend anterior to the posterior end of the external naris. Due to the lack of a modern description of *Aetosaurus* it is difficult to quantify these characters and therefore to support the erection of an inclusive sub-family solely for this taxon. The teeth of *Aetosaurus* are not truly “recurved,” rather they possess bulbous crowns and slightly recurved apices (Walker, 1961). The anterior portion of the dentary is edentulous (Walker, 1961). The third character is ambiguous and represents a condition that is similar in *Aetosaurus*, *Stagonolepis*, and *Desmatosuchus* (Walker, 1961; Small, 2002). In fact, most of the differences between *Stagonolepis* and *Aetosaurus* are related to size and possibly ontogeny, something originally suggested by Walker (1961). Since these two taxa are close enough to be almost congeneric they certainly belong to the same subfamily.

Aetosaurus ferratus **O. Fraas 1877**

1877	*Aetosaurus ferratus*:	O. Fraas, p. 1, figs. 2-3, pl. 1-3
1896	*Aetosaurus ferratus*:	E. Fraas, p. 17, tab. 4.
1902	*Aetosaurus ferratus*	Huene, p. 54, fig. 68
1908	*Aetosaurus ferratus*:	Huene, p. 392, figs. 345-346, 350.
1914	*Aetosaurus ferratus*:	Huene, p. 18, fig. 9.
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. 62, fig. 5.
1956	*Aetosaurus ferratus*:	Huene, p. 450, fig. 484a, b.
1956	*Aetosaurus*:	Romer, p. 131, fig., 69e.
1961	*Aetosaurus ferratus*:	Walker, p. 164, figs. 24a, 40-45.
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, p. 2, figs. 1-3, 4a.
1994	*Aetosaurus ferratus*:	Jenkins et al., p. 13, figs. 8-9.
1998	*Aetosaurus* sp.:	Small, p. 287, figs. 2-4
2000	*Aetosaurus ferratus*:	Heckert and Lucas, p. 1547, figs. 3a, d.

Lectotype -- SMNS 5770, individual number XVI, complete adult specimen from a block containing approximately 22 individuals (Walker, 1961).

Type locality -- Lower Stubensandstein; Sandstone quarry in Stutgart-Kaltental, Germany.

Diagnosis -- Dorsal paramedian plates with an elongate keel and deeply incised ornamentation. Total adult length is less than one meter.

Aetosaurus crassicuada **E. Fraas 1907**

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
2000 *Aetosaurus crassicauda*: Heckert and Lucas, p. 1549, figs. 3c, f.

Holotype -- SMNS 11837, a partial skeleton consisting of an articulated carapace, complete from the mid-dorsal to anterior-caudal regions and an incomplete pelvis.

Type Locality -- Middle Stubensandstein, Pfaffenhoffen, Baden-Württenburg, Germany.

Diagnosis -- Paramedian scutes with a median knob instead of a keel and deeply incised pitting; strong transverse arching of the anterior caudal paramedian plates. Larger adult body size (~ 1.5 m.) than other species of *Aetosaurus*.

Aetosaurus arcuatus **(Marsh 1896)**

1896 *Stegomus arcuatus*: Marsh, p. 60, pl.1.
1914 *Stegomus arcuatus*: Huene, p. 19, fig. 49
1915 *Stegomus arcuatus*: Lull, p. 99, fig. 9, pl. 7.
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., p. 1216, figs. 2-4. pls. 1-2.
2000 *Aetosaurus arcuatus*: Heckert and Lucas, p. 1550, fig. 3b.

Holotype -- YPM 1647, natural cast of the ventral surface of a portion of the dorsal carapace.

Type Locality – Clark Quarry, New Haven Formation, Fair Haven, Connecticut.

Diagnosis -- Dermal plates with a very faint radial pitting, high (3.5/1) width:length ratio of the dorsal paramedian scutes, tail narrows rapidly posteriorly (Heckert and Lucas, 1998).

Discussion -- *Aetosaurus* is potentially one of the better-known aetosaur genera due to the existence of 22 mostly articulated specimens in the German Lower Stubensandstein, including the type of *A. ferratus*. However, until this taxon is restudied in accordance with our current state of knowledge regarding aetosaurs, *Aetosaurus* will continue to be poorly understood. Although occurring in strata of Norian age, *Aetosaurus* is believed to be the most primitive aetosaur, an idea that is weakly supported by phylogenetic analysis (Parrish, 1994; Heckert and Lucas, 2000). A new analysis (Chapter 8, this thesis) based upon information from Walker (1961) suggests that *Aetosaurus* is not the most primitive aetosaur but instead is closer to *Stagonolepis*.

Walker (1961) and Krebs (1976) argued that *A. ferratus* and *A. crassicauda* could only be distinguished on the basis of size and therefore did not represent distinct species. However, Wild (1989) in his revision of the genus showed that the two differed stratigraphically as well as morphologically with *A. crassicauda* occurring in the Upper Stubensandstein, possessing a knob on the dorsal paramedian plates rather than an elongate keel as found in *A. ferratus*, and in having caudal paramedian plates that are strongly arched transversely.

Lucas et. al. (1998) argued convincingly that *Stegomus arcuatus* from the Newark Supergroup of the eastern United States was remarkably similar to the European

Aetosaurus, differing only in the presence of weaker sculpturing in the dermal plates and a rapidly tapering tail in *Stegomus*. Accordingly, Lucas et. al. (1998) synonymized the two genera, creating the new combination *Aetosaurus arcuatus*, a synonymy that is supported by Small (1998) and Heckert and Lucas (1999; 2000).

Specimens of *Aetosaurus ferratus* have recently been found in Colorado and New Mexico extending the range of that species to North America (Small, 1998; Heckert and Lucas, 1998). Previously, *A. ferratus* was known only from Europe and Greenland. In addition, plates found in fissure-fill at Cromhall, Avon in the U. K. are referred to *Aetosaurus* by Heckert and Lucas (2000) as was suggested by Fraser (1988) and Wild (1989). Kitching and Raath (1983) make a reference to the occurrence of *Aetosaurus* from the Karroo beds of South Africa but this material has not been described and this claim cannot be substantiated.

Aetosaurus is an index taxon for the Revueltian land vertebrate faunachron of Lucas and Hunt (1993). However, it has recently been pointed out by Sues et. al. (1999) that since *Aetosaurus* is a primitive form with an extensive ghost lineage (Heckert and Lucas, 1999; 2000) the possibility strongly exists that similar species could be found in Carnian deposits as well, thus this indicator should be used with caution especially when dealing with isolated occurrences and elements. This is also true regarding the new phylogenetic position of *Aetosaurus* postulated in this chapter.

***Stagonolepis* Agassiz 1844**

Type species -- *Stagonolepis robertsoni* Agassiz 1844

Distribution -- Lossiemouth Sandstone, Lossiemouth, Scotland; Chinle Formation, Arizona and New Mexico; Tecovas Formation, Dockum Group, west Texas; ?Blasensandstein, Germany; Ischigualasto Formation, Argentina; Santa Maria Formation, Brazil.

Revised diagnosis – Relatively narrow dorsal paramedian plates with a radial pattern of pits and grooves radiating from a prominent keel or knob that contacts the posterior margin of the plate; paramedian plates moderately angulated at the center of ossification; ventral bar present on some paramedian plates; ventral armor with maximum of eight transverse rows; anterior bars well-developed on dorsal lateral and ventral plates; lateral plates equant to rectangular in shape, ranging from flat to strongly angulated with a dorsal eminence with either a distinct longitudinal keel that is closest to the medial edge or a hook-like boss, depending on location in the body; posterior blade of the ilium greatly thickened, short, and sub-rectangular in lateral view; neural spines of vertebrae tall, especially in the posterior dorsal, sacral, and anterior caudal regions; transverse processes of the posterior dorsal region flattened and expanded antero-posteriorly (Walker, 1961; Heckert and Lucas, 2000). This character is as described by Walker (1961) for *S. robertsoni* and is also apparent in the type specimen of *S. wellesi* (Case, 1932). The posteriormost dorsal vertebrae in aetosaurs, evident in *Stagonolepis*, *Desmatosuchus*, and *Typothorax*, are extremely specialized in relation to the rest of the series. These modifications probably had structural ramifications for the heavy carapace. Long and Murry (1995); Heckert and Lucas (1999; 2000; 2002a) repeatedly list the presence of extremely elongate transverse processes in the dorsal series as a synapomorphy for *Stagonolepis*, however, this character was based on the posteriormost dorsals in the type of *S. wellesi*. Analysis of *Stagonolepis* vertebrae from the rest of the dorsal series shows no distinct differences from the dorsal vertebrae of other aetosaurs. As previously mentioned, the "dorsal" vertebral column of *S. scagliai* in Heckert and Lucas (2002a: fig. 2.8) is actually the anterior caudal series, which possesses elongate, flattened transverse processes in all stagonlepidids.

***Stagonolepis robertsoni* Agassiz 1844**

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.
1902 *Staganolepis* [sic] *robertsoni*: Huene, p. 54, figs. 62-67, 72, 73.
1907 *Stagonolepis robertsoni*: Huene, p. 392, figs. 347-348.
1936 *Stagonolepis robertsoni*: Huene, p. 207, fig. 3.
1942 *Stagonolepis robertsoni*: Huene, p. 223, figs. 45-49.
1961 *Stagonolepis robertsoni*: Walker, p. 103, figs. 2-23, 24b, 25b, pl. 9-12.
1976 *Stagonolepis robertsoni*: Krebs, p. 40, figs. 3, 4, 9, 10d, 12, 15, 16, 17c-e, 19d-e, 20d-e, 26b, 27.
1978 *Staganolepis* [sic]: Bonaparte, p. 300, figs. 137b, 138.
1986 *Stagonolepis*: Parrish, p. 8, fig. 6, 14c3.
1988 *Stagonolepis*: Carroll, p. 273, figs. 13.15, 13.16.
1988 *Stagonolepis*: Fraser, p. 132, fig. 5b.
1991 *Stagonolepis*: Sereno, p. 11, fig. 10, 27f.
1996 *Stagonolepis*: Lucas and Heckert, p. 57, fig. 4.
2000 *Stagonolepis robertsoni*: Heckert and Lucas, 2000, p. 1552, figs. 4c,e.
2001 *Stagonolepis robertsoni*: Lucas and Heckert, p. 719, figs. 2,3.
2002 *Stagonolepis robertsoni*: Gower and Walker, p. 7, figs. 1-4, 6.

Holotype – EM 27R, impression of a portion of the ventral carapace of a small individual.

Type Locality – Findrassie Quarry, Lossiemouth Sandstone Formation, Lossiemouth, Scotland (Heckert and Lucas, 2000)

Diagnosis – Paramedian plates possess a pattern of grooves and pits radiating from a low, central keel or knob; paramedian eminence is situated on the posterior margin of the plate; pubis possesses two foramina; tooth counts of the dentary and maxilla slightly reduced, maxillary tooth count 11 or 12; dentary tooth count 9 or 10; teeth possess denticles along the mesial edge and distinct wear facets.

Discussion – Stagonolepis robertsoni was described by Agassiz (1844) based on a sandstone impression of a portion of the ventral carapace. The type locality was believed to be in the Devonian Old Red Sandstone, therefore Agassiz mistook the specimen for that of a fish. Huxley (1859, 1877) was the first to determine its reptilian affinities and he also realized its taxonomic position between "belodonts" (phytosaurs) and crocodylians. Walker (1961) provided an excellent description of the Findrassie material and also made the first detailed comparisons with other aetosaur taxa. Unfortunately, most of this material is preserved as natural sandstone molds, and although Walker developed ingenious ways to obtain even the slightest details from these molds, it has proven difficult for modern workers to examine this material. Recently, however, a paper was published on new casts of the braincase (Gower and Walker, 2002). Since this material is not available it has been almost impossible to make detailed comparisons with other *Stagonolepis* specimens, particularily in the southwestern United States, and in Argentina, and Brazil. This is especially true for the dermal armor, which was not described in great detail by either Huxley or Walker.

Heckert and Lucas (1999, 2000) and Lucas and Heckert (2001) have synonymized many of the *Stagonolepis*-like aetosaurs worldwide with *S. robertsoni*, including *Stagonolepis* (=*Calyptosuchus*) *wellesi* (Long and Murry, 1995), *Aetosauroides scagliai* (Casamiquela, 1960); *Argentinasuchus bonapartei* (Casamiquela, 1960); *Ebrachosaurus singularis* (Kuhn, 1936), and "*Aetosauroides subsulcatus*" (Zacharias, 1982). However, these same authors have recently (Heckert and Lucas, 2002a) stated that *S. wellesi* is a valid species of *Stagonolepis* and tentatively assigned the type material of *Argentinasuchus bonapartei* to this taxon. All of these taxa possess strong similarities to *S. robertsoni*, particularily in the armor patterning, however, the type of *Ebrachosaurus* is lost and cannot be directly compared to *Stagonolepis* and as stated earlier all comparisons are limited due to the preservation of the type material of *S. robertsoni*. *Stagonolepis wellesi*, is known only from a partial carapace and vertebral column, including a crushed pelvis (Case, 1932), however, Long and Ballew (1985) and Long and Murry (1995) have briefly described isolated material from the *Placerias* Quarry and Petrified Forest National Park in Arizona. In addition, another partial skeleton attributable to this taxon was recently excavated in the park (Parker, in prep).

Because of the biostratigraphic utility of aetosaurs, synonymies must be carried out with care, especially since many genera are proving to have longer stratigraphic ranges and the taxonomic diversity of aetosaurs is greater than previously believed. Heckert and Lucas (2002a) and Lucas and Heckert (2001) have made a seemingly strong case for assigning all of the South American material to *Stagonolepis*. However, in an abstract, Desojo (1999) has contested this point of view, citing several differences between the specimens but unfortunately the detailed information has yet to be formally published this information. In view of these potential differences, the recent retraction of their synonymy of *S. wellesi* by Heckert and Lucas (2002a), and the limited access to type materials, it is best to simply assign the Argentinian material to *Stagonolepis scagliai*, and the Brazilian material to *Stagonolepis* sp. until the armor and postcrania of *S. robertsoni* and *S. wellesi* can be more completely described.

Stagonolepis wellesi **(Long and Ballew 1985)**

1922 Phytosaur: Case, p.70, fig. 27, pl. 13a.
1929 Phytosaur: Case, p. 49, fig. 21.
1932 Phytosaur: Case, p. 57, figs. 1-6, pl. 1-3, pl. 4 (fig. 1).
1985 *Calyptosuchus wellesi*: Long and Ballew, p. 45, figs. 13-16, pl. 4-5.
1986 *Calyptosuchus*: Parrish, p. 15, fig. 17h.
1995 *Stagonolepis wellesi*: Long and Murry, p. 1, figs. 68-70, 71a, b, c, d, 72-84.
2000 *Stagonolepis robertsoni*: Heckert and Lucas, p. 1552, figs. 4a,b.

Holotype – UMMP 13950, almost a complete carapace from the posterior dorsal to the mid-caudal region, including the associated vertebrae and a crushed pelvis (Case, 1932).

Type Locality – Northeast of Rotten Hill, near the breaks of Sierrita de la Cruz Creek, Tecovas Formation, Dockum Group, Texas.

Revised Diagnosis – Paramedian plates moderately to strongly flexed ventrally along the center of ossification; paramedian and lateral plates thickened dorsoventrally with a ventral bar present on some specimens; dorsal eminence is extremely enlarged on posterior paramedians, often overhanging the posterior margin of the plate; postcranial elements robust.

Discussion -- Long and Ballew (1985) erected the genus *Calyptosuchus* based on armor plates from Arizona that were identical to a partial carapace from Texas described by Case (1932). Murry and Long (1989) noted strong similarities between this new form and *Stagonolepis robertsoni*, and formally synonymized *Calyptosuchus* with *Stagonolepis* in 1995 (Long and Murry, 1995). The two main features that these authors felt distinguished *S. wellesi* from *S. robertsoni* were the presence of small cervical lateral horns and greatly elongate transverse processes in the dorsal region of *S. wellesi*. Long and Murry (1995:85-86) list numerous other differences but most of these are a result of

S. wellesi being a larger, more robust animal. Most workers feel that the cervical horns have erroneously been assigned to *S. wellesi*, indeed they are difficult to substantiate since the type specimen only contains the posterior half of the animal. This led Heckert and Lucas (1999, 2000) to disregard *S. wellesi* as a valid species, a stance they have since reversed based on other characters (Heckert and Lucas, 2002a). The transverse processes of the dorsal series in *S. wellesi* are not very different than in other aetosaurs (Long and Murry: fig. 75d-f). The last three presacrals are expanded and elongate, however, the processes in this position are also similarily modified in *S. robertsoni* (Walker, 1961: fig. 9), *Desmatosuchus*, and *Typothorax* (Hunt et. al, 1993).

Mehl (1916) described an aetosaurian pelvis from the lower Chinle Formation near Fort Wingate, New Mexico as *Acompsosaurus wingatensis*. Although this specimen is currently lost, it most likely pertains to *Stagonolepis wellesi* (Case, 1929; Long and Murry, 1995; Heckert and Lucas, 2000). Nonetheless, if it ever is recovered and a positive correlation can be made, *S. wellesi* would become a junior synonym of this taxon.

Heckert and Lucas (2002a) tentatively assigned the type specimen of *Argentinasuchus bonapartei* (Casamiquela, 1960) to *Stagonolepis wellesi* based on overall similarity and large size. However, although the type materials of *A. bonapartei* are clearly distinct from those of "*Aetosauroides*" *scagliai*, they are too fragmentary, and are not comparable to *S. wellesi*. These authors also assign larger elements of "*Aetosauroides*" *scagliai* to *S. wellesi*, but this would infer that *S. wellesi* is distinct only by its size, a hypothesis that cannot be substantiated by existing data. *Argentinasuchus* *bonapartei* should remain a *nomen dubium* and the possible presence of *S. wellesi* in South America negated for now.

Lucas and Heckert (2001) noted that a few specimens of *Stagonolepis* from the *Placerias* Quarry may be referable to *S. robertsoni* or alternately could be juveniles of *S. wellesi*. While it is possible that *S. wellesi* could simply represent an ontogenetic stage or sexual dimorph of *S. robertsoni*, there is simply not enough information available to reach a sound conclusion. Until conclusive evidence is found, it is best to keep these taxa separate.

***Stagonolepis scagliai* (Casamiquela, 1961)**

1960	*Aetosauroides scagliai*: Casamiquela, p. 2, figs. 1,2.
1961	*Aetosauroides scagliai*: Casamiquela, p. 4, figs. 1-26, pl. 1.
1967	*Aetosauroides scagliai*: Casamiquela, p. 173, figs. 1-3, pls. I-XV.
1971b	*Aetosauroides scagliai*: Bonaparte, p. 671, figs. 15, 16.
1978	*Aetosauroides scagliai*: Bonaparte, p. 300, figs. 137b, 138.
1982	*Aetosauroides*: Bonaparte, p. 108, fig. 4d.
2000	*Stagonolepis robertsoni*: Heckert and Lucas, p. 1552, fig. 4d.
2002a	*Stagonolepis robertsoni*: Heckert and Lucas, p. 852, figs. 2-4.

Holotype – PVL 2073, partial skeleton including articulated carapace and vertebral column, incomplete girdles and limbs.

Type Locality – Ischigualasto Basin, Ishigualasto Formation, San Juan, Argentina.

Revised Diagnosis – Medium sized aetosaur, very similar to *S. robertsoni*, but considered by Casamiquela (1967) to be an intermediate form between *Stagonolepis robertsoni* and *Aetosaurus ferratus*. Dorsal paramedian plates ornamented with grooves and pits radiating from a low, sharp longitudinal keel just medial to the mid-line. Paramedian plates moderately flexed ventrally along the center of ossification; humerus gracile, with a more elongate shaft, and reduced “flaring” of the proximal end; femur with extremely hypertrophied 4th trochanter; tibia with an elongate shaft and gracile build; dentition unreduced, maxillary tooth count of 13 and dentary tooth count of 11; dentition “primitive” (Casamiquela, 1967), crown apices are more recurved and less bulbous than in aetosaurs such as *Stagonolepis* or *Desmatosuchus* and more closely resemble the teeth of *Aetosaurus*.

Discussion – “*Aetosauroides*” *scagliai* was preliminarily described by Casamiquela in 1960 followed by a more complete description in 1961. Shortly after publishing his manuscript, Casamiquela received a copy of Walker’s 1961 monograph on *Stagonolepis robertsoni*. Although Casamiquela recognized many of the similarities between the two he was even more impressed by the characters shared by “*Aetosauroides*” with both *Stagonolepis* and *Aetosaurus* and was a “transitional” form (Casamiquela, 1967). Although, considered synonymous with *S. robertsoni* by Heckert and Lucas (2002a), “*Aetosauroides*” does possess differing characters, especially of the dentition, that suggest that it should be retained as a separate species. *Stagonolepis scagliai* appears to be a more primitive form of *Stagonolepis* in comparison to *S. robertsoni*, and *S. wellesi*.

***Stagonolepis* sp.**

Zacarias (1982) described a new aetosaur taxon, “*Aetosauroides subsulcatus*,” from a partial carapace from the Alemoa Member of the Caturrita Formation of Brazil, in an unpublished Masters Thesis. Subsequently, Lucas and Heckert (2001) assigned this material to *Stagonolepis robertsoni*. This specimen is indeed referable to *Stagonolepis* based on the armor patterning, the presence of eight plates in a transverse row of ventral scutes, and the keeled, equant lateral plates. In addition, the dorsal paramedians are slightly arched transversely from the center of ossification, which is slightly medial. These characters are shared by all three species of *Stagonolepis*. Notable, is the dorsal eminence of the paramedian plates, which does not appear to be keel-like or even possess a developed knob. Instead it appears to be a low, indistinct pyramidal boss in contact with the posterior portion of the plate, similar to that found in *Longosuchus*. Although these differences do not necessarily warrant erection of a new species it is probably best to refer these specimens to *Stagonolepis* sp. until more conclusive material is discovered.

TYPOTHORAXINAE (new taxon)

Typothoraxinae is a stem-based taxon defined here as all stagonolepinids closer to *Typothorax* than *Stagonolepis*. Typothoraxinae contains two clades, Typothoraxini and Paratypothoraxini.

TYPOTHORAXINI (new taxon)

Typothoraxini is a node-based taxon defined here as containing *Typothorax* and Paratypothoraxini and all descendents of their recent most common ancestor. *Chilenosuchus* as recently redescribed by Desojo (2003) is most likely also a member of this clade. Typothoraxini is robust being defined by eight synapomorphies: 1) transverse processes of dorsal vertebrae elongate and buttressed ventrally (unknown in *Typothorax reseri*, “*Tecovasuchus*” and *Heliocanthus*); 2) presacral neural spine height generally low, less than the height of the centrum (unknown in *Typothorax reseri*, “*Tecovasuchus*”, and *Heliocanthus*, convergent in *Desmatosuchus*); 3) width to length ratio of widest dorsal paramedian plates more than 4:1 (incompletely known in *Heliocanthus*); 4) angle of flexion between the dorsal and lateral flanges of the anterior lateral plates approximately 90° or less (unknown in *Typothorax reseri*); 5) dorsal and lateral flanges of anterior lateral scutes asymmetrical with lateral flange being longest (unknown in *Typothorax reseri* and *Heliocanthus*); 6) narrow region ("waist") in the carapace anterior to the sacrum absent (unknown in *Typothorax reseri*, "*Tecovasuchus*" and *Heliocanthus*, convergent in *Desmatosuchus* and *Longosuchus*); 7) posterior lateral plates possess a semicircular ventrolateral border and a hook-like eminence (unknown in *Typothorax reseri*); and 8) anterior lateral plates triangular in lateral view (unknown in *Typothorax reseri*). This node is robust, receiving a bootstrap proportion of 85 for 1000 replications.

Typothorax Cope 1875

Type Species – *Typothorax coccinarum* Cope 1875

Distribution – Chinle Formation, Arizona and New Mexico; Dockum Group, Eastern New Mexico and Texas.

Diagnosis – Aetosaur with dorsal paramedian scutes having a high width/length ratio, random, sub-circular ornamentation that is finer, more densely spaced, and shallower than in *Desmatosuchus,* arching about 15° - 45° at the center of ossification in most of the post-cervical region; plates have straight, anterolaterally sloping margins in the posterior dorsal paramedian scutes in adults, a raised anterior bar, thick rounded ventral keel more prominent lateral and immediately adjacent to center of ossification and flattens out both sides of the line of arching: plates lack beveling of the dorsal posterior margin (from Martz, 2002).

Typothorax coccinarum Cope 1875

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 *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.
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.
2000 *Typothorax coccinarum*: Heckert and Lucas, p. 1557, figs. 5a-c.
2002 *Typothorax coccinarum*: Heckert and Lucas, p. 195, figs. 4, 5.

Lectotype – USNM 2585, dorsal paramedian plate fragment (Cope, 1877; Lucas and Hunt, 1992; Hunt and Lucas, 1993b; Heckert and Lucas, 2002d). Heckert and Lucas (2000) erroneously list this specimen as USNM 2586.

Type Locality – Upper Petrified Forest Member, Chinle Formation, Rio Arriba County, New Mexico.

Diagnosis – Larger size than *T. reseri*; arching in the dorsal paramedians around 15° - 30°; less pronounced ventral keel; pyramidal boss on posterior dorsal and caudal paramedian plates; premaxillary teeth absent; dentary extremely shallow with ten teeth; cervical vertebrae short in adult specimens; dorsal vertebrae with greatly expanded transverse processes that are buttressed ventrally; gracile humerus; humerus with enclosed epicondylar foramen; ilium with greatly elongate anterior blade and strong constriction above the acetabulum; extremely shortened distal pubis; angulated lateral scutes with reduced dorsal flanges and pitted ornamentation; dorsal flange of lateral scutes triangular in adults with raised ridge at line of angulation, no lateral horn, large lateral flange bearing fine pitting posterodorsally, but elongate grooves radiating from the region on rest of flange (Martz, 2002).

***Typothorax reseri* (Hunt and Lucas, 1991)**

1985 *Typothorax* 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. 3,4.
2000 *Redondasuchus reseri*: Heckert and Lucas, p. 1558, figs. 5d-e.

Holotype – UCMP 64515, right dorsal paramedian plate (Hunt and Lucas, 1991: fig. 2a-c)

Type Locality – Apache Canyon Quarry 2 (UCMP loc. 6148), Redonda Formation, Quay County, New Mexico.

Diagnosis -- Smaller size relative to *T. coccinarum*; dorsal paramedian scutes with a greater degree of arching (45°); prominent ventral keel relative to size of paramedian plate, keel more abruptly flattened medial to the line of arching (Martz, 2002). *Redondasuchus* was originally distinguished from other aetosaurs by having dorsal paramedian plates that are strongly flexed about two thirds of their length from the “medial” edge (Hunt and Lucas, 1991), and by its lack of a continuous ventral keel (Heckert et.al., 1996). Martz (2001) has demonstrated that these are also characters of *Typothorax coccinarum* and accordingly has provided a revised diagnosis.

***Typothorax antiquum* Lucas et al., 2002**

1989 *Typothorax* sp.: Hunt et. al., p. 65, fig. 3c.
1995b new aetosaur 3: Hunt and Lucas, p. 244.
1995b *Typothorax coccinarum*: Hunt and Lucas, fig. 2k.
1995 *Typothorax coccinarum* (in part): Long and Murry, p. 234
2002 *Typothorax antiquum*: Lucas et. al., p. 221, figs. 3-10

Holotype – NMMNH P-36075, partial skeleton consisting of cervical, dorsal, sacral, and caudal vertebrae, both ilia and ischia, partial scapulocoracoid, limbs, and a partial armor carapace (Lucas et. al., 2002: figs: 3-9).

Type Locality – NMMNH loc. 3108, Tres Lagunas Member of the Santa Rosa Formation, Dockum Group, Santa Fe County, New Mexico.

Diagnosis – Distinguished from *T. coccinarum* by possessing relatively narrow paramedian plates (width:length ratio ~2-3); paramedian plates possess coarser and less dense pitting; lateral scutes with more pronounced radial ridges; ilium robust, with more prominent and thicker peduncles, lateral buttress, and iliac blade.

Discussion – *Typothorax* is probably the most common aetosaur taxon recovered from Late Triassic strata in the southwestern U.S. where it is known from the upper beds of both the Chinle Formation and Dockum Group and also from the lower beds of the Dockum. However, presently it is restricted to this region unlike *Stagonolepis, Aetosaurus*, and *Paratypothorax*, which are much more cosmopolitan. Recently considered monospecific (Heckert and Lucas, 2000), *Typothorax* is now known from three species, which can mainly be distinguished by size and stratigraphic occurrence. *Typothorax coccinarum* was described by Cope in 1875 from material from the Chama Basin of New Mexico (Upper Petrified Forest Member of the Chinle Formation). Since this time, *T. coccinarum* has been recovered from the Bull Canyon (=Cooper Canyon) Formation of the Dockum group in west New Mexico and eastern Texas, and the Upper Petrified Forest and Owl Rock Members of the Chinle Formation in Arizona (Lucas et. al., 1985; Small, 1989; Murry and Long, 1989; Kirby, 1989). Heckert and Lucas (2002b) redescribe, refigure and emend the syntype and lectotype material.

Hunt and Lucas (1991) described a new small aetosaur from the Redonda Formation of New Mexico as *Redondasuchus reseri*. These authors noted its similarities to *Typothorax coccinarum* but were convinced it was a valid taxon and provided a redescription in 1996 (Heckert et. al., 1996) after Long and Murry (1995) questioned its validity. Martz (2002) has recently provided strong evidence that many of the distinguishing characters of *Redondasuchus* are shared by *Typothorax,* however, he did feel that the consistently small size of the Redonda material allowed for species separation. The assignment of *Redondasuchus* to *Typothorax* is also supported by phylogenetic analysis (Heckert et. al., 1996; Harris et. al., 2003). *Redondasuchus* has been described as not possessing lateral plates based on the downward flexure of the dorsal paramedians, which supposedly preclude the presence of a lateral plate (Heckert et. al., 1996). However, Martz (2002) has suggested that the holotype paramedian scute was interpreted incorrectly and demonstrated that if the plate is reversed, not only is it similar to the same plates in *T. coccinarum* but it can articulate with a lateral plate.

Martz (2002) described a probable juvenile specimen of *T. coccinarum* from the Post Quarry in Texas, providing an excellent morphological study of the braincase, armor, and much of the postcrania from not only this new specimen, but from material from the Canjillon Quarry as well. This description is very useful in clarifying and improving many of the identifications for the partial skeleton of *T. antiquum*, described by Lucas et. al. (2002). *Typothorax antiquum* is very similar in its overall morphology to *T. coccinarum* and is seemingly distinguished only by stratigraphic position and a few minor details of the skeleton. However, I do agree with the authors that this does warrant erection of a new species. Unfortunately, the paper describing this material contains several errors that should be pointed out: 1) the armor plates (Lucas et. al., 2002: figs. 3a,b) are caudal paramedians, not cervicals; 2) the "dorsal" vertebra (fig. 5a, b) is actually an anterior-mid caudal, which explains the unique characteristics described by the authors; 3) the "caudal" vertebra (fig. 5c, d) is actually a mid to posterior dorsal, which again explains its "uniqueness"; 4) the pelvis orientation in fig. 6c is posterior not anterior; 5) the pelvis orientation in fig. 6e is anterior not posterior; 6) the calcaneum (fig. 9a, b) is actually from the right side and the orientations need to be reversed, the same for the astragalus (fig. 9e, f); and 7) the fibula (fig. 8g) is upside down. Once these corrections are made it can be seen that *T. antiquum* is indeed very similar to *T. coccinarum* especially in the characters of the tarsals, and the vertebrae. Lucas et. al. (2002) are probably mistaken that the cervical paramedians are longer than wide since this description is based on caudal paramedians. Figure 3c of their paper depicts what probably is a cervical paramedian (note the weak ornamentation and that it is longer than wide), unfortunately they inexplicably identify it as a ventral plate. Of great interest are the elements of the lower front limb and the pelvis since these have never previously been described for *Typothorax*, unfortunately the pubes are missing so it is not possible to verify whether they were extremely short ventrally as is suggested by the Canjillon Quarry material (Long and Murry, 1995). Even more interested is the apparently extreme width of the pelvis and the almost horizontal orientation of the ilia so that the acetabula face ventrally. This is markedly different from the pelves of other known aetosaurs and more like those of rauisuchians.

Chilenosuchus Casamiquela 1980

Type Species – *Chilenosuchus forttae* Casimiquela 1980

Distribution – Estrados El Bordo, Chile

Diagnosis – Aetosaur that differs from other stagonolepidids by the recticular pattern of ornamentation on the paramedian armor; differs from all aetosaurs except *Typothorax* by possessing paramedian, lateral, and ventral plates devoid of grooves and ridges; and differs from *Typothorax* by possessing plates with pits of uniform size (Desojo, 2003).

Chilenosuchus forttae Casimiquela 1980

Syntype – SNGM 987, impression of a portion of the disarticulated postcrania and dermal armor.

Type Locality – Cerro Quimal, Cordillera Domeyko, Antofagasta Region, Chile.

Diagnosis – Same as for the genus.

Discussion – Casimiquela (1980) provided the original description of this taxon, which he felt showed a Late Triassic age for the Estratos El Bordo, a volcanic-sedimentary succession in Northern Chile. This age has been disputed by the discovery of microfossils and plant fossils of supposed late Paleozoic age (Desojo, 2003). Based on this biostratigraphic evidence and because the type materials were considered lost, Heckert and Lucas (1999; 2000) argued that *Chilenosuchus* does not represent an aetosaur. Recently the type materials have been relocated, and Desojo (2003) has provided a redescription in which she argues that *Chilenosuchus* is indeed an aetosaur. The armor of *Chilenosuchus* appears to be very similar to *Typothorax*, however, because of the incomplete condition of the materials it was not included in the phylogenetic study presented in this thesis. Despite this it has been placed within the Typothoraxini based on this resemblance (Desojo, 2003). Nonetheless, due to the strength of Desojo's argument, it does appear that *Chilenosuchus* is indeed a valid aetosaur taxon, although its stratigraphic position is still enigmatic (Desojo, 2003). Hopefully, future research will provide a more complete description of this taxon and determine whether the Estratos El Bordo are unquestionably late Triassic in age.

PARATYPOTHORAXINI (new taxon)

Paratypothoraxini is a node-based taxon that includes "*Tecovasuchus*," *Heliocanthus* gen. nov., and *Paratypothorax* as well as all descendents of their recent most common ancestor. Paratypothoraxini is currently diagnosed by three synapomorphies: 1) dorsal eminence of the paramedian plates never or almost never contacts the posterior margin of the plate (convergent in *Desmatosuchus*, *Lucasuchus*, and *Aetosaurus*); 2) paramedian plates flat lying with little or no ventral flexure at the center of ossification (convergent with *Longosuchus*, *Lucasuchus*, and *Desmatosuchus*); 3) dorsal eminence on paramedian plates strongly offset medially; and 4) angle of flexion between the dorsal and lateral flanges of the anterior lateral plates approximately 90° or less. This node was recovered a majority of the time with a bootstrap proportion of 88 for 1000 replicates.

"*Tecovasuchus*" Martz and Small, in press.

"*Tecovasuchus*" is a new undescribed aetosaur taxon from the Tecovas Formation of Texas. The details of this animal will not be covered in the thesis except to note that it shares many synapomorphies with *Paratypothorax*.

***Heliocanthus* gen. nov.**

Type Species – *Heliocanthus chamaensis* (Zeigler et. al, 2002)

Distribution – Petrified Forest Member, Chinle Formation, New Mexico, Arizona; ?Bull Canyon (=Cooper Canyon) Formation, Dockum Group, New Mexico.

Etymology – From "*helios,*" Greek for sun, and "*acanthus,*" Greek for spike. Refers to numerous armor spikes radiating from the carapace and also honors the state of New Mexico from which the holotype was collected, and the state emblem, which is a "spiky" sun.

Diagnosis – Aetosaur known only from the dermal armor; anterior dorsal and posterior cervical armor crescentic in dorsal view (as in *Typothorax*); posterior cervical and anterior dorsal paramedian plates possess a distinct dorsal eminence, which consists of an elongate, gracile, recurved spike; posterior dorsal paramedians possess a reduced eminence, which takes the form of either a very short, straight spike or a very low, rounded knob; dorsal eminence of cervical and dorsal paramedian plates is situated just lateral to the medial edge of the plate, being strongly offset as in *Paratypothorax* and "*Tecovasuchus*"; ornamentation of the paramedian plates consists of elongate grooves, ridges, and pits, radiating from the dorsal eminence; lateral plates possess incised grooves radiating from the eminence (as in *Paratypothorax*); caudal paramedian plates equant in shape with a strong anterior bar and robust, short, hook-like eminence, which contacts the posterior margin of the plate; anteromedial corner possesses a small, sharp process that projects anteriorly; median edges of paramedian plates are straight while the lateral edges are sinuous; ventral surfaces of paramedian plates are flat and smooth except for a slight emargination beneath the dorsal eminence; anterior lateral plates possess two distinct flanges at an acute angle which meet to form an elongate, slightly recurved spike that projects laterally, the spike is compressed dorsoventrally with a sharp anterior edge and a rounded posterior edge; posterior lateral plates possess a sinuous medial margin, and a semi-circular ventrolateral edge (as in *Typothorax* and *Paratypothorax*); the anterior edge of the posterior lateral plates are straight with a raised anterior bar; posterior lateral plates possess a radial pattern of incised grooves from a sharp, hook-like eminence, with the plate being slightly flexed ventrally along this center of ossification.

Heliocanthus chamaensis **(Zeigler et. al., 2002)**

1985 *Desmatosuchus* sp.: Carpenter and Parrish, p. 197-198.
1986 *Desmatosuchus* sp.: Parrish and Carpenter, p. 152, fig, 11.3.
2000 *Desmatosuchus* n. sp.: Zeigler et. al., p. 46
2001 *Desmatosuchus* n. sp.: Hunt, p. 139.
2002 *Desmatosuchus chamaensis*: Zeigler et. al., p. 215, fig. 2.
2003 *Desmatosuchus chamaensis*: Heckert et. al, p. 115, figs. 2-8.

Holotype – NMMNH P-32793, right anterior dorsal paramedian plate (Zeigler et. al., 2002: fig. 2d).

Type Locality – Snyder Quarry, NMMNH loc. 3845, Petrified Forest Member, Chinle Formation, Rio Arriba County, New Mexico.

Paratypes – NMMNH P-32795, presacral paramedian plate; NMMNH P-31295, right posterior lateral plate; NMMNH P-32797, partial right dorsal paramedian plate; NMMNH P-32796, left posterior lateral plate; NMMNH 33099, partial right anterior dorsal or posterior cervical paramedian plate; NMMNH 33100, partial anterior dorsal or posterior cervical paramedian plate; NMMNH P-29045, partial spike (Zeigler et. al., 2002).

Topotypes - NMMNH P-37300, partial left? posterior lateral plate; NMMNH P-39520, right posterior lateral plate; NMMNH P-35806, partial right dorsal paramedian plate; NMMNH P-34887, right dorsal paramedian plate; NMMNH P-33101, lateral? plate; NMMNH P-35993, partial anterior right lateral plate; NMMNH P-37349, partial left dorsal paramedian plate; NMMNH P-35436, right anterior dorsal paramedian plate; NMMNH P-35991, left caudal paramedian plate; NMMNH P-35807, left dorsal paramedian plate; NMMNH P- 33820, left dorsal paramedian plate; NMMNH P-36052, left anterior? lateral plate; NMMNH P-35459, left paramedian plate; NMMNH P-35357, left anterior caudal plate; NMMNH P-34892, left lateral plate; NMMNH P-34891, lateral plate; NMMNH P-32794, partial left anterior lateral plate; NMMNH P-37348, partial mid-dorsal paramedian plate; NMMNH P-35349, partial lateral plate; NMMNH P-36502, partial lateral plate; NMMNH P-39184, partial ?caudal lateral plate; NMMNH P-33931, right calcaneum; NMMNH P-33932, right astragalus; NMMNH P-33927, left astragalus.

Referred Material –NMMNH P-4894, partial lateral plate (Zeigler at. al., 2002: fig. 2c); UCM 47725, cervical anterior dorsal paramedian plate (Parrish and Carpenter, 1986: fig. 11.3; Zeigler et. al., 2002: figs. 2h,i), both from the Bull Canyon (=Cooper Canyon)

Formation of New Mexico. PEFO 31162, anterior paramedian? plate from the Karen's Point Locality (PFV 075), Petrified Forest National Park, Petrified Forest Member, Chinle Formation.

Diagnosis – same as genus

Discussion – *Heliocanthus chamaensis* was originally described by Zeigler et. al. (2002) and then redescribed by Heckert et. al. (2003) as a new species of *Desmatosuchus* based on several supposed synapomorphies. However, inspection of this material does not reveal any shared synapomorphies with *Desmatosuchus* except perhaps that the dorsal eminence of the paramedian plates does not contact the posterior edge of the plate. The plates of *Heliocanthus* possess a radial ornamentation that is reminiscent of *Paratypothorax*. In fact, *Heliocanthus* shares several characters with *Paratypothorax,* specifically the morphology of the posterior lateral plates. These plates are identical in both taxa with the exception of larger size in *Heliocanthus* (Figure). The type specimen includes armor from the posterior cervical, dorsal, and caudal paramedian areas, as well as representative lateral plates from several areas of the body. Unfortunately many of the plate edges are incomplete making orientation and placement in the body difficult. Position of some of the plate ornamentation is puzzling as well, differing from what is typical for aetosaurs. For example, the holotype scute (NMMNH P-32793; Zeigler, et. al., 2002: fig. 2d) is crescentic in dorsal view, similar to the cervical and anterior dorsal paramedian plates of *Typothorax*. However, in *Typothorax* the shorter, concave margin is the anterior margin, while in *Heliocanthus* the elongate, convex margin of the plate possesses what appears to be an anterior bar, making the orientation opposite to that of *Typothorax*. This is puzzling since this would make the recurved spike face anteromedially, an unlikely orientation, although on several other plates this opponent orientation can be seen as well (e.g. NMMNH P-33099). *Heliocanthus* possesses two, possibly three distinct late plate morphologies. The most anterior are formed by two flanges, which meet at an acute angle to form an elongate, dorsoventrally compressed, slightly recurved spike with a sharp anterior edge (NMMNH P-35993). This is very similar to anterior lateral plates in *Paratypothorax* except that they are longer and thinner. More posterior lateral plates have a straight anterior edge, a highly sinuous medial edge, and a semi-circular posterolateral edge making the plate roughly triangular in dorsal view (NMMNH P-31295; Zeigler at. al., 2002: fig. 2f). This type of plate is exactly similar to those in *Paratypothorax* except that the hook-like boss is a bit longer and sharper. The possible third type of lateral plate consists of a thin quadrilateral plate with an elongate recurved spike (NMMNH P-33101), however, it is unclear where they would be situated in the carapace due to the lack of comparable material in other taxa. The purported "third lateral cervical horn" (Zeigler et. al., 2002: fig. 2k, l) is actually a spike broken from an anterior paramedian plate (compare to fig. 2a in Zeigler et. al., 2002) and is not analogous in any way to the lateral cervical horns in *Desmatosuchus*. More posterior dorsal paramedian plates lack the elongate recurved spike and instead have a low, rounded knob as a dorsal eminence. However, these bosses are strongly offset medially on the plate similar to *Paratypothorax* and "*Tecovasuchus*" and also contain the radial pattern of elongate grooves, ridges and pits also found in those taxa.

As a result of the lack of shared characters it is extremely unlikely that *H. chamaensis* represents a valid species of *Desmatosuchus* as postulated by Zeigler at. al. (2002) and Heckert et. al. (2003). The lateral plates are completely different, and

Desmatosuchus does not possess a radial pattern of grooves and ridges on the paramedian plates. In addition, the dorsal eminences are strongly offset in *Heliocanthus*, a character that never occurs in *Desmatosuchus*, and there is an anterior bar present in *Heliocanthus*. The morphology of the lateral plates, ornamentation of the paramedian plates, and the strongly medial offset of the dorsal eminence suggests a strong relationship with *Paratypothorax*. However, the lack of a high width/length ratio and the presence of recurved spikes on the paramedian plates warrant generic distinction.

Paratypothorax **Long and Ballew, 1985**

Type Species – *Paratypothorax andressi* (lapsus calami of Long and Ballew, 1985)

Paratypothorax andressorum (justified emendation, Heckert and Lucas, 1999)

Distribution – Chinle Formation, New Mexico and Arizona; Dockum Group, New Mexico and Texas; Lower and Middle Stubensandstein, Germany.

Revised Diagnosis – Aetosaur with narrow paramedian plates with a high width/length ratio; ornamentation of paramedian plates consists of a combination of a distinct, raised anterior bar and a pattern of grooves and ridges that radiate from a prominent boss; surrounding this boss is radiate, coarse pitting; the boss is strongly offset medially from the center and set close to the posterior edge of the plate; boss ranges in size from a low rounded knob, to a robust, short, hook-like spike than can rarely contact or project posteriorly past the plate margin; antero-medial corner of the plate has a short flange that projects anteriorly as in *Typothorax*; lateral edge is highly sinuous for articulation with the lateral plate, but lacks the thickened tongue and groove articulations found in *Desmatosuchus* and *Longosuchus*; some paramedian plates possess thickened ventral bar;

dorsal posterior margin of paramedian plates can be slightly beveled but never to the degree seen in *Tecovasuchus*; posterior lateral plates possess a sinuous medial margin, and a semi-circular ventrolateral edge (as in *Typothorax* and *Heliocanthus*); the anterior edge of the posterior lateral plates are straight with a raised anterior bar; posterior lateral plates possess a radial pattern of incised grooves from a sharp, hook-like eminence, with the plate being slightly flexed ventrally along this center of ossification; anterior lateral plates possess two distinct flanges at an acute angle which meet to form a short, but broad, slightly recurved spike that projects laterally, the spike is compressed dorsoventrally with a sharp anterior edge and a rounded posterior edge; and dorsal vertebrae possess elongate, ventrally buttressed transverse processes as in *Typothorax*.

***Paratypothorax andressorum* (Long and Ballew, 1985)**

1861 *Belodon*: Meyer, p. 337, pl. 43 (figs. 1, 2, 4, 5).
1865 *Belodon*: Meyer, p. 118, pl. 28 (figs. 1-9)
1911 *Phytosaurus kapfii*: Huene, p. 103, fig. 25.
1913 *Phytosaurus kapfii*: Huene, p. 282, fig. 13.
1932 *Phytosaurus*?: Case, p. 72, pl. 4, (figs. 5, 6)
1953a Pseudosuchian: Gregory, p. 1, fig. 1.
1953b cf. *Typothorax* sp.: Gregory, p. 1, fig. 16.
1974 *Nicrosaurus*: Wild, p. 22, fig. 9
1985 *Paratypothorax andressi*: Long and Ballew, p. 45, fig. 17, pl. 6,7.
1989 *Paratypothorax*: Small, p. 301, pl. 5g-h.
1992 *Paratypothorax andressi*: Hunt and Lucas, p. 147, figs. 2-4.
1992 *Paratypothorax*: Lucas and Hunt, p. 164, fig. 13b.
1995 *Paratypothorax andressi*: Long and Murry, p. 1., figs. 113-115.
1997 *Paratypothorax sp.*: Heckert, p. 29, fig. 3f.
1999 *Paratypothorax andressorum*: Heckert and Lucas, p. 50.
2000 *Paratypothorax andressorum*: Heckert and Lucas, p. 1592, figs. 6d-f.
2000 *Paratypothorax andressorum*: Lucas, p. 1, figs. 1-3.

Holotype – SMNS (no number assigned) left dorsal paramedian plate (Long and Ballew, 1985: pl. 6).

Type Locality – Heslach, near Stuttgart, Lower Stubensandstein, Würtemburg, Germany.

Diagnosis – same as genus.

Discussion – The aetosaur currently known as *Paratypothorax* was a taxonomic enigma for over 100 years. Meyer described and figured the first plates belonging to this taxon in 1861. They came from the Stubensandstein of Germany, however, since they were found with skull materials of the phytosaur "*Belodon*" they were long believed to represent the dermal armor of certain forms of parasuchians. This confusion persisted through the next century, causing problems in phytosaur taxonomy (see discussions in Camp, 1930:147; Gregory, 1962a:16; Gregory, 1962b:682; Gregory and Westphal, 1969). It was not until Long and Ballew's (1985) seminal work on the taxonomic value of armor ornamentation in aetosaurs that the true identity of these plates was recognized. Long and Ballew (1985) assigned the armor from Germany to a new genus of aetosaur, *Paratypothorax*, an assignment that has been strongly supported by the discovery in the southwestern U.S. of similar plates with aetosaur postcrania (Hunt and Lucas, 1992).

Currently *Paratypothorax* is monospecific with a stratigraphic range worldwide from the early late Carnian through at least the early Norian (Heckert and Lucas, 2000). However, morphological differences between many of the armor plates assigned to this taxon, in conjunction with the long stratigraphic range, suggest that several species may be present. This includes material from the Maleri Formation of India (Huene, 1940; Kutty and Sengupta, 1989) and from the Fleming Fjord Formation of Greenland (Jenkins et. al., 1994). Conversely, plates from the Eagle Basin of Colorado assigned to *Paratypothorax* by Small and Sedlmayr (1995) and Small (2001) probably belong to a distinct genus (pers. obs.).

Because Long and Ballew (1985:57) erected the species *P. andressi* to honor the entire Andress family (Chris Andress was the Chief Ranger at Petrified Forest National Park), Heckert and Lucas (1999) justifiably emended the species epithet to *P. andressorum*. Lucas (2000) described pathological armor of *P. andressorum* from the Lower Stubensandstein of Germany, which is the first published case of a pathology in aetosaur armor. Martz (2002) has since documented another case in *Typothorax*.

DESMATOSUCHINAE Huene 1942

Heckert and Lucas (2000:1555) defined Huene's Desmatosuchinae as a stem-based taxon that includes all aetosaurs more closely related to *Desmatosuchus* than the last common ancestor of *Desmatosuchus* and *Stagonolepis*. This definition is still valid for this revised phylogeny. Desmatosuchinae consists of *Neoaetosauroides* + *Longosuchus* + (*Lucasuchus* +*Desmatosuchus*). *Lucasuchus* is considered here to be a valid taxon but restricted to the dorsal paramedian plates with the conical eminences that Sawin (1947) originally assigned to *Typothorax coccinarum*. *Acaenasuchus* (Long and Murry, 19995) is considered to be a chimera, consisting of the material of several juvenile aetosaur taxa, most likely *Stagonolepis* and *Desmatosuchus* (Heckert and Lucas, 2002e; 2002f).

Unnamed Clade (*Neoaetosauroides* + *Longosuchus* + (*Lucasuchus* + *Desmatosuchus*)

These taxa are united by two synapomorphies: 1) dentary tooth count less than 9 (unknown in *Lucasuchus*); 2) cervical centra unkeeled ventrally (unknown in *Lucasuchus*).

Neoaetosauroides Bonaparte, 1967

Type Species -- *Neoaetosauroides engaeus* Bonaparte, 1967

Distribution – Los Colorados Formation, Argentina; ?Redonda Formation, Dockum Group, New Mexico.

Heckert et. al. (2001) document a possible occurrence of *Neoaetosauroides* sp. from the Redonda Formation of New Mexico. If this ID is accurate it would represent the first occurrence of *Neoaetosauroides* outsideArgentina.

Diagnosis – Medium sized aetosaur with a robust dentary possessing 6-7 teeth; premaxillary tooth count of four; lateral armor apparently rectangular as in *Longosuchus* and *Desmatosuchus* but without spikes; limbs robust; humerus with an epicondylar foramen rather than a groove; fifth metatarsal extremely reduced; coracoid with a postglenoid process; dorsal paramedian plates narrow and faintly ornamented; caudal armor rows reduced in number, only 26 compared to *Aetosaurus* and *Stagonolepis*, which each possess 40-45.

1969b *Neoaetosauroides engaeus*: Bonaparte, p. 283, figs. 7-8.
1971a *Neoaetosauroides engaeus*: Bonaparte, p. 87, figs. 34-42.
1971b *Neoaetosauroides engaeus*: Bonaparte, p. 171, fig. 17.
1978 *Neoaetosauroides engaeus*: Bonaparte, p. 300, fig. 139.
1982 *Neoaetosauroides*: Bonaparte, p. 108, fig. 4e.
1985 *Neoaetosauroides*: Cruickshank and Benton, p. 716, fig. 2a.
2000 *Neoaetosauroides engaeus*: Heckert and Lucas, p. 1555.

Holotype – PVL 3525, partial skeleton including lower jaws, maxillary and premaxillary fragments, left scapulocoracoid, sacrum, limbs, and an almost complete but badly preserved carapace (Bonaparte, 1969; 1971a).

Type Locality – Ischigualasto Villa Unión Basin, upper part of the Los Colorados Formation, Gral Lavalle, La Rioja Province, northwestern Argentina.

Diagnosis – as for the genus.

Discussion – *Neoaetosauroides* is known mainly from three partial specimens from the Los Colorados Formation of Argentina. Although most of the skeleton is present, Bonaparte's description deals mainly with the postcranial axial skeleton. The armor ornamentation is poorly known due to the poor preservation of the carapace (Bonaparte, 1971a). Desojo (2002) has documented the existence of better cranial material including two new complete skulls, although this material has not been described yet. Further discussion of these taxa most wait on future study of the existing and new specimens.

Unnamed Clade (*Longosuchus* + (*Lucasuchus* +*Desmatosuchus*))

These taxa are united by six synapomorphies: 1) dorsal presacral paramedian scutes possess tongue and groove articulations for lateral scutes; 2) lateral cervical armor possesses well-developed elongate spikes (unknown in *Lucasuchus*); 3) presence of spikes on dorsal and caudal lateral scutes (unknown in *Lucasuchus*); 4) lengths of dorsal and lateral flanges of anterior lateral scutes asymmetrical with dorsal flange being longest (unknown in *Lucasuchus*); 5) presence of a narrow region ("waist") in the carapace anterior to the sacrum (unknown in *Lucasuchus*); and 6) lateral spikes in dorsal and pelvic regions well-developed (unknown in *Lucasuchus*). This node has a bootstrap proportion of 51 for 1000 replicates.

Longosuchus Hunt and Lucas, 1991

Type species -- *Longosuchus meadei* (Sawin 1947)

Distribution -- Colorado City member (= Cooper Canyon Member?), Dockum Formation, west Texas; ?Timesgadiouine Formation, Argana Group, Morocco. Early late Carnian (Heckert and Lucas, 2000).

Lucas and Hunt (1992) list the presence of *Longosuchus* in New Mexico based solely on a small fragment of aetosaur plate(NMMNH P-11005) from the Salitral Shale Tongue of the Chinle Formation. This assignment was based primarily on the sigmoidal shape of the plate in lateral view, which they claimed was diagnostic of the genus. However, other aetosaurs including *Desmatosuchus* have plates that are sigmoidal in lateral view. Recently, Lucas et. al. (2003) reassigned this fragment to *Desmatosuchus haplocerus*, presumably to conform with the supposed Adamanian age of this unit. However, this fragment (Lucas et. al. (2003: figs. 10G, H) is barely diagnostic, certainly does not belong to *Desmatosuchus haplocerus* due to its pyramidal shaped dorsal eminence, and cannot be identified below Stagonolepididae indet. As a result, the biostratigraphic use of this specimen should cease (contra Lucas and Hunt, 1992; Hunt and Lucas, 1993; Heckert and Lucas, 1999; Heckert and Lucas, 2000; Lucas et. al., 2003). Furthermore, the presence of *Longosuchus* in New Mexico should not be regarded with any certainty until more diagnostic material pertaining to this genus is found. This deletion should also pertain to *Desmatosuchus* since none of the plate fragments assigned by Lucas et. al. (2003: figs. 10B, G, H) belong to this taxon.

Lucas (1998) also assigned three partial lateral plates from Morocco to *Longosuchus meadei*. Although clearly aetosaurian, this assignment is probably premature based on the recent discoveries of other spiked aetosaurs from North America that have not yet been described. Assignment to a specific taxon should be delayed until associated, diagnostic paramedian plates are recovered.

Removal of *Longosuchus* from faunal lists in New Mexico, North Carolina (see discussion below for *Lucasuchus*), and Algeria restrict the presence of this taxon to the Otis Chalk region of Texas. Thus is usefulness as a biostratigraphic index taxon is negated.

Type locality -- TMM quarry 3a, 3 miles north of Otis Chalk, Colorado City Member (= Cooper Canyon Member?), Dockum Formation, Texas (Heckert and Lucas, 2000)

Revised Diagnosis -- Medium sized aetosaur possessing seven teeth in the dentary; dentary excluded from the ventral margin of the lateral mandibular fenestra by the angular; premaxillary teeth present; maxillary tooth count 10 – 13; teeth, simple, conical with no distinct wear facets; splenial exposed laterally; dorsal paramedian plates possess a combination of a well-developed anterior bar, and a faint radial pattern of pits emanating from a low pyramidal boss that contacts the posterior margin of the plate; dorsal paramedian plates are sigmoidal in lateral view and possess the complex tongue-and-groove articulations for adjacent plates as in *Lucasuchus* and *Desmatosuchus;* seven longer than wide cervical plates cover the nine vertebrae in the cervical series; cervical plates are thickened dorsoventrally and possess tongue and groove articulations; lateral plates with well-developed spikes throughout the cervical, dorsal and caudal regions; lateral spikes faceted in cross-section and not recurved; lateral plates possess two flanges that meet approximately at right angles to form an elongate spike at the point of flexure; base of the lateral spikes not solid and round as in *Desmatosuchus* but instead are “V” shaped in posterior view; lateral plates of the cervical and dorsal regions asymmetrical with the dorsal flange being longer than the lateral flange; neural spines of cervical and dorsal region tall; area between the greater and fourth trochanters of the femur strongly convex. (Sawin, 1947; Hunt and Lucas, 1990; Parrish, 1994; Long and Murry, 1995; Small, 2002).

Discussion – *Longosuchus* was originally described by Sawin (1947) as a distinct species of "*Typothorax*," this animal was believed to be generically distinct by several workers (e.g. Long and Ballew, 1985; Small, 1989) and was finally placed in a new genus, *Longosuchus*, by Hunt and Lucas (1990). Previous to 1990 most references to *Typothorax* actually refer to *Longosuchus* or other taxa including *Stagonolepis* or *Paratypothorax*. This is a result of *L. meadei* having an armor ornamentation very similar to these taxa and very different from true *Typothorax* specimens.

Longosuchus meadei **(Sawin 1947)**

1947 *Typothorax meadei*: Sawin, p. 201, figs. 1-13, 15a, b1, b3; 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. 2c-f, 3i-j.
1994 *Longosuchus meadei*: Parrish, p. 196, figs. 1-6.
1995 *Longosuchus meadei*: Long and Murry, p. 67, figs. 58-63.
2000 *Longosuchus meadei*: Heckert and Lucas, p. 1561.

Holotype-- Colorado City Member (= Cooper Canyon Member?), Dockum Formation, west Texas: TMM 31185-84b, partial skeleton consisting of skull, lower jaws, incomplete vertebral column, limb bones, fragmentary girdle elements, and paramedian and lateral plates (Sawin, 1947: Figs. 1, 2, 6, 15 a, 15 b (1,3); Hunt and Lucas, 1990: Fig. 2 c-f; Parrish, 1994: Figs. 1 a-b, 2 a-b, 3, 4, 5, 6).

Diagnosis – As for the genus.

Discussion -- Sawin (1947) did not formally designate a holotype in his original description. His description is based on two specimens, TMM 31185-84a, a partial postcranial skeleton, and TMM 31185-84b, a skull and additional postcrania. Hunt and Lucas (1990) later designated TMM 31185-84b as the lectotype and referred much of the material to *L. meadei*. Long and Murry (1995) argued that the lectotype contained material from more than one individual and that the proper catalogue number for the material is TMM 31185-97. They removed the skull from this lot, assigned it a new number, TMM 31185-98, and designated this specimen as the new holotype. Examination of the TMM collection shows that on many, but not all, of the elements TMM 31185-84b, the 84b has been crossed out and replaced with the number 97. It is not clear when or why this was done and this change is not reflected in the actual cataloguing, thus the original number should be retained to avoid confusion. Additionally, Long and Murry (1995) designated a skull for the holotype of *L. meadei* however; in their diagnosis for the species they list only characters for the dermal armor. It is therefore suggested that the number TMM 31185-98 be abandoned, the skull placed back in TMM 31185-84b and the entire collection be retained as the holotype until further studies are conducted.

***Longosuchus* sp.**

1995 ?*Lucasuchus hunti*: Long and Murry, p. 73, figs. 65a-d, f-h; 66-67.

Discussion -- Long and Murry (1995) tentatively refer much of the material from the Otis Chalk Quarries to *Lucasuchus* based mainly on size of the elements. This includes lateral armor, vertebrae, girdle and limb material, most of which is still unprepared. Although *Lucasuchus* is considered a valid taxon in this thesis based on the morphology of several dorsal paramedian plates, the association of these plates with the rest of the material referred to *Lucasuchus* cannot be demonstrated. Sawin (1947) explicitly states on page 233 that "no large horns were found in association with the plates of [*Lucasuchus hunti*]". This material was not included in the original description of "*Typothorax*" *meadei* and is labeled as "*Desmatosuchus*" in the TMM collections. It is not clear whether this material was known to Sawin and its relationship with other material in the quarry in ambiguous. It does, however, bear close resemblance to the holotype material of *Longosuchus*. Therefore, at this time, it is best to assign this material to *Longosuchus* sp. until more complete material of *Lucasuchus* is recovered.

Unnamed node (*Lucasuchus* + *Desmatosuchus*)

These taxa share a single synapomorphy, dorsal eminence never contacts the posterior margin of the paramedian plates. Admittedly based on the scrappy material of *Lucasuchus*, its validity and relationships will always be suspect. However, as currently diagnosed it is a valid taxon (Harris et. al., 2003, this study) unless future new material shows it to be otherwise (see discussion below).

Lucasuchus Long and Murry, 1995

Type species – *Lucasuchus hunti* Long and Murry, 1995

Distribution – Colorado City member (= Cooper Canyon Member?), Dockum Group, Texas, Pekin Formation, Newark Supergroup, North Carolina.

Type Locality – TMM locality 31100, Quarry 3, Howard County, Texas.

Diagnosis -- Paramedian plates with deeply incised patterning of pits and grooves radiating from a large, central conical eminence, and with a distinct anterior bar; dorsal eminence never contacts the posterior margin of the plate; paramedian plates are sigmoidal in lateral view and possess complex tongue-and-groove lateral and medial margins for articulation with other plates.

Lucasuchus hunti Long and Murry, 1995

1947 *Typothorax coccinarum*: Sawin, p. 233, figs, 15b2, b4.
1990 *Longosuchus meadei*: Hunt and Lucas, p. 321, figs. 2a-b, 3a-h.
1995 *Lucasuchus hunti*: Long and Murry, p. 73, fig. 64.

Holotype -- Colorado City Member (= Cooper Canyon Member?), Dockum Formation, west Texas: TMM 31100-257, paramedian scutes (Long and Murry, 1995: Figs. 64 f-g).

Diagnosis – as for the genus.

Discussion -- Excavations near Otis Chalk, Texas in 1940 resulted in the collection of a large amount of aetosaur material. Approximately one-half of this material was referred to "*Typothorax*" *meadei* by Sawin (1947), and later referred to *Longosuchus meadei* by Hunt and Lucas (1990). The remainder of the Otis Chalk material in the TMM collection has either never been prepared or is identified as "*Desmatosuchus.*" Examination of this material shows that this identification is erroneous. This material is very similar to that of *Longosuchus meadei*, except that it is of greater size (Long and Murry, 1995). This erroneous identification is most likely what led Elder (1978) to argue that *Desmatosuchus* and *"Typothorax"* were congeneric, a statement that has since been shown to be inaccurate by Small (1989). Included in this material are several paramedian plates of a distinct nature that were originally mistakenly referred to *Typothorax coccinarum* by Sawin (1947: fig. 15b (2,4)). For unclear reasons, despite the uniqueness of these plates Hunt and Lucas (1990) referred the material to *Longosuchus meadei*.

Long and Murry (1995) recognized the distinctness of these plates and reassigned them to a new genus and species, *Lucasuchus hunti*. In addition, they tentatively referred most of the TMM material that had been identified as *Desmatosuchus* to their new genus based mostly on size, although they note the great similarity in the material to that of *Longosuchus meadei* (Long and Murry, 1995: 71). Reexamination of the material shows that although the paramedian plate ornamentation is truly distinct and warrants taxonomic separation, the association of the plates with the other larger postcranial elements cannot be established. Indeed, as previously stated Sawin (1947: 233) notes that "no large horns were found in association with the plates of *T. coccinarum* (*Lucasuchus*)." Thus the majority of the material referred to *Lucasuchus hunti* by Long and Murry (1995) should be referred to *Longosuchus* sp. (see previous discussion). Of course, if it could be unquestionably proven that the distinct plates do in fact belong with this material, *Lucasuchus* would become a junior synonym of *Longosuchus,* on the basis of the clear similarities argued by Heckert and Lucas (1999; 2000) and noted by Long and Murry (1995). Unfortunately, due to the lack of quarry data, this problem will not be resolved with the material at hand and will require new associated material. Thus, until new material is uncovered it is best to keep *Lucasuchus* as a valid taxon, although restricted only to the distinct paramedian plates.

Long and Murry (1995) correctly argue that *Longosuchus meadei* does not occur in the Pekin Formation of North Carolina and that plates from this formation referred to *L. meadei* by Hunt and Lucas (1990) should instead be referred to *Lucasuchus hunti*. The Pekin plates are similar in morphology to the plates attributed to *Typothorax coccinarum* by Sawin (1947) and are considered distinct by Long and Murry (1995). Hunt and Lucas (1990) also err in arguing that in the original assignment of the Pekin material, Baird and Patterson (1967) were comparing the North Carolina material with "*Typothorax*" (=*Longosuchus*) *meadei*, not *Typothorax coccinarum* (Hunt and Lucas, 1990: 321). Sawin never referred the plates with the tall conical eminences to "*Typothorax" meadei*, instead as previously stated, he referred them to *Typothorax coccinarum* (Sawin, 1947: 233). Thus, Baird and Patterson (1967) probably followed this assignment. However, Hunt and Lucas (1990) are correct that this material clearly does not belong to *Typothorax coccinarum*. The cause for this misidentification is most likely a description by Huene (1915; p. 489) in which he describes rectangular plates belonging to *Typothorax coccinarum* as possessing a "high spine like elevation from which the sculpture radiates." In any case, the North Carolina material with large conical eminences should be referred to *Lucasuchus hunti* as contended by Long and Murry (1995).

Lucas and Hunt (1990), Lucas (1998), and Heckert and Lucas (2000) address the biochronological significance of *Longosuchus* based on their assignments of material to this taxon. They erected a *Longosuchus* biochron, that established that the Pekin

Formation of the Newark Supergroup, the Salitral Shale Tongue of the Chinle Formation, and the Timesgadiouine Formation of the Argana Group of Morocco were equivalents based on the occurrence of this taxon. However, as noted previously, these assignments are based either on scrappy, undiagnostic material or on material of *Lucasuchus*. Thus, until better material is recovered, these correlations cannot be substantiated as was argued by Long and Murry (1995).

Desmatosuchus **(Cope, 1892)**

Type Species – Desmatosuchus haplocerus (Cope, 1892)

Distribution – Bluewater Creek and Blue Mesa Members, Chinle Formation, Arizona and New Mexico; Tecovas and Cooper Canyon (=Bull Canyon) Formations, Dockum Group; ?Colorado City (= Cooper Canyon?) Member, Dockum Group, Texas.

Revised Diagnosis – Large aetosaur, four meters or more in length; premaxilla edentulous; tooth crowns bulbous though slightly laterally compressed; tooth crowns posses very small, rounded denticles on mesial and distal edges; infratemporal fenestra reduced; infratemporal fenestra oval in outline; external mandibular fenestra relatively small; humerus with epicondylar foramen instead of groove; posterior-most dorsal vertebra completely fused to first sacral vertebra; posterior dorsal vertebra possess broad, flat ribs fused to transverse processes; dorsal vertebra possess accessory articulations (hyposphenes and hypantra); pubes extremely deep; axial skeleton extremely robust; paramedian plates possess ornamentation of pits, grooves, and ridges in a random, not radial pattern; dorsal eminence consists of a low rounded boss that is generally situated slightly posterior of the center of the plate; paramedian and lateral plates possess thin anterior laminae rather than thickened, raised bars; cervical paramedian plates longer than wide and extremely thickened dorsoventrally; paramedian and lateral plates possess complex tongue-and-groove articulations; cervical lateral plates possess well-developed, recurved spikes, especially in the 5th series where the spikes are extremely large; anteriormost dorsal lateral plates possess large knobs instead of spikes; dorsal lateral spikes become more pointed and elongate posteriorly with the best developed in the pelvic and anterior caudal regions; dorsal, pelvic, and anterior caudal plates are rectangular, flexed at approximate right angles at the center of ossification (spike), and asymmetrical with the dorsal flange being much longer than the lateral flange.

Desmatosuchus haplocerus (Cope, 1892)

1892 *Episcoposaurus haplocerus*: Cope, p. 129.
1920 *Desmatosuchus spurensis*: Case, 1922, p. 524, figs. 1-4.
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 Phytosaur: Case, p. 72, pl. 4 (figs. 2,3).
1942 *Desmatosuchus spurensis*: Huene, p. 233, fig. 50.
1950 *Episcoposaurus haplocerus*: Wilson, p. 113, fig. 2,3.
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
1989 *Desmatosuchus haplocerus*: Long et al., p. 69, figs. 2b,c.
1993 *Desmatosuchus haploceros* [sic]: Parrish, p. 298, fig. 6b.
1995 *Desmatosuchus haplocerus*: Long and Murry, p. 89, figs. 85-98.
1995 *Acaenasuchus geoffreyi* (in part): Long and Murry, p. 114, figs. 117-118.
1995 *Episcoposaurus haplocerus*: Spamer and Daeschler, p. 430, fig. 21.
2000 *Desmatosuchus haplocerus*: Heckert and Lucas, p. 1559, figs. 6a-c.
2002c *Desmatosuchus haplocerus*: Heckert and Lucas, p. 193, figs. 1, 2, 3a,b.
2002d *Acaenasuchus geoffreyi* (in part): Heckert and Lucas, p. 205, fig. 3.
2002d *Desmatosuchus*: Heckert and Lucas, p. 205, fig. 4.

Lectotype **--**ANSP 14688, articulating right cervical lateral, and cervical paramedian plates (Gregory, 1953: figs. 1-3; Spamer and Daeschler, 1995: fig. 21b, Heckert and Lucas, 2002: figs. 1a-e). It should be noted that in figure 1 of Heckert and Lucas (2002) they mistakenly refer to these elements as being from the left side.

Paralectotypes--The remainder of ANSP 14688 can be assigned to *Desmatosuchus*, specifically the dermal armor (Gregory, 1953: figs. 9-14; Spamer and Daeschler, 1995: fig. 21e; Heckert and Lucas, 2002: figs. 1f, g, 2a-k) and the partial scapula (Gregory, 1953: figs. 4, 5; Spamer and Daeschler, 1995: fig. 21a; Heckert and Lucas, 2002: figs. a, b). The sacral vertebra (Gregory, 1953: figs. 6-8; Spamer and Daeschler, 1995: fig 21d; Heckert and Lucas, 2002: figs. 3c, d) and the two fragmentary caudal vertebrae (Cope, 1892:130; Gregory, 1953:17) should not be included as paralectotypes for reasons given below. Note that the caption for figure 2c in Heckert and Lucas (2002) is erroneous. This figure actually represents conjoined anterior dorsal right lateral and paramedian plates. Figures 2a and 2c in Heckert and Lucas (2002) are upside down.

Topotypes--TMM 18569, two lateral plates (Wilson, 1950: figs. 2-3; Spamer and Daeschler, 1995:434). The dorsal vertebra (Wilson, 1950: fig. 1) is very likely phytosaurian and should be excluded (Heckert and Lucas, 2002; pers. obs.).

Type Locality – Windmill pasture, 5km north of Dickens, Dickens County, Texas. Tecovas Formation, Dockum Group. Late Carnian.

Revised Diagnosis – Spikes on anterior cervical lateral armor not highly developed, being very short; spikes on posterior dorsal lateral not elongate, nor recurved; hemispherical fontanelle of the basipterygoid deep; almost no gap apparent between the basal tuber and basipterygoid process; elongate pit present in the dorsal region of the supraoccipital; exoccipitals meet at the midline in the foramen magnum; maxillary tooth count of 12-13 (Small, 1985; 2002).

Discussion – *Desmatosuchus haplocerus* has been discussed earlier in this thesis.

Desmatosuchus smalli nov. sp.

1985 *Desmatosuchus haplocerus*: Small, p. 1, figs. 3-11.
1986 *Desmatosuchus haplocerus*: Murry, p. 122.
1986 *Desmatosuchus*: Chatterjee, p. 145.
1989 *Desmatosuchus haplocerus*: Small, p. 301, fig. 1B, pl. 5A-F, I.
1995 *Desmatosuchus haplocerus*: Long and Murry, p. 89, fig. 86A.
2002 *Desmatosuchus haplocerus*: Small, p. 97, figs. 1-9.

Type Specimen – TTUP 9024: relatively complete skull with a complete right mandible, pelvis, femora, nearly complete cervical series of armor, and assorted dorsal armor.

Paratypes – TTUP 9023: well-preserved skull, including braincase and mandibles, scapulocoracoid, humerus, a single dorsal vertebra, lateral cervical spike, assorted dorsal armor; TTUP 9025: partial skull including teeth; TTUP 9170: right humerus and ulna.

Type Locality – Post Quarry, Garza County, Texas. Cooper Canyon Formation, Dockum Group. Norian.

Etymology – Species epithet in honor of Bryan Small for his detailed work on *Desmatosuchus* and on aetosaurs in general.

Diagnosis -- The anterior cervical lateral armor and posterior dorsal lateral armor possesses elongate gracile spikes that are much more developed than those in *D. haplocerus*; hemispherical fontanelle of the basipterygoid extremely shallow; sizeable gap occurs between the basal tubera and the basipterygoid process; exoccipitals do not meet at the midline of the foramen magnum; maxillary tooth count of 10-12.

Discussion – *Desmatosuchus smalli* was discussed in detail in chapter 6.